The Ecology of

THE SYMPOSIA OF THE NATIONAL ZOOLOGICAL PARK

ARBOREAL FOLIVORES

G. GENE MONTGOMERY, ***Editor***

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Foreword

The maintenance of mammalian arboreal folivores in captivity is a difficult problem for zoological curators. In the New World, the three-toed sloth, *Bradypus*, has been a vexing problem in captivity, and to assist us in assessing its dietary needs the National Zoological Park sponsored research by G. G. Montgomery and M. E. Sunquist for some five years. Their pioneering efforts brought to light some of the many problems which an arboreal mammal must solve before it can efficiently exploit the seemingly abundant leaf resources of a tropical evergeen forest. Intriguing questions were posed concerning individual differences in dietary preferences and the acquisition of feeding traditions.

Since sloth ecology was only one aspect of the whole problem of plant and animal coevolution, it was decided to convene a symposium dealing with the problem of plant ecology and animal adaptations for feeding on leaves. The participants were selected from a variety of research areas by Dr. Montgomery and the staff of the National Zoological Park. The Conservation and Research Center at Front Royal, Virginia, was designated as the meeting place. We are indebted to Dr. Christen Wemmer and his staff for attending to the many small problems which preceded this successful symposium.

The conference was supported by the Smithsonian Research Foundation, and the publication of the proceedings has been generously supported by a grant from the Friends of the National Zoo. Dr. Montgomery served as editor of this volume, assisted by Mrs. Wyotta M. Holden. The efforts of Mr. Joe W. Reed, Dr. Yael D. Lubin, and Mr. E. Kohn are gratefully acknowledged.

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Editor's Note

When I conceived the arboreal folivores conference and the resulting book which you now hold, I certainly did not expect that so many diverse ideas and new challenges could result. The contributors to this volume have transformed what was then a broad outline of topics (see Table of Contents) into an exciting, in-depth exploration of the many unique facets of the life of animals which live in trees and eat leaves.

It has been a very rewarding task to attempt to convey to you some fraction of the excitement and growth that we experienced at Front Royal during the conference, and to help the authors present the many ideas which were shared among the participants. I thank all the authors for their patience and cooperation. We all owe thanks to Wy Holden and John Eisenberg, who shared the editing with me.

The book is arranged to follow the format of the conference, except that space did not permit summarizing the discussion sessions which followed each major part of the conference. Likewise, space and cost considerations prevented inclusion of a subject index.

Perusal of the table of contents will show you that we discussed the resource base for arboreal folivores, and limitations which are placed on its use; the general features of the lives of invertebrate and vertebrate folivores; and some examples of arboreal folivores from recent field studies. There was a strong bias toward vertebrate examples and, because of their prominence as subjects in current field studies, from the leaf-eating primates. This bias reflects my interests, as well as the tendency for most zoos to exhibit primarily the mammalian arboreal folivores.

The book did not require an introductory paper because the major questions which we addressed at the conference are repeatedly dealt with by the various authors. I do not feel it particularly worthwhile to impose my own interpretation of the ideas given at the conference by writing a summary paper, because the authors have done such an excellent job of presenting their own ideas and data. I would prefer that you read all of the papers contained herein and form your own interpretation of them.

I feel that we made a major step toward understanding some of the restraints which limit exploitation of the arboreal folivore niche, and how diverse life forms cope with those limitations. By reading this collection of papers, you can share in that understanding, and perhaps be inspired to add to it. I and the contributors to this book can expect no more.

G. Gene Montgomery, *Editor*

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Arboreal Folivores in Captivity—Maintenance of a Delicate Minority

In years past, the principle aim of zoological gardens was to acquire and exhibit to the public various species of exotic animals. Because wild animals were deemed abundant and an almost constant supply could be assured, little regard was paid to long-term survivorship and captive reproduction of the various species. The result was that little practical husbandry information accumulated through the years. Today zoological gardens are becoming aware of the fact that they can no longer afford to be consumers of wildlife but must quickly produce enough specimens to become self-sufficient in terms of animal supply.

For many zoological gardens the synthesis of a strong and coherent husbandry program for each species is the first step toward the goal of effective management of captive populations of exotics, especially rare and endangered species and those species reputed to be difficult to maintain in captivity. Traditionally, the most difficult species to maintain have been those with specialized dietary requirements, such as insectivores, myrmecophages, and folivores. Captive management of these specialists has been difficult, principally because either the specific dietary requirements in nature were unknown or because of the difficulties of duplicating a known natural diet. Recent field and captive research has made available the proper quantity and quality of information to enable many of these food specialists to be successfully maintained in captivity.

This paper will discuss the maintenance of those mammalian arboreal folivores in captivity which have high public impact and zoological interest. Although arboreal folivory is expressed in 7 of the 19 mammalian orders, this review treats only 4: primates, marsupials, edentates and carnivores, excluding rodents, dermopterans, and hyracoideans owing to the limited amount of information available.

During recent times there have been 4 separate primate adaptations to exploit the arboreal folivore niche. These include the Lemurinae and Indriidae of Madagascar, the Alouattinae of South America, and the Colobinae of Africa and Asia, by far the most successful in terms of species diversity.

The 2 most successful taxa, the Colobinae and the Alouattinae, exhibit adaptations of the digestive system analagous to those of the polygastric and monogastric herbivorous ungulates, respectively. The Colobinae possess a sacculated stomach in which cellulysis and fermentation occurs (Kuhn, 1964; Hollihn, 1973; Hungate, 1959; Drawert, et al., 1962), as in the ruminants. Fundamental differences do occur in the digestive system of the Colobinae when compared with the ruminants, including a noncompartmentalized stomach, glandular epithelial stomach lining, and utilization of glucose as the primary form of metabolic energy in the Colobinae as opposed to a compartmentalized stomach lined with squamous epithelium and a dependence on volatile fatty acids (VFA's) as the primary energy source in ruminants. The Alouattinae possess a simple stomach (nonsacculated), short illeum, enlarged cecum, and large intestine analagous to the digestive system in the Perissodactyla (Hill, 1964; Cramer, 1968; Machado and Di Dio, 1963).

Both the Colobinae and Alouattinae specialize in the extraction of nutrients from foliage, a food resource which is fundamentally low in nonstructural and high in structural carbohydrates. This requires that a considerable period of time during the course of a day be devoted to the location, gathering, consumption, and digestion of food. Indeed, it has been estimated that *Colobus* spends fully 50 percent of its waking hours feeding or engaged in activities related to feeding (Clutton-Brock, 1974). Comparable figures have been reported for *Alouatta* (Carpenter, 1965) and *Lepilemur* (Martin, personal communication). Analysis of feeding data from several studies indicates that *Alouatta* may spend more time actually eating than do the *Colobus*. If this is the case, the data correspond with that concerning ungulates which reveals that the monogastric species spend more time grazing or browsing than do the polygastric species. Of course, the ruminants spend considerable additional time quietly digesting and masticating their food.

Physiologically, a unit of food consumed by a monogastric herbivore has a transit rate through the digestive system three times as fast as that of a polygastric species is utilized. The Alouattinae appear far less catholic in their tastes than the Colobinae, and field to eat more than a ruminant of comparable size to obtain the same amount of nutrition. If the Alouattinae and Colobinae demonstrate a similar disparity in physiological function (which remains to be demonstrated), it may explain the preliminary conclusion that Alouattinae spend more time feeding than do the Colobinae.

In nature the colobines appear to be more highly folivorous than the Alouattinae. Although fruits, bark, flowers, and nuts are eaten by some members of the Colobinae, most species consume mature leaves, young leaves and shoots as 60 percent or more of their total diet (Muckenhirn, 1972; Rudran, 1970; Clutton-Brock, 1974; Hladik and Hladik, 1972; Sabater Pi, 1973; Dunbar and Dunbar, 1974). In many cases only a small percentage of available tree and shrub species is utilized. The Alouattinae appear far less catholic in their tastes than the Colobinae, and field studies have indicated that fruits and nuts are often preferred food items when available (Hladik and Hladik, 1969; Carpenter, 1965). Therefore, fruits and other related, nonfolivorous plant material appear to be far more important in the diet of the Alouattinae than that of the Colobinae.

In captivity it is rarely possible to supply folivorous primates with the quantity and quality of folivorous foodstuffs they would normally obtain, and thus it is necessary to acclimate the animals to a captive diet. The success of colobine husbandry is dependent on this period of acclimatization. A sudden change or a change to an improper diet will result in gastrointestinal disorders including enteritis, constipation, diarrhea, gastritis, dysentery, and aspiration of food eructed, all of which are the major causes of death (Hollihn, 1973; Hill, 1964; personal communications from T. Hunt, D. Allen, and B. Beck). It seems necessary to feed only natural, fresh, and preferred foliage at first while gradually substituting increasing amounts of the desired captive diet. When the animals are finally acclimated to captivity, the ultimate diet should contain from 60 to 70 percent bulky, fibrous foodstuffs, especially leafy vegetables and fresh browse from suitable domestic species (see Table 1).

It appears that only a small percentage of captured colobines successfully make the critical transition, most succumbing to the above-mentioned gastrointestinal disturbances. Helminths and amoebae contribute to this induced gastroenteritis syndrome, and may render the animal susceptible to infection of other organs and organ systems.

Secondary to feeding a diet of insufficient bulk,

Table 1—Families and genera of tree and shrub species fed to captive colobines. (From Hollihn, 1973; Lang, 1973; and Miles Roberts, unpublished data.)

Family	*Genus*
Fagaceae	*Fagus*
Salicaceae	*Salix*
	Populus
Moraceae	*Morus*
	Ficus
Ulmaceae	*Celtis*
	Ulmus
Aceraceae	*Acer*
Aquifolaceae	*Ilex*
Tiliaceae	*Tilia*
Betulaceae	*Betula*
	Alnus
Cornaceae	*Cornus*
Leguminosae	*Robinia*
Platanaceae	*Prunus*

the primary cause of gastrointestinal problems in colobines appears to be the consumption of a diet too rich in carbohydrates. Consumption of large quantities of carbohydrates leads to a condition in colobines comparable to that of bloat in cattle in which the stomach becomes acutely distended as a direct result of the animal's being unable to eliminate gases from the foaming digesta in the stomach (Bolt, 1959; Tanner, 1959). In ruminants, this inability to eruct is attributed to changes in the eructation reflex, respiration, and blood pressure (Kay and Phillipson, 1959) and can be directly traced to high carbohydrate meals of sweet potatoes, legumes, and boiled rice. In addition to the bloat in colobines, deaths have resulted in aspiration of the frothy egesta of a high carbohydrate meal resulting in pneumonia and pulmonary embolism.

Once acclimation has been achieved and reproduction begins, problems related to digestion lessen as the offspring, through imitation, tend to develop food preferences similar to the adults. In colobines, infant sharing and food "stealing" are seen (Horwich and Manski, 1975; Hill, 1972; Emerson, 1973). Infants began mouthing and eating foods acquired by the adults that carry them at about 4 to 6 weeks of age, and demonstrate preferences for foods chosen by their mothers and the female or females that carry them most frequently (Miles Roberts, unpublished data). Such food preferences are retained through life (Hollihn, 1973) and thus, if original stock animals can be acclimated to a suitable diet, the offspring should adapt readily also.

In captivity colobines appear to be somewhat fastidious in their choice of forages but will indeed accept a wide variety (Hollihn, 1971, 1973), although their food preferences in nature appear to be rather narrow (Dunbar and Dunbar, 1974; Sabater Pi, 1973).

It is interesting to note that, until the food requirements of colobines were understood, the greatest degree of success in captive maintenance was often obtained by private individuals who kept single animals or pairs. This seemed true regardless of whether the private animalkeeper kept his animal in the country of origin or abroad. This paradox seems to result from the fact that private pet owners allowed their animals a fair degree of freedom to roam the garden or the surrounding woods. During these excursions, the animals apparently were able to obtain enough browse of a suitable nature to offset the negative aspects of the diet offered by their owners.

Of the New World primates, the Alouattinae are the most specialized folivores. As mentioned earlier, the Alouattinae process folivorous material in an enlarged caecum and large intestine and do not possess a sacculated stomach (Hill, 1962; Cramer, 1968). The Alouattinae are partially frugivorous and apparently the processing of sugars and carbohydrates in fruits occurs in the stomach with absorption of glucose in the small intestine. Cellulysis, if it occurs, must take place in the greatly enlarged caecum and large intestine which houses a large population of cellulytic bacteria. Presumably fermentation and the resultant release of VFA's, CO_2, and methane occurs here and VFA absorption occurs through the wall of the caecum. As digestive efficiency in monogastric species is approximately 50 percent of that in the polygastric, it can further be speculated that digestive efficiency of foliage in Alouattinae is less than that for the Colobinae with the result that either Alouattinae must ingest more folivorous material or depend less on foliage and more on fruits for energy.

In captivity, howler monkeys (*Alouatta*) do not suffer as severely from improper dietary management as colobines, but rather seem to adapt to a more "standard" primate fare. This is undoubtedly a reflection of the fact that they exhibit broader natural food preferences than the Colobinae. As with the Colobinae, however, it appears necessary to provide a reasonable amount of bulk to the diet of captive howler monkeys, as they also seem predisposed toward bloat-type digestive disturbances (Crandall, 1964). Respiratory infection and general physical deterioration brought about by moroseness seems to be the major cause of premature death in howlers. Such deterioration is probably more related to psychological factors than diet-related ones. It is interesting to note that the National Zoological Park has successfully maintained a pair of *Alouatta palliata* for 6 years on a diet consisting largely of cottage cheese, concentrated primate food, and canned baby food with a small amount of leafy greens. These animals were hand-raised and it is probable that this fact lessened the psychological trauma of captivity and enabled the animals to adapt better than wild-caught animals.

The marsupials are an extremely interesting group of mammals to ponder in regard to the diversity exhibited in their form and function. In Australia, where they evolved without competition from eutherians, they achieved adaptations to exploit a great diversity of foodstuffs. Marsupial carnivores, insectivores, and omnivores filled niches that paralleled those of their placental counterparts. Herbivorous marsupials diversified into forms that grazed and browsed (macropods) and even fed on pollen and nectar (*Tarsipes*). Others, primarily the phalangers, climbed to exploit the arboreal habitat. Of this group, 7 genera (*Phalanger, Trichosurus, Cercartetus, Dactylopsila, Pseudocheirus, Phascolarctos,* and *Schoinobates*) feed on leaves to a greater or lesser degree. Of these 7 genera, 2 (*Phascolarctos* and *Schoinobates*) have become obligate folivores.

The koala (*Phascolarctos cinereus*) inhabits dry sclerophyll forests of eastern Australia from Queensland south to Victoria. The koala is a highly specialized folivore feeding solely on the leaves of eucalyptus trees. Carrying specialization to a yet higher degree, *Phascolarctos* feeds on only approximately 20 out of the 350 available eucalypt species and shows strong preference for only 5 of these 20 (Grzimek, 1972). Adult animals weight up to 13.6 kg and consume approximately 1.14 kg of leaves a day.

Dietary demands are complicated further by the nature of the eucalypt leaves themselves. Grzimek relates how seemingly healthy koalas kept in the Melbourne Zoo would suddenly expire. Veterinary medical treatment did not help and autopsies revealed nothing. At about this time, chemists and pharmacists began investigating eucalyptus leaves. They found that *E. mana*, one of the koalas' favorite trees, seasonally produced hydrocyanic acid in its shoots and leaves. During the winter a greater percentage of this acid was produced than during the summer months. In addition, more is produced in young leaves and shoots than in the more mature leaves. Logically, in the wild, koalas change over to other trees and avoid the fresh sprouts, but captive animals may be forced to eat these leaves out of pure necessity. Some of the young leaves and shoots are highly toxic containing as much as .09 percent hydrocyanic acid. Twenty-five grams of these leaves will kill a sheep. The animalkeepers at Melbourne had unknowingly forced their koalas to commit suicide by feeding them (with the best of intentions) solely on the tender leaves and shoots of the manna gum.

Two other chemicals, cineol and phellandren, found in eucalypt leaves are also of great interest. Cineol decreases blood pressure, relaxes muscles, and lowers body temperature, while phellandren seems to increase body temperature. It has been hypothesized that the smaller koalas of warm Queensland prefer the eucalypt species containing cineol and avoid those containing phellandren. The larger koalas of cooler southern Australia prefer eucalypt species whose leaves contain phellandren and avoid those with cineol (see Eberhard, 1978, for a refutation).

One method of insuring that a captive koala receives the proper foliage is to present it with a great variety of eucalyptus leaves and let it choose. This is the primary reason for the lack of koalas in most zoos outside of Australia. North temperate zoos simply cannot provide a continuous and abundant selection of fresh leaves from tropical eucalyptus trees. To date, no one has formulated an adequate substitute diet. The London Zoo maintained a specimen for 14 months following its arrival at that institution in 1880. Its death was accidental. At first the koala was fed on dried leaves brought with it from Australia and then on fresh leaves, probably from a botanical garden. Subsequent attempts at maintaining this species at the London Zoo proved less successful.

The only koala acquired by the New York (Bronx) Zoo arrived at that institution on October 30, 1920. Crandall (1964) reports that during the journey it had been fed on eucalyptus leaves, both dried and refrigerated, but that the supply was already exhausted when the animal was received. Fresh foliage of many sorts was offered and refused. As eucalyptus leaves were not then available, the koala died 5 days later. California zoos, blessed with an abundance and variety of eucalyptus, have had much more success with these animals. Both the San Francisco Zoo and the San Diego Zoo have maintained groups of koalas that thrived and bred (Pournelle, 1961).

Unless a suitable substitute for the koala's natural diet of eucalyptus leaves is formulated, it is doubtful that we will see these animals in zoos outside the range of the eucalyptus tree in the near future. Even if a successful substitute diet were formulated, obtaining these animals from Australia would be extremely difficult at this time, since they, along with the platypus and lyrebird, are among that country's three most highly protected animals.

The greater marsupial glider (*Schoinbates volans*) inhabits the canopy of tall trees and is restricted to the wet and dry sclerophyll forests of eastern Australia from Queensland south to Victoria (Tyndale-Biscoe and Smith, 1969). Greater marsupial gliders are specialized in their dietary habits, ingesting each night approximately 20 grams (dry weight) of leaves, buds, and bark from a variety of species of eucalyptus trees (Marples, 1973). Troughton (1967) notes that eucalypt blossoms are also eaten, and relates one account of this species feeding on the leaves and blossoms of apple trees. Regarding its folivorous diet, Fleay (1947) comments that in this respect it resembles the koala for, remarkable to relate, this largest of the gliders is the only one that is a leaf-eater, and, unless able to get a regular variety of eucalypt leaves according to its own fastidious requirements, it simply will not live.

Jones (1963) reports that *Schoinobates* was maintained at the Earl of Derby's Knowsley Menagerie in England in 1850, but no other details (diet, longevity, etc.) are available. This is the only record we can find of this species having been transported outside of Australia. Troughton (1967) observes that, as early as 1853, Gould expressed surprise that so interesting and attractive an animal had not been sent alive to England, as with the smaller members of its family. Strangely enough, the largest species appears to need more careful nursing in captivity than the smaller but hardier gliders. This may be because of its greater dependence on a fresh supply of suitable leaves, like the koala, with which it shares an inability to thrive solely on unnatural foods.

The Sydney Zoo feeds its captive *Schoinobates* a variety of eucalypt leaves and blossoms, bottle brush, wattle, and other native foliage. In addition, banana, apple, fruit bread, and carrot are fed as supplements. Fleay (1933) notes that captive animals may be persuaded to acquire an additional taste for bread and milk spread with a sweet jam or honey, but this is only possible as an adjunct to the diet of eucalypt leaves. Although several authors are of the opinion that *Schoinobates* is dependent upon eucalypt leaves for its survival in captivity, it would seem that this species has been kept in captivity outside of Australia far less frequently than the koala and that no one has made serious attempts at formulating a totally "unnatural" but acceptable diet for this phalanger. We see no reason why California zoos with their access to a variety of eucalypts could not maintain this species in addition to the koala.

Although the Edentata consists of genera that are primarily terrestrial, insectivorous, and myrmecophageous, the family Bradypodidae is exclusively arboreal and highly herbivorous. Like the colobine primates, sloths have stomachs and digestive systems showing convergence with the ruminants, possessing pouched stomachs capable of storing large quantities of bulky food material in which fermentation apparently occurs (Grassé, 1955, Jeuniaux, 1962). That *Bradypus* has a more complex stomach than *Choloepus* (Wislocki, 1928) is probably a reflection of its more highly folivorous habits (Montgomery and Sunquist, 1975).

It is interesting to note that while *Bradypus* represents approximately 40 percent of the total fauna biomass in selected Central American rainforests and *Choloepus* only 12 percent (Eisenberg and Thorington, 1973), *Choloepus* is by far the most commonly represented in zoological collections. This apparently is a result of the difficulty in acclimating *Bradypus*, since its particular feeding habits make it an obligate folivore (Herbig-Sandreuter, 1964; Montgomery and Sunquist, 1975). Acclimatization of *Choloepus* to a captive diet has been vastly more successful than for *Bradypus*, probably because of its predisposition to eating fruits, flowers, buds, and possibly some animal material in addition to foliage (Beebe, 1926; Eisentraut, 1932; Tirler, 1966; McCrane, 1966; Montgomery and Sunquist, 1975). Even *Bradypus* that have been maintained on a natural leafy diet in captivity have demonstrated poor longevity (Beebe, 1926). It is possible that the more docile and even timid nature of *Bradypus* (Montgomery, personal communication) contributes to its poor adaptability to captivity.

Recent research reveals that there may be considerable variability among members of any single sloth population in terms of food preferences. Individual sloths concentrate large percentages of their time using a single "modal tree" species (Montgomery and Sunquist, 1975). Jeuniaux (1962) believes there is variability in the cellulytic power of the stomach contents from individual to individual and this fact, coupled with the discovery that certain individuals become strongly attached to specific tree species, may mean that there is a strong difference in digestive efficiency, over the range of food eaten, from specimen to specimen. Thus, when an attempt is being made to acclimate sloths to captivity, especially *Bradypus*, it may be useful to know the individual animal's "modal tree" and feed a high percentage of leaves from that tree species at first while gradually substituting components of the desired captive diet.

The difficulty of maintaining *Bradypus* in captivity is so well known that few zoological gardens even attempt to acquire the animal, although Herbig-Sandreuter (1964) did manage to maintain 1 male and 2 female *Bradypus infuscatus* for 3 years in the tropics with 1 young born. In captivity, *Choloepus* is successfully maintained on a diet of fruits, vegetables, bread, and leafy greens. Although reproduction is infrequent, several institutions have managed to breed *Choloepus* with a fair degree of regularity.

One unique species that we have had the opportunity to study at the National Zoological Park during the past 4 years is the giant panda (*Ailuropoda melanoleuca*). Although not strongly arboreal as an adult, it is quite definitely a folivore. Bamboo of the genus *Sinarundinaria* appears to be the principal food item in the diet of free-living specimens of this "carnivore turned herbivore" (Morris and Morris, 1966). The same authors list 8 genera and 9 species of bamboo that are acceptable to the giant panda as food. While *Bambusa* sp., *Phyllostachys* sp., and *Pseudosasa japonica* have all been accepted as food by our 2 pandas, selectivity is shown in the feeding process. When offered a large quantity of *Pseudosasa japonica*, the leaves are eaten but the culms or canes are left. In this particular species, the culms are small in diameter while the leaves are exceptionally large. It does not appear energetically efficient for the animal to attack the smaller, tough canes for the amount of usable tissue extracted, thus, unless a limited amount of bamboo is fed, the culms of this species are simply dropped after the leaves are snipped off. In the species exhibiting larger culms, both the leaves and culms are eaten. Naturally, the younger, more tender stalks are preferred and fresh shoots of all 3 species of bamboo are readily eaten.

Pseudosasa japonica may also be preferred by our specimens because the thicker, tougher leaves of this bamboo retain their moisture and freshness long after they have been cut. The paper-thin leaves of the other bamboo species wither and curl rapidly after cutting.

Although somewhat more arboreal than *Ailuropoda*, the red panda (*Ailurus fulgens*) also demonstrates a high degree of folivory in nature. Ranging in the high, cool, mixed rhododendron/bamboo forests of southern China, Tibet, and Nepal, *Ailurus* nests, dens, and sleeps in trees, but apparently descends to the ground to forage for herbivorous foodstuffs, primarily the various species of bamboo. Although both *Ailurus* and *Ailuropoda* exhibit strong herbivorous tendencies, *Ailuropoda* appears to be the more highly folivorous showing a strong preference for bamboo, with *Ailurus* being less inclined to folivory. In captivity, *Ailurus* is maintained in a manner similar to *Ailuropoda*, receiving large allotments of bamboo and sometimes eating as much as 1 to 1.5 kg of bamboo per day per animal. In addition, supplementary food items such as oatmeal, milk, apple, and banana are offered daily. Although highly herbivorous, *Ailurus* is able to survive in captivity even when no bulky foodstuffs are offered; however, survivorship is reduced under these conditions and digestive problems including dysentery and bloat have been reported.

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Semideciduous tropical forest in Sri Lanka. The ubiquity of leaves and their seasonal abundance present both opportunities and problems to folivorous animals. (Photo by C. M. Hladik).

FOLIAGE AS A FOOD SOURCE

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Forest Leaf Production

Introduction

The object of this paper is to describe the quantities of leaves available to arboreal folivores in forests. Leaves are the principal appendage borne by the stem. In some plants the leaves have arisen as a lateral outgrowth of the stem; in others the leaf is interpreted as a branch system limited in growth and differing from the main branch system. While there are a variety of different types of leaves, those on trees are mainly foliage leaves which function in photosynthesis. Leaves show determinate apical growth as contrasted with continuous growth of the stem from the apical meristem and, therefore, are restricted in their capacity to restore their tissues exposed to weathering and other harmful influences. In perennial plants new leaves are repeatedly formed and old ones shed. Thus, leaves are usually limited in growth and longevity and are restricted in mass.

The length of time leaves remain on the tree varies greatly with species and environment. In deciduous species the leaves are lost during seasons of extreme cold or dryness; in evergreen species leaves may persist for several years. The mass of leaves present on a tree is, of course, a measure of the quantity available at that instant of time but is a relatively poor predictor of availability if the tree occurs in an area with seasonality. In this case it is much more useful to know the quantity of leaves produced or lost per year. Leaf production is a well-studied phenomena in forests since both energy capture and transpiration depend upon this vegetation process. Leaf production is usually measured as part of primary net production which also considers the increase in mass of roots, stems, and other plant parts, as well as leaves.

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Leaf production can be determined by measuring the leaf-mass at sequential intervals of time in the forest canopy or by collecting the leaves as they fall to the forest floor. In the first method the leaves may be collected directly and measured or weighed or the leaf-mass may be estimated from some more easily studied part of the vegetation, such as the diameter and height of the stems. This is called the allometric technique, and it can involve a very detailed analysis of the vegetation (Whittaker, 1965). It is much easier to capture the falling leaves and weigh this litter over a season or annual cycle. There are literally dozens of such studies and several reviews of leaf-litter fall (for example, Bray and Gorham, 1964). The following comments will discuss leaf-mass, distribution, and production from these two points of view.

Observations

Leaf-mass.

The mass of leaves in forests and associated vegetation varies with the type of forest and conditions within forests (Table 1). The maximum leaf-mass is sustained on the average by tropical forests and temperate coniferous forests. In both cases the leaf-mass is maintained over the year. Deciduous forests have a substantially lower leaf-mass and, as expected, deserts and tundras have even less than deciduous forests.

The vertical distribution of biomass of the leaf-mass can be exceedingly important to foliage feeders since this distribution regulates the animal distribution patterns. Two examples, from a tropical mangrove forest and a Japanese birch forest, illustrate the typical pattern (Figure 1). Initially leaves are distributed throughout the vegetation height but, as the plants mature, leaves in the lower strata are shed and are not replaced owing partly to low intensities of light beneath the canopy. The curve of light intensity and leaf-mass parallel one another.

Table 1.—Some selected average forest leaf-mass estimates. (From Rodin and Brazilevich, 1965 and Ovington, 1965.)

Vegetation	*Average leaf mass*	*Range*
Tropical forest	10.3	2.5-25.4
Temperate coniferous	10.2	4.7-24.6
Temperate deciduous	3.8	1.1-6.4
Shrub tundra	3.2	—
Deserts	1.8	0.01-10.0
Arctic tundra	1.0	—

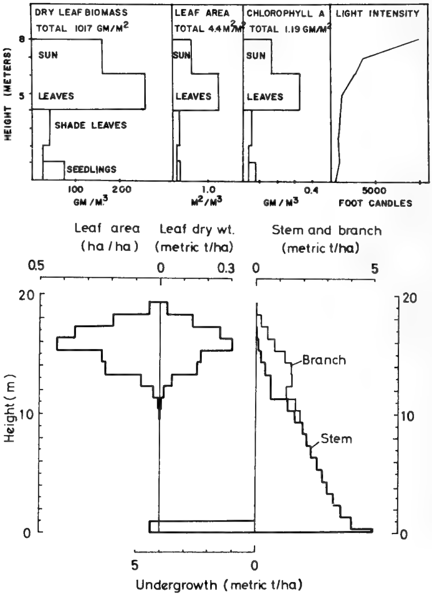

Figure 1. Structural features of the leaf mass of a red mangrove forest in Puerto Rico (Golley, et. al., 1962) (upper part of figure) and a Japanese birch forest (Satoo, 1970).

The seasonal distribution of leaf-mass is exceedingly important in deciduous forests and also probably significant in tropical evergreen forests, but relatively few data are available on these seasonal changes. Trends in leaf-mass and leaf-area over the growing season in a plot of *Ulmus* is shown in Figure 2. There is a period of rapid growth in the spring, then a period of gradual decrease until leaf-fall.

The above comments refer to the forest as a simple entity but, actually, forests are most often complexes of species populations. Since animals often are associated with single species plant populations, it may be useful to know the mass of leaves by species. Data of this type are often less common than data for the leaf-mass of a forest in toto, but see A. Hladik (1978). An example is an oak-pine forest on Long Island (Whittaker and Woodwell, 1969) (Table 2). In this case, several species of oak and a pine share dominance in leaf biomass.

Leaf-mass also varies with age of the stand. The leaves reach equal levels to those of the mature forest relatively early in the sere. This is partly because photosynthesis and transpiration depend upon the

Table 2.—Biomass of the Brookhaven oak-pine forest, Long Island. (Adapted from Whittaker and Woodwell, 1969.)

Species	*Stem, wood, and bark*	*Branch live wood and bark*	*Branch dead wood and bark*	*Current twigs*	*Leaves*	*Fruits*	*Flowers*	*Above-ground total*	*Total roots*	*Full total*
				Biomass, dry g/m²						
Quercus coccinea	1964	705	110	26	164	7	1	2967	1335	4302
Q. alba	1280	345	19	16	109	8	1	1788	1485	3272
Pinus rigida	808	262	35	9	116	5	—	1235	315	1550
Quercus velutina	271	98	16	4	23	1	—	413	190	603
Tree-stratum total	4323	1410	180	55	412	21	2	6403	3325	9728
Quercus ilicifolia	6.2	2.9	0.9	0.2	1.6	—	—	11.8	50.9	62.7
Gaylussacia baccata	47.4	23.1	4.4	4.5	15.6	0.6	0.2	95.8	160.9	256.7
Vaccinium vacillans	5.1	5.1	0.4	1.9	7.6	1.0	0.2	21.3	66.8	88.1
V. angustifolium	—	3.0	0.5	0.6	1.8	—	—	5.9	12.3	18.2
Other shrub species[a]	4.0	2.3	0.3	0.2	1.4	—	—	8.2	14.6	22.8
Tree sprouts[b]	8.0	4.0	0.4	0.4	2.7	—	—	15.5	—	15.5
Shrub-stratum total	70.7	40.4	6.9	7.8	30.7	1.6	0.4	158.5	305.5	464.0
Total woody plants	4393	1450	187	63	443	23	2.4	6561	3631	10192

[a] Current twig clippings (dry g/m²) for minor shrub species: *Myrica pensylvania* 0.750, *Kalmia angustifolia* 0.624, *Pyrus arbutifolia* (L.) L. F. 0.103, *Rubus* sp. 0.048, *Lyonia mariana* (L.) D. Don 0.024, *Amelanchier stolonifera* Wieg. 0.016, *Vaccinium corymbosum* (L.) 0.015, *Comptonia peregrina* (L.) Coult. 0.002, *Smilax rotundifolia* 0.0002.

[b] Current twig clippings (dry g/m²) for tree sprouts and seedlings not reaching 1 cm breast height: *Quercus coccinea* 1.57, *Q. alba* 1.04, *Q. prinoides* Willd. 0.266, *Pinus rigida* 0.030, *Sassafras albidum* 0.018.

leaf-mass, and these processes provide both the energy and nutrients required for growth and maintenance of the forest. Data from tropical moist forest in Panama illustrate the trend (Figure 3). In this example, leaf-area and canopy cover reach the level of the mature forest in six years. Leaf-mass is still somewhat below the mature leaf-mass because the weight of individual leaves is less at this stage of stand development.

Leaf production

Although leaf production can be measured directly by harvest over the growth period, it is much easier to collect leaves as they fall to the forest floor. Leaf-fall then is a measure of the leaf production, integrated over the seasons of growth and influenced by environmental factors such as wind, storm, and so on. Further, leaf-fall data also must be corrected to take into consideration the herbivores' consumption of leaves and the loss of leaf weight by translocation to the branch and so on. Thus, leaves collected as they fall may underestimate true leaf production; nevertheless, leaf-litter data provide an unusually good source of information on leaf production, since so many separate estimates exist.

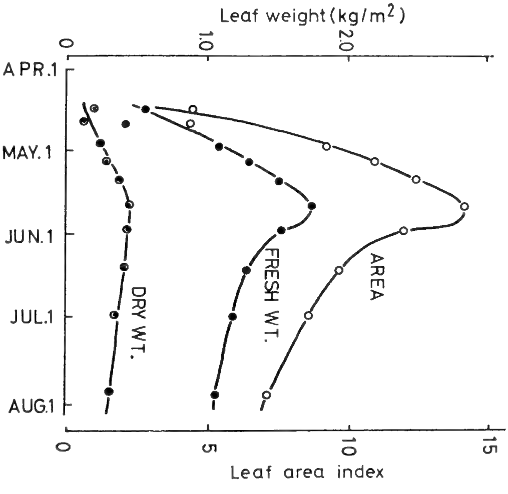

Figure 2. Seasonal change in leaf area and leaf biomass in a plot of *Ulmus* (Satoo, 1970).

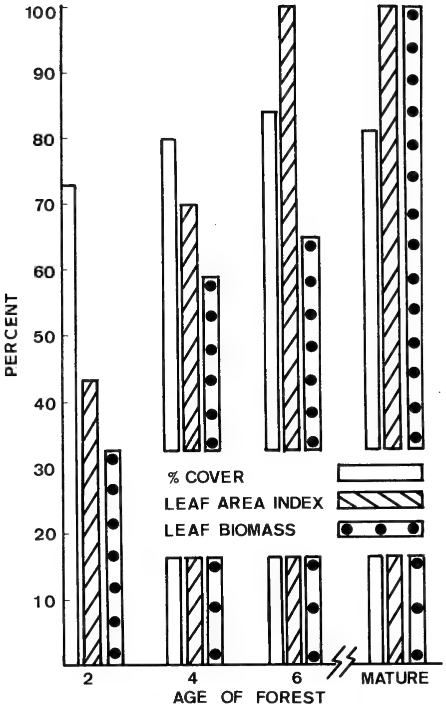

Figure 3. Characteristics of Panamanian Tropical Moist forest leaf-mass at different ages.

Leaf-litter production in the major climatic zones (Bray and Gorham, 1964; Golley, 1975; and A. Hladik, 1978) show that leaves are produced at a higher rate in equatorial forests (Table 3). Jordan (1971) pointed out that on a gradient of decreasing solar energy, wood production tends to be constant, while leaf production decreases. However, on a gradient of decreasing precipitation, leaf production tends to be constant and wood production is highly variable from forest to forest (Table 4). Leaf production is lowest in very dry tropical environments, and probably also in cold, high-altitude habitats although data for these are not available. The average leaf production for tropical forests, based on leaf litter fall, is 5.4 mt/ha/yr.

Table 3.—Annual leaf-litter production in major climatic zones. (From Bray & Gorham, 1964 and Golley, 1975.)

Climatic zone	*Number of samples*	*Leaf mt/ha*
Arctic-Alpine	1	0.7
Cool temperate	15	2.5
Warm temperate	8	3.6
Equatorial	20	5.4

Estimation of Leaf-Mass and Production

Measurement of the leaf-mass or leaf production has been described by Newbould (1967) in the IBP Handbook on methods of estimating the primary production of forests. My comments will be paraphrased from his directions.

As mentioned previously, there are two ways of estimating leaf biomass and production: (1) as part of the branch component of trees, or (2) as litter fall. There are also two ways of regarding leaf production: (1) as the maximum dry weight of foliage during the year minus the minimum quantity (for deciduous species this minimum may be zero), or (2) as the dry weight of the foliage at the end of the growing season. The maximum dry weight is a true measure of leaf production and represents the quantity of foliage available to folivores. In contrast, leaf dry weight at the end of the season may be less than the maximum dry weight because of translocation losses, leaching by rainfall, insect consumption, and the fact that respiration may exceed assimilation during part of the season.

Maximum leaf production can be estimated by taking representative samples of leaves from different parts of the canopy at regular intervals throughout the year and determining the maximum dry weight of a given number of leaves. This estimate can be combined with an estimate of the maximum number of leaves in the stand derived from harvest of a selection of branches or from litter fall.

Estimates of litter fall have been discussed earlier. There are a variety of collection devices reviewed by Newbould. It is important that the litter can fall directly into the trap, not blow out again, and not decompose in the trap between collection periods. Usually litter traps have an opening of about 1 meter square and are placed in the forest by some stratified random method. Probably not less than 20 traps are needed for the general forest leaf production. If production of minor species is required the number of traps may need to be much larger than 20. Traps are best emptied of litter weekly.

Table 4.—Estimates of litter fall in tropical forests (units in metric tons per hectare per year). Leaf litter is presented separate from total litter which includes fruit and flower parts and twigs, as well as leaves. (Authorities taken from Golley, 1975, World Status Report on Tropical Forests. Unpublished.)

Forest	*Location*	*Leaf litter*	*Total litter*
Equatorial Rain	Khao Chong, Thailand	11.9	23.2
Lowland Dipterocarp	Pasoh, Malaya	8.3	12.6
Lower Montane	El Verde, Puerto Rico	4.8	11.4
Dry Deciduous	Varanasi, India	—	7.7
Secondary forest 40 yrs.	Kade, Ghana	6.9	10.5
Mature forest	Omo, Nigeria	7.2	—
Mature forest	Olokemeji, Nigeria	4.8	—
Derived Savannah	Olokemeji, Nigeria	0.9	—
Teak plantation	Dehra Dun, India	—	7.8
Sal plantation	Dehra Dun, India	—	10.9
Chir plantation	Dehra Dun, India	—	7.8
Montane	Rancho Grande, Venezuela	—	7.8
Dry forest	Calabozo, Venezuela	—	8.2
Miombo forest	Lubumbashi, Zaire	3.0	4.0
Tropical Moist	Darien, Panama	—	11.3
Premature Wet	Darien, Panama	—	10.5
Gallery	Darien, Panama	—	11.6
Rain Forest	Colombia	—	8.5
Rain Forest	Colombia	—	10.1
Second growth	Canal Zone, Panama	—	6.0
Dry Woodland	Nigeria	—	5.6
Moist Semideciduous	Nigeria	—	4.6
Evergreen	Nigeria	—	7.2
Evergreen	Banco, Ivory Coast	8.2	11.9
Evergreen	Yapo, Ivory Coast	7.1	9.6
Lowland Dipterocarp	Malaya	—	7.2
Lowland Dipterocarp	Malaya	—	5.5
Upland Dipterocarp	Malaya	—	6.3
Secondary forest	Malaya	—	8.3
Secondary forest	Malaya	—	10.5
Secondary forest	Malaya	—	14.4
Semideciduous	Tafo, Ghana	—	20.9
Mixed forest	Yangambi, Zaire	—	12.4
Brachystegia	Yangambi, Zaire	—	12.3
Macrolobium	Yangambi, Zaire	—	15.3
Musanga	Yangambi, Zaire	—	14.9
Dry Evergreen	Lubumbashi, Zaire	4.7	9.2
Miombo	Lubumbashi, Zaire	2.9	7.5
Riparian	Lubumbashi, Zaire	4.5	5.9
Dipterocarp Savannah	Thailand	—	7.8
Mixed Savannah	Thailand	—	8.0
Evergreen gallery	Thailand	—	25.3
Temperate Evergreen	Thailand	—	18.9
Terminalia-Shorea	Chakia, India	6.2	—
Tectona	Chakia, India	5.0	—
Diospyros-Anogeissus	Chakia, India	4.2	—
Shorea-Buchanania	Chakia, India	3.1	—
Butea	Chakia, India	1.0	—
Amazonian upland	Manaus, Brazil	5.6	11.3
Evergreen Seasonal (Mora)	Trinidad	7.0	—

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Interaction of Plant Life History Components as Related to Arboreal Herbivory

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Introduction

The interaction between herbivorous animals and plants has often been portrayed as similar to a foot race between two evenly matched opponents; first one competitor surges ahead, but is eventually overtaken by his opponent, and on and on. It cannot be denied that the mutual co-adaptations of animals and the plants upon which they rely as food resources is one of continual fine-tuning and tracking of adaptations, but it is usually overlooked that their mutually related characteristics are strongly related to a complex of other features which combine to form what may be called a "life-history strategy." In this contribution I wish to synthesize many kinds of evidence illustrating how leaf persistence, leaf chemistry, reproductive strategy, growth, longevity, and successional status of plants may form co-evolved syndromes and how these not only relate to, but restrict, the characteristics of herbivores which feed upon them.

The physical harshness or permissiveness of the environment is an important restraining factor on the nature of plant life-history adaptations, but is less so for their animal defoliators. Similar climates usually favor similar plant communities and the herbivores which occur in similar plant communities will probably display analogous life-history adaptations.

In this paper I will first indicate how physical environmental factors may be limiting to certain life-history features of trees, and then discuss how various characteristics of trees, especially those which relate to external biotic and abiotic environmental features, combine to form several co-adaptive alternative strategies. The characteristics of monophagous arboreal folivores will then be related to their resources, and, finally, the life-history features of generalist folivores will be related to community characteristics of the constituent tree species in space and time.

The Physical Environment and Plant Life History

Physiological tolerance

As one proceeds toward the poles of the earth or upwards in elevation a point is reached beyond which the physical environment is inimical to the growth of trees (Hustich, 1953). Similarly, as one follows gradients of increasing aridity a point may be reached beyond which trees cannot grow. These kinds of phenomena relate to the extreme physical limits for the growth of trees. It has been demonstrated that the altitudinal or latitudinal limits relate to a complex interrelationship between the lower temperature limits for photosynthesis, and water transport and balance (Anderson and McNaughton, 1973), while aridity is usually limiting with regard to soil moisture availability (Strain, 1969). Naturally, other site characteristics, such as steep unstable slopes, strong winds on ridge tops, unfavorably harsh soils (chemistry or pH), or frequent fire, may preclude the presence of trees, but such qualifications do not relate to the physiological tolerance of the plants themselves (Kramer, 1958). Such trees as do survive under such conditions, particularly fire and unfavorable soil, have evolved mechanisms which allow them to survive there.

Ecological tolerance

Given the geographical area within which trees may grow and survive as viable populations, how do physical factors further limit their phenotypic characteristics? The most obvious is that the evergreen habit in angiospermous trees occurs far to the south, and at lower elevations than that for deciduous species (Figure 1). The microphyllous coniferales, because of their leaf form and physiological adaptations, may sustain the evergreen habit to greater latitudinal and elevational extremes than angiosperms. Yet a deciduous conifer (*Larix lyallii* Parl.) lives in perhaps the most exacting climate in the Americas (Arno and Habeck, 1972).

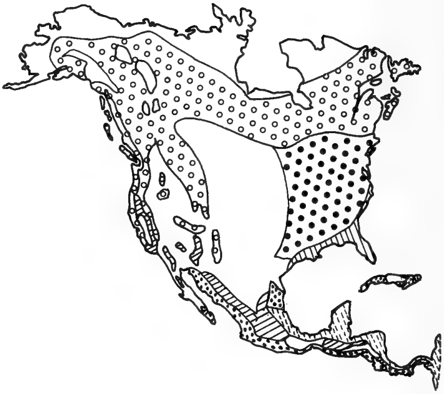

Figure 1. Map of North and Central America diagrammatically depicting major forested areas highlighted by different degrees of leaf persistence. Adapted from information in Shelford, *The Natural Vegetation in North America,* 1966.

A similar situation prevails in extremely arid situations with deciduous trees occurring in the most arid sites, although evergreen phreatophytes may persist where ground-water reserves are within reach of their root systems (Strain, 1969).

Within the areas where trees may grow, and where both deciduous and evergreen habits may survive, it is well known that local expression of such factors as precipitation, temperature, humidity, wind, and substrate features may favor certain morphological and physiological characteristics of trees. Even in such cases, however, other sorts of expression may not be prevented, and different trees of diverse characteristics may exist. Such concepts as life zones (Merriam, 1899; Holdridge, 1967), biomes, and plant formations have been based on the existence of such apparent ecological maxims. The latter phenomenon, phenotypic diversity under similar physical bounds, is a central focus to the present discussion. Genotypic flexibility, as determined by prior evolutionary events, and interspecific adjustment among tree species (competition), and most importantly, extant herbivores, pollinators, and dispersal agents may allow different tree species to utilize quite different life-history strategies in the same environment. Obviously, quite different permutations of phenotypic characters may be combined to form successful life-history strategies in a similar environment, but it is equally obvious that most possible permutations would not be selectively advantageous. We should be particularly concerned here with the sorts of permutations that would be selectively advantageous in a given environment and how these might relate to ecological opportunities for arboreal herbivores. I will now examine evidence relating various character sets for trees.

Plant Life-Support Functions

We may look at a tree, in the generalized sense, as having five primary structures with associated essential functions: leaves (transformation of sun energy to highly ordered chemical energy, gas exchange, and water balance), stems (supportive and conductive), roots (anchoring, storage, and uptake), flowers (meiosis and genetic exchange), and fruits (reproduction and dispersal). All of these are interactive in both the contemporaneous functional and evolutionarily adaptive senses. Fitness, the relative ability to insert an individual's genome into succeeding generations, is highly dependent upon a plant's reproductive system, which in turn is highly dependent upon its vegetative support system. A number of studies have dealt with interactions of the reproductive system (Bawa and Opler, 1975; Opler et al., 1976b), while the interactivity of reproductive and vegetative systems has been demonstrated by others (e.g., Carr and Pate, 1967; Rockwood, 1973; Dement and Mooney, 1974). Since we are concentrating our thoughts in this symposium on foliar characteristics, I will not dwell at length on interactions between reproductive characteristics.

Vegetative Interactions

Leaf phenology

Most trees have characteristic annual periodicities with regard to leaf production, persistence, senescence, and abscission. Changes in the chemical constituents in leaves undergo both quantitative and qualitative changes with time (Sanger, 1971; Dixson, 1966; Dement and Mooney, 1974; Feeny and Bostock, 1968). Chemicals produced or stored in other plant organs may be transferred to leaves, and energy-rich chemicals produced by photosynthesis are transferred from leaves to other structures (Carr and Pate, 1967).

A portion of the chemical changes in leaves is highly related to defense against herbivores, and is a phenomenon referred to as allelochemics (Whittaker and Feeny, 1971; Jones, 1962).

With regard to palatability and nutritive value, newly produced leaves are eminently suited to herbivores, while mature leaves are relatively unsuitable (Feeny and Bostock, 1968; Feeny, 1968, 1970). Others have shown chemical changes in senescent leaves may again endow relative palatability and nutritive value, at least to some insects (Dixson, 1966; Opler, 1974b).

Leaf persistence

Leaf persistence may be defined as the length of time a leaf remains attached to a plant while remaining functional. Plants which are devoid of leaves for variable periods each year are referred to as deciduous. By definition their leaves persist for periods less than 12 months. Plants which always have some leaves are referred to as evergreen. Although such plants could conceivably have overlapping leaf sets, each with less than 12-month persistence periods, the leaves of most evergreens persist for at least a year. Some evergreens are known to have persistence periods up to 3 years (Trelease, 1924; Molisch and Fulling, 1938), and much longer periods are not inconceivable.

The relationship of leaf persistence to the absolute permissiveness of the physical environment was discussed earlier, but other features may be mentioned here. A notable trend is for the leaves or leaflets of evergreen trees to be elongate with entire margins. While the leaves of deciduous trees may possess these traits, they are often lobed and deeply dissected. In addition, the leaves of evergreen species seem to be thicker and more heavily cuticularized than those of deciduous species. These differences in leaf morphology may well be related to the physical environment, but also relate to herbivore defense, as will be discussed later.

In plant succession the earliest seral stages represented by trees are often dominated by deciduous species (Budowski, 1961), while these are often replaced by evergreens. In Costa Rica, lowland tropical forest successional sequences are dominated in their early stages by such genera as *Cecropia, Cordia, Muntingia, Ochroma,* and *Trema,* all deciduous.

Succeeding stages in a succession are characterized by trees with longer periods of leaf persistence (most climax species).

Growth rate and longevity of trees also seem to be correlated with leaf persistence. Evergreen trees grow at slower rates than deciduous species, but have increased longevity (Molisch and Fulling, 1938). These trends when related to the successional trends show that species in successive seral stages display decreasing growth rates, but increased longevity.

Presumed increases in allelochemic defense are also associated with increased leaf persistence and will be treated later in this discussion.

Foliar and Reproductive Events

As mentioned previously, the components of a plant's reproductive system are integrated and form a co-adaptive system. Each plant's vegetative characteristics are also closely integrated with its reproductive traits.

Leaf phenology and reproduction

For most trees, flower production immediately precedes, is simultaneous with, or directly follows foliation. This is not surprising since floral structures are ontogenetically derived from leaves. Fruit and seed maturation are often associated with leaf senescence and abscission, but not as intimately as are floration and foliation events. Energetic reserves for flower production must be drawn from those produced by photosynthesis of prior "leaf generations," while fruit maturation may rely upon energy transfer from current photosynthetic production.

It has been shown that timing of chemical changes involved in fruit maturation is closely integrated with that taking place in the leaves of *Heteromeles arbutifolia* (Rosaceae) (Dement and Mooney, 1974).

It is selectively disadvantageous for a plant's fruits to be eaten by animal dispersal agents until their seeds are mature, and allelochemicals in the fleshy exocarp of unripe fruits are probably frequent. As fruits ripen, these chemicals can be transferred to leaves or broken down into harmless by-products (Dement and Mooney, 1974).

Leaf persistence and reproductive effort

The above-mentioned correlation of leaf persistence, growth rate, and longevity is also closely tied to reproduction. The proportion of accrued energy devoted to reproduction and growth in fast-growing deciduous trees is far greater than that devoted to vegetative maintenance and defense.

Leaf persistence may also be closely correlated with pollination, seed dispersal, and breeding systems. Bawa and Opler (1975) have reported that in a Costa Rican semideciduous forest a significantly high proportion of dioecious trees are evergreen, these having small inconspicuous flowers of a generalized pollination syndrome, and large single or few-seeded, fleshy animal-dispersed fruits. Extending this correlation for all trees in the same forest (Table 1), we find that a significantly high proportion of evergreen species has small flowers and large, single, or few-seeded animal-dispersed fruits; while deciduous trees tend to have larger flowers, adapted for more specialized pollination, and fruits with large numbers of physically dispersed (wind, propulsion, or gravity) seeds. Some deciduous trees, particularly those of low stature and early successional position, have animal-dispersed fruits containing many small seeds. McKey (1975) has referred to the latter as leading to "low-quality dispersal" and to the large-seeded fruits of evergreen trees as leading to "high-quality dispersal." In more temperate regions these correlations apparently do not hold, since many deciduous trees may have tiny wind-pollinated flowers and large fruits, although small flowers and large-seeded animal-dispersed fruits are still the general rule for nonconiferous evergreens.

Table 1.—Correlation of reproductive traits of lowland tropical dry forest trees with leaf persistance traits.

	Evergreen (N Spp)	*Deciduous* (N Spp)	χ^2	*P*
Seeds/Fruit				
1	27	26	14.5	<0.005
>1	15	63		
Pollinators				
Specialized	17	58	6.8	<0.01
Generalized	25	31		
Dispersal				
Animal	36	34	25.9	<0.005
Physical	6	55		

Reproductive Strategies of Trees

r- and K-selection

Through the simultaneous consideration of the various vegetative and reproductive characteristics of trees, we may devolve a further generalization, one which possesses predictive power capable of being tested experimentally. As one proceeds from physically exacting environments to those which are more benign, or as one proceeds from early to late successional stages one expects to find that several associated trends in the vegetative and reproductive characteristics of trees (or other plants) are closely correlated (Table 2). Various authors have contrasted the seed-dispersal characteristics and colonizing abilities of plants found in pioneer habitats with plants in later successional stages (Salisbury, 1942; Gadgil and Solbrig, 1972; Baker, 1974; Horn, 1974; Opler, et al., 1976a). These authors all concur that plants in the former category have many light, physically dispersed seeds in each fruit or infructescence. Cates and Orians (1975) have presented data which strongly support the notion that early succession plants are not as highly defended chemically as are climax plants. Data from studies of the reproductive biology of trees in Costa Rica (Baker, Frankie, and Opler, unpublished) support the above generalizations and bring to light additional correlations (Table 1). By tallying selected characteristics (number of seeds/fruit, generalized versus specialized pollination syndrome, animal versus physical seed dispersal) and by correlating the relative frequency of each with leaf-persistence traits, we find that various character states of each trait not only compare favorably with leaf persistence levels but can be integrated with the pioneer-climax comparison presented previously for trees in semideciduous forest habitats of northwestern Costa Rica.

Table 2.—Some characteristic extremes of r- and K-selected trees.

	r-selected	*K-selected*
Leaf Persistence	Deciduous	Evergreen
Chemical Defense	Low	High
Net Productivity/Year	High	Low
Dispersal	Physical	Animal
Seeds/Fruit	Many	Few
Pollination	Specialized	Generalized

These two sets of traits are not absolutes but are extremes of a continuum, and can be thought of as relatively r-selected and K-selected, respectively. The more theoretical aspects of these extremes in reproductive behavior were first proposed by MacArthur and Wilson (1967), and have been elaborated upon by Pianka (1970) for animals and by Gadgil and Solbrig (1972) as well as Odum (1969) for plants. In this sense, the correlation of leaf persistence with reproductive traits of plants has not been previously propounded.

Herbivore Defense

The mechanisms whereby plants protect their leaves from herbivores are extremely varied, just as are the feeding adaptations of their animal defoliators. The major kinds of defense can be roughly categorized as chemical, physical, temporal, spatial, and symbiotic.

Chemical defense involves secondary chemicals, or allelochemicals, previously assumed to be metabolic by-products, which render a plant's leaves toxic, unpalatable, and/or nutritionally poor. Much has been written on this topic in the last decade, and this probably is the most widespread kind of plant defense (Dethier, 1954, 1970; Feeny, 1975; Whittaker and Feeny, 1971; Jones, 1962).

Physical defense involves the heavy cuticularization of leaves, spines, heavy tomentosity, etc. (Feeny, 1970). This process makes leaves physically difficult to approach, ingest, or chew.

Temporal defense is the phenomenon of foliation at a time when potential herbivores are not at peak numbers (or even absent). This may involve foliation of trees at a time when ovipositing insect females have completed their activity (Varley, in litt.; Opler, 1974b), or the production of leaves at a season unfavorable to herbivore activities (Janzen, 1970).

Spatial defense can involve several forms. By one strategy, principally involving short-lived annual plants, new populations are continually being established in colonizing situations, and their leaves and reproductive structures may be formed before their discovery by herbivores. For long-lived perennials, such as trees, low density per unit habitat or small total area of occurrence may result in low herbivore diversity, and possibly, but not necessarily, low abundance as well (Opler, 1974a).

Symbiotic defense is the provision by plants of living sites and/or food substances for predaceous or omnivorous insects, especially ants. The adaptations of plants for ants have been described by Wheeler (1910) and repeatedly documented by Janzen (e.g., 1966, 1967, 1972, 1974). The role of extra-floral nectar in the protection of leaves has been recently dealt with by Jeffrey, et al. (1970), as well as by Carroll and Janzen (1973). Even the provision of slender thorns, leaf spines, and other plant projections have probably evolved principally as attachment sites for the nests of larvivorous Hymenoptera (especially social Vespidae), while broader projections, usually on trunks and branches, are especially adaptive as dwellings for colonies of predaceous ants.

It has recently been shown that the relative degree of palatability decreases with the successional status of plant species, both in temperate areas (Cates and Orians, 1975) and in the tropics (Waltz, in litt.). As an allegory these biologists both infer increased chemical defense with successional position. This is probably also true of the progression from deciduous to evergreen trees (see below). Against these generalizations is the evidence presented by Feeny (1975) that the chemical defense of early successional plants is directed toward specialist herbivores, while the defenses of forest trees are more generalized.

Folivore Strategy

Putting this evidence together with that discussed earlier for the temporal changes in chemical defense of leaves, we may begin to visualize the various resource availabilities for different herbivores in a forest through space and time.

The complex, ever-changing mosaic of resource types and opportunities through evolutionary time has resulted in an equally complex set of folivores and life-history adaptations. Nevertheless, several generalities may be put forward that enable us to better understand the principles involved.

Specificity

First, with regard to specificity among arboreal folivores, we find that generalist folivores feed upon newly produced tender leaves that may have very low levels of allelochemicals, although many specialists may feed on young leaves as well, e.g., Rockwood (1974). As we find by reading the later papers of this symposium, mammalian folivores almost entirely restrict their feeding to young leaves. Leaf cutting ants (*Atta* spp.), which are extremely generalized, also preferentially select young leaves of their various host plants (Rockwood, 1975, 1976). The most generalized Lepidoptera, e.g., *Argyrotaenia citrana* (Powell, 1964), which feeds on a wide variety of trees in many families, also feed on young leaves. Mature leaves, at their peak of allelochemic content and "toughness," are fed upon by only a few specialist herbivores (Varley, 1967).

Finally, senescent leaves, probably with higher nutritive availability than mature leaves, but with no lessening of chemical defense (Dixson, 1966), are fed upon by specialists, greater in density and richness than those feeding on mature leaves (Opler, 1974b).

Leaf persistence

There are striking differences in the suitability of evergreen and deciduous trees to folivores. The relative degree of chemical defense is probably much greater for evergreen trees than for their deciduous brethren. The best evidence for this assertion is derived from studies of leaf-mining insects on oaks (*Quercus*) in California. These insects are primarily specialists on either mature or senescent leaves (Opler, 1974b). Foliage samples from several populations of both evergreen and deciduous species showed a highly significant difference in the frequency of leaf-mining activity. Furthermore, evergreen species with persistence periods approaching 2 or 3 years had still lower levels of feeding than did those whose leaves persisted for about a year (Table 3). Further observation of plants in genera with both deciduous and evergreen members, e.g., *Prunus* (Rosaceae), *Rhamnus* (Rhamnaceae), and *Rhus* (Anacardiaceae), indicated similar differences. In addition, greater proportions of specialist folivores will probably be found to feed upon the young leaves of evergreen trees.

Table 3.—Correlation of leaf-mining activity on California oaks with leaf persistence.

Host species	*Leaves mined (%)*	*Persistence (Months)*	*Localities (N)*
Quercus douglasii	17	7	4
Quercus kelloggii	19.7	7	4
Quercus lobata	28.3	9	9
Quercus agrifolia	4.7	24	8
Quercus wislizenii	3.5	24	4
Quercus chrysolepis	7.5	36	4
Quercus durata	2.2	36	12

Successional position

It has been previously mentioned that the first trees to appear in a successional progression are often deciduous, and that their leaves have been found to be more palatable than those of trees in later seral stages (Cates and Orians, 1975). In addition, Odum (1969) has illustrated that net production (measured as biomass/area/time) is at its greatest level early in a seral sequence. These three factors, which are interrelated, point out that greater herbivore biomass, usually translated into greater density, occurs at early forest stages. Later, as evergreen trees become more dominant, as palatability decreases, and as net production lowers, herbivore biomass may decrease (although diversity may actually increase).

r- and K-selection

As was discussed earlier, there may be documented changes from r-selected trees to relatively K-selected trees as one proceeds either in a seral sequence or with increasing degrees of leaf persistence. It may be stated that the reproductive strategy of a folivore is dependent upon the strategy of its resources. Force (1972) has previously documented that the reproductive strategies of parasitoid insects coincide with those of their hosts. Additionally, herbivore communities of a particular reproductive strategy seem to be associated with plants of similar strategy. Again data from leaf-mining insects of California oaks may be used to illustrate this phenomenon. Each oak has its own set (guild) of host specific leaf-miners (Opler, 1974b), and the sets which feed on different hosts are composed largely of congeneric representatives. Thus, communities of homologous herbivores which feed on congeneric hosts, differing most notably in leaf persistence features, may be compared. Several generalizations may be made concerning congener sets found on deciduous and evergreen hosts, respectively. Those leaf-miners on deciduous oaks have brief larval feeding periods (Opler, 1974b), are small in size, and occur at much higher densities than their homologues specializing upon evergreen oaks (Table 4).

Table 4.—Size of leaf-mining moths which fed on California oaks (*Quercus*) as correlated with leaf persistence of hosts.

Genera of leaf-mining moth	*Adult Leaf-miner Wing-span (mm)*				
	Evergreen		*Deciduous*		*E/D*
	Span	*N Spp*	*Span*	*N Spp*	
Phyllonoryctor	8.3	10	7.3	10	1.14
Lithocolletis	8.0	6	7.2	7	1.11
Coptodisca	4.3	3	3.7	3	1.16
Nepticula	5.5	3	4.1	3	1.37
Tischeria	7.9	3	7.5	3	1.05
Bucculatrix	7.4	1	6.4	2	1.16

Grain

The same forest may be treated on quite different scales by different herbivores. Relative specialization and life span are the chief determinants of this phenomenon. A forest is coarse-grained to any specialist which feeds only upon leaves of a single host. If leaves of the proper age are available only for a small portion of the year, the remainder of the year must be passed by some inactive stage, often in physiological arrest. Needless to say, this group is almost entirely composed of insects and mites. This group may be functionally subdivided into those species which feed on young leaves and those which feed on mature and senescent leaves.

Those herbivores which are generalized with regard to the kinds of trees they feed upon are relatively fine-grained. For most insects in this group, i.e., short-lived generalists, a given individual larva will only feed upon leaves of the plant upon which it finds itself; however, adults may move freely about the forest, and females may deposit eggs on plants other than those upon which they fed as larvae. Long-lived generalist herbivores, those living longer than a single year (leaf-cutter ant colonies could thus be construed), must live in an environment where there is a continual supply of young leaves throughout each year, albeit by different tree species. Thus, it is not surprising that almost all mammalian arboreal herbivores are tropical denizens. Even then, these fine-grained herbivores occasionally feed upon flowers or fruits (Rockwood, 1975, 1976; Glander, and other papers in *The Ecology of Arboreal Folivores,* G. Gene Montgomery, editor, 1978). These long-lived species must have relatively greater mobility than the relatively sedentary feeding stages of insects, as they must be able to undergo fairly frequent changes in feeding sites as the chemical and nutritional suitability of their food resources change with the seasons (Rockwood, 1975, 1976; Glander, and other papers in Montgomery, 1978).

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Leaf Production, Leaf Consumption, and the Regulation of Folivory on Barro Colorado Island

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Introduction

How much foliage does a tropical forest grow in a year? How much of this foliage do vertebrates and insects eat? Why do they not eat more? These questions require answers if we are to set arboreal folivores in proper ecological perspective.

Data on litter fall, seasons of flowering, fruiting, and leaf flush in a variety of trees, rainfall, runoff, and catches of insects in light-traps and of mammals in live-traps have been collected on Barro Colorado Island (BCI), Panama, for over 4 years on behalf of the Environmental Sciences Program of the Smithsonian Institution (Smythe, 1974). These data will help us to suggest answers to our questions.

The major study area on BCI is a 10-hectare watershed in secondary forest, little disturbed except by landslips in the past 50 years, but partly cleared for farms before 1924. BCI receives over 2500 mm of rain a year, but suffers a marked dry season lasting 4 or 5 months; most years less than 100 mm of rain fell between January 1 and April 1. How representative is the forest on BCI of tropical rain forests elsewhere in the world? How typical are the modes of herbivore control on BCI? To answer, we compare data from BCI with results of other tropical studies wherever possible.

Litter fall

About 6500 kg dry weight of litter falls per hectare per year in the BCI study watershed; 7490, 7442, 6060, and 5550 kg fell in the 4 successive study years beginning December 1, 1971. These figures are from weekly collections of the litter falling into 100 tubs, each a twelfth of a square meter in area, which Robin Foster placed about the watershed. The fallen leaves were dried in an oven at 60°C for between 1 week and 1 month before weighing. Perhaps leaf-fall has declined in recent years because many of the very large nonstrangling figs (*Ficus*, sect. Pharmacosycea) in the watershed (Milton, 1978) have been dying. These figs are second-growth species, and the watershed may be experiencing a change in its progress towards climax.

The seasonal rhythm of leaf-fall is remarkably regular (Table 1). December is unpredictable, because the dry season may start at any time during that month and leaf-fall is always very heavy at the beginning of the dry season.

Leaf-fall on BCI is typical of that of lowland rain forests around the world. Indeed, yearly leaf-fall varies little from one lowland tropical forest to another: leaf-fall in well-drained terrestrial rain forest, in the blackwater swamp forest of the Amazon basin, in mangrove swamps of the rainy tropics, is close to 7000 kg dry weight per hectare per year (Table 2; A. Hladik, 1978). Leaf-fall is much higher in certain montane forests, and much lower in cloud forests and mesic temperate forests (Leigh, 1975).

Table 1.—Seasonal variation in fall of leaf litter on Barro Colorado Island

Litter-fall in secondary forest on Barro Colorado Island, in grams dry weight per square meter per day, for each month of the Environmental Monitoring Program (Smythe, 1974, and unpublished data). Standard error is about one-tenth the mean.

Month	*1971*	*1972*	*1973*	*1974*	*1975*
January		3.72	3.64	3.44	3.02
February		2.74	2.83	2.71	2.53
March		2.47	2.59	2.19	2.20
April		2.47	2.38	2.03	1.84
May		1.55	2.10	1.72	1.39
June		1.54	1.32	1.15	0.92
July		1.15	1.16	1.04	0.76
August		1.32	1.10	1.03	0.63
September		1.18	1.12	0.92	0.82
October	1.72	1.24	1.13	0.76	1.01
November	1.74	1.71	1.64	1.22	1.11
December	3.58	3.56	1.57	2.18	

Table 2.—Annual fall of leaf litter in lowland forests around the world

Annual fall of leaf litter, in metric tons dry weight per hectare per year, for selected tropical and mesic temperate forests.

Locality (Authority)	*Leaf fall*
Bélem, Brazil, tirra firme (Klinge, 1975)	7.8
Bélem, Brazil, varzea (Klinge, 1975)	7.5
Bélem, Brazil, igapo (Klinge, 1975)	6.7
Barro Colorado Island, Panama (Foster, personal communication; Smythe, 1974 and personal communication)	6.5*
Ipassa, Gabon (A. Hladik, 1978)	6.5
Banco, Ivory Coast (Bernhard, 1970)	8.2*
Omo, Nigeria (Hopkins, 1966)	7.2
Pasoh, Malaya (Lim, 1974)	7.5
Mangroves, several sites (Lugo and Snedaker, 1974)	7.3*
Glendon Hall, Toronto, Canada (Bray and Gorham, 1964)	3.2*
Mendocino Co., California, redwoods (Westman and Whittaker, 1975)	2.1

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* Average for different sites and/or different years.

Leaf-fall underestimates leaf production. Bray and Gorham (1964) suggest, on the basis of some measurements on *Ficus elastica*, that nearly a fifth of a leaf's dry matter is resorbed into the tree before the

Table 3.—Total area of leaves falling in successive seasons on a ten-hectare watershed on Barro Colorado Island

Total area of leaves, in square meters of leaf per square meter of ground, falling in successive seasons and successive years (mean ± standard error), and number of weeks in each season that leaves were sampled for area measurement. The area of leaf falling in a given season is calculated as the average area of leaf falling per square meter per week of sample, multiplied by the number of weeks in the season (22 for the dry season, and 30 for the rainy).

Year		*December–April (Dry season)*	*May–November (Rainy season)*	*Total for year*
1973–74	Area of falling leaves	4.45 ± 0.39	3.52 ± 0.28	7.97 ± 0.46
	Number of samples	17	14	31
1974–75	Area of falling leaves	4.17 ± 0.26	2.80 ± 0.16	6.97 ± 0.32
	Number of samples	16	25	41

leaf is dropped. Moreover, animals may eat over one-tenth of the leaf production, as we shall see.

Leaf area

Between December 1, 1973, and December 1, 1975, 7.45 ± 0.32 hectares (mean ± standard error) of leaves fell per hectare of ground per year in the watershed study area of BCI (Table 3). These figures are based on leaves sampled from the litter tubs. In those weeks leaf area was measured, all leaves were removed from the litter collected in every tenth tub among the first 100 in the watershed. Tubs were sampled for leaf-area measurements on a rotating basis—tubs 1, 11, 21 for one week; tubs 2, 12, 22 for the next, etc. The outlines of these leaves and of their holes and gaps were traced on sheets of paper, and from the tracings the areas of these leaves, and of their holes and gaps, were measured with a planimeter. To evaluate standard errors, the area of leaves falling into tubs 1–10, that falling into tubs 11–20, etc., was totaled separately, then the standard deviation among these ten subtotals was calculated and divided by three.

The forest of BCI is partly deciduous, so we suspect that few leaves last over a year. If we assume the average leaf is replaced once a year, then a yearly fall of over 7 hectares of leaves per hectare of ground implies that during the rainy season when all trees are in leaf, the forest supports over 7 hectares of leaves per hectare of ground. By sampling leaves on trees clear-felled from a 2/10 hectare rainforest plot in the Pasoh Reserve, Malaya, one finds that this forest supported 8 hectares of leaves per hectare of ground (Yoda, et al., 1975); by counting the leaves that touch vertical threads suspended from above the canopy, one finds that the submontane rain forest at El Verde, Puerto Rico, supports 6 hectares of leaves per hectare of ground (Odum, 1970, Table 8); by dividing the weight of fallen leaves by the weight per unit area of typical leaves of the region, one finds that the mesic temperature deciduous forest at Hubbard Brook, New Hampshire, also supports 6 hectares of leaves per hectare of ground (Whittaker, et al., 1974).

The spectrum of leaf size.

Seventy-eight percent of the total area, but less than half the total number, of the fallen leaves we sampled were of Raunkiaer's mesophyll size class (Richards, 1952), which comprises leaves with area between 20.25 and 182.25 cm². The total area of a tree's leaves reflects the tree's phytosynthetic importance far better than their total number, e.g., a breadfruit tree cannot increase its photosynthetic surface by dividing its great leaves into myriads of tiny leaflets. As one might expect, the distribution of the total area of leaves over Raunkiaer's size classes matches rather closely the percentages of species in other lowland forests with leaves of these sizes, whereas the distribution of numbers of leaves over these size classes is very different indeed (Table 4). Similarly, exactly half the simple-leaved canopy tree species of the Mucambo forest, Belém, have leaves over 50 cm² in area (Cain, et al., 1956: Table 4, Megaphanerophytes), and half the total area of our sampled leaves belongs to leaves over 45 cm² in area, but the median size of our sampled leaves was only 19 cm²: that is to say, half the sampled leaves were less than 19 cm² (Table 5).

The distribution of both leaf numbers and leaf area over size classes above the mode is nearly normal, but there are too many small leaves for the entire distribution of leaf size to follow the log normal law (Table 5). The distribution of leaf area over these size classes is more nearly normal than the distribution of numbers.

Table 4.—Proportion of foliage in different size categories

Percentages of species of trees with leaves of different size classes in the Mucambo and Castinhal forests near Bélem, Brazil (Cain, et al., 1956), in the lowland Amazonian forest at Shinguipino, Ecuador (Grubb, et al., 1963), in the *Agathis* forest on Vanikoro, Melanesia (Whitmore, 1966), in the Shasha forest reserve, Nigeria (Richards, 1952) and at 450 m on Mt. Maquiling in the Philippine Islands (Brown, 1919), and the percentages of leaf area and numbers of leaves in different size classes among the fallen leaves sampled in the study watershed at Barro Colorado Island, Panama.

Leaf size class	*Mucambo*	*Castinhal*	*Ecuador*	*Melanesia*	*Nigeria*	*Philippines*	*BCI (Area)*	*BCI (Numbers)*
Leptophyll ($<.25$ cm^2)	3	2	0	0	0	0	0	0
Nannophyll (.25-2.25 cm^2)	1	1	0	2	0	0	0	2
Microphyll (2.25-20.25 cm^2)	12	13	9	12	10	4	18	50
Mesophyll (20.25-182.25 cm^2)	75	74	64	84	84	86	78	47
Macrophyll (182.25-1630.25 cm^2)	9	9	27	2	6	10	4	1
Megaphyll (1630.25 cm^2 +)	0	1	0	0	0	0	0	0

Table 5.—Size composition of fallen leaves

Total area, and total number, of fallen leaves sampled during the two years starting Dec. 1, 1973, in each size class, compared with the areas and numbers expected from log normal distributions. Two log normal curves were calculated, one to fit the distribution of area, and the other of number of leaves, over the size classes greater than 18.3 cm^2.

	Total area of leaves in each size class		*Total number of leaves in each size class*	
Leaf area class (cm^2)	*Observed*	*Expected*	*Observed*	*Expected*
<6.5	1999.4	219.4	507	93
6.5-9.1	2865.7	642.0	376	129
9.1-12.9	2871.6	1861.1	265	229
12.9-18.3	5491.5	4380.5	360	334
18.3-25.8	8278.1	8232.7	380	407
25.8-36.5	12142.0	12418.1	396	407
36.5-51.6	15098.7	14945.7	351	334
51.6-73.0	14628.9	14563.7	241	229
73.0-103.2	10076.8	11321.0	118	129
103.2-145.9	6706.5	7168.1	56	60
145.9-206.5	5457.4	3421.5	31	23
206.5-291.9	992.0	1414.1	4	7
291.9+	298.7	601.4	1	2

Leaves falling in the dry season are somewhat smaller than those falling during the rest of the year (Table 6). It is hard to test the significance of this difference, as the falls of two leaves from the same tree are not independent events, nor are they part of the same event. For example, a chi-square test would reveal a "significant" difference in the size compositions of the leaves from the two dry seasons, which is largly due to the greatly increased fall of *Platypodium elegans* leaflets of area between 6.5 and 9.1 cm^2 in the second dry season. What should this mean?

Leigh (unpublished manuscript) has measured the average lengths of litter leaves in 12 lowland forests in Panama, Puerto Rico, Dominica, Peru, Malaysia, and New Guinea. How do leaf sizes in these forest compare with leaf sizes in our watershed?

We did not tabulate the lengths of all leaves sampled in the watershed, but our data do suggest that a leaf's area is, on the average, about three-tenths the square of its length. Using this formula to calculate length from area, we find that the average length, weighted by area, of the leaves we sampled in the watershed, is about 13.1 cm, varying from 11.2 to 16.2 cm from month to month, while the numerical average was 8.6 cm, varying from 7.2 to 10.2 cm in the months we sampled (Table 7).

Leigh obtained his figures by laying from 1 to 7 transect lines in each forest he studied, choosing 4 points 8 meters apart on each line, and measuring the lengths of the 10 leaves that either covered the point or had their edges closest to it. If all 10 leaves covered the point, their average would estimate the average length, weighted by area, of leaves in their neighborhood, as the chance of a leaf actually covering the point would increase with its area. If no leaf covered the point, a leaf's nearness might depend less on its size and more on where its center was, so the average of the sampled leaves would estimate more nearly the numerical average length of the neighborhood leaves. In practice, transect estimates should lie

Table 6.—Seasonal changes in size composition of fallen leaves

Total area of leaves in each size class (total numbers in parentheses) falling into sampled tubs in successive seasons. These figures are based on 17 weeks of sampling during the first dry season, 16 during the second, 14 weeks of sampling during the first rainy season, and 25 during the second.

Leaf area class (cm^2)	Total area (total number) of leaves in each size class			
	Dec. 1973–Apr. 1974	*Dec. 1974–Apr. 1975*	*May 1974–Nov. 1974*	*May 1975–Nov. 1975*
$<$ 0.6	1.3 (4)	0.3 (1)		0.3 (1)
0.6–1.2	3.2 (5)	1.9 (3)	0.6 (1)	2.6 (4)
1.3–1.8	16.8 (13)	3.9 (3)	3.9 (3)	5.2 (4)
1.9–2.5	36.8 (19)	9.7 (5)	9.7 (5)	1.9 (1)
2.6–3.1	61.9 (24)	18.1 (7)	15.5 (6)	12.9 (5)
3.2–3.8	96.8 (30)	61.3 (19)	51.6 (16)	29.0 (9)
3.9–4.4	143.2 (37)	73.5 (19)	46.5 (12)	23.2 (6)
4.5–5.1	108.4 (24)	117.4 (26)	49.7 (11)	72.3 (16)
5.2–5.7	170.3 (33)	211.6 (41)	15.5 (3)	46.5 (9)
5.8–6.4	174.2 (30)	180.0 (31)	69.7 (12)	52.2 (9)
6.5–9.1	946.4 (125)	1265.8 (164)	277.4 (36)	376.1 (51)
9.1–12.9	971.6 (90)	976.8 (91)	307.1 (28)	616.1 (56)
12.9–18.3	1878.1 (123)	1566.4 (104)	880.6 (57)	1166.4 (76)
18.3–25.8	2612.3 (121)	2487.1 (114)	1400.6 (64)	1778.1 (81)
25.8–36.5	3845.2 (124)	4311.0 (140)	1412.3 (47)	2573.5 (85)
36.5–51.6	5129.7 (119)	4432.9 (104)	2513.5 (58)	3022.6 (70)
51.6–73.0	4827.7 (78)	3527.1 (60)	2780.6 (45)	3493.5 (58)
73.0–103.2	3483.9 (41)	2828.4 (33)	1336.1 (16)	2428.4 (28)
103.2–145.9	1879.4 (16)	1875.5 (16)	1707.1 (14)	1244.5 (10)
145.9–206.5	2025.2 (11)	1174.8 (7)	514.2 (3)	1743.2 (10)
206.5–291.9	242.6 (1)		263.3 (1)	487.1 (2)
291.9+				298.7 (1)
Total area	28654.8	25123.2	13655.5	19474.3
Total number	1068	988	438	592
Average length (by area)	13.0	12.2	13.5	14.0
Average length (numerical)	8.4	8.3	9.2	9.4

between the areal and the numerical average. In the rain forests Leigh studied, the average length of the litter leaves he sampled lay between 8.5 and 12.9 cm: the average length of the leaves Leigh sampled in his transects on the mature forest of BCI was 11.5 cm. The size of leaves in the watershed, thus, seem eminently normal.

Death and Growth in the Tropical Forest

Montgomery and Sunquist (manuscript in preparation) have watched 486 trees near the watershed on BCI, where they happened to find sloths, for an average of 2.033 years apiece. Twenty-two trees died during the watch, suggesting an average lifetime of 45 years. Trees in the secondary forest at Sungei Menyala, Malaya, have the same average lifetime, but trees in primary lowland forests generally live longer (Table 8). Baas Becking's (1948) record suggests that trees live longer in the mountains, as they do in virgin temperate-zone forests.

In primary forests, but not in secondary, trees of all sizes die at the same rate, as can be shown by applying the chi-square test to the data in Table 9, lumping categories where necessary to insure that the expected number of tree-falls is at least five for each size class. Where data are sufficient to check, as at

Table 7.—Seasonal variation in characteristics of falling leaves

Average length (numerical and weighted by area) of fallen leaves; total area, and total number, of leaves falling per square meter of ground per week, average area per unit dry weight of fallen leaves, number of weeks in which fallen leaves were sampled for area measurements, and rainfall, month by month.

Month	*Average leaf length*		*Area (cm^2) of leaves falling per m^2 per week*	*Number of leaves falling per m^2 per week*	*Leaf area per unit weight (cm^2/g)*	*Number of sample weeks*	*Rain (mm)*
	Weighted by area	*Numerical*					
Dec. 1973	11.7	8.1	1570	64	103	2	58
Jan. 1974	13.8	9.1	2193	71	82	5	6
Feb. 1974	13.6	9.1	2754	89	126	3	14
Mar. 1974	11.7	7.4	1946	93	117	3	41
Apr. 1974	12.5	7.9	1545	64	97	4	12
May 1974	12.6	9.3	1498	49	130	2	100
June 1974	11.8	8.4	1083	41	123	2	271
July 1974	13.7	8.7	1194	41	152	2	330
Aug. 1974	12.9	9.6	1325	41	169	2	279
Sep. 1974	14.4	9.1	1231	38	161	2	249
Oct. 1974	12.8	9.4	825	26	148	2	452
Nov. 1974	16.2	10.1	1037	26	103	2	396
Dec. 1974	12.4	9.0	1729	60	97	3	119
Jan. 1975	12.8	9.3	2146	70	94	4	5
Feb. 1975	11.2	7.2	1849	96	98	4	18
Mar. 1975	11.6	7.9	1972	86	119	3	41
Apr. 1975	13.5	10.2	1531	42	129	2	58
May 1975	15.6	9.1	1207	37	106	2	315
June 1975	12.3	9.2	693	23	97	2	229
July 1975	12.8	9.7	698	21	121	4	226
Aug. 1975	15.1	10.1	651	17	140	4	333
Sep. 1975	12.8	9.0	919	32	151	5	315
Oct. 1975	14.3	9.7	1025	30	135	4	424
Nov. 1975	15.0	9.5	1371	40	165	4	356

Sungei Menyala and Bukit Lagong, the giants of the forest die as fast as smaller trees.

Since new trees can reach the canopy only in gaps where older trees have fallen, one would expect the death rate to pace growth rate. It does not; the trees at Sandakan and Sungei Menyala, for example, grow equally fast despite very different death rates (Table 10), and average growth rates in tropical forests generally differ far more than death rates.

Growth in the secondary forest at Sungei Menyala, which was disturbed and perhaps partly burnt during the clearing of a nearby rubber plantation in 1917, definitely slowed between 1953 and 1959. Calculations from Table 7 of Wyatt-Smith (1966) suggest that the 28 trees over 40 cm dbh grew a sixth as fast from 1953 to 1959 as during the previous 6 years, and growth in the 70-odd trees between 20 and 40 cm dbh slowed by half during the same period. There was no such slowdown in the adjoining primary forest: seemingly, a number of successional species simultaneously attained their limits of growth in that very crowded plot of secondary forest. Perhaps litter-fall in the BCI study watershed, with its numerous large trees of successional species of *Ficus, Spondias,* etc., is slowing down for a similar reason.

Similarities of Lowland Tropical Forests

Leigh (1975) has argued that lowland tropical forests are alike in structure and production because they transpire at similar rates. Whether or not he is right is something of a mystery.

Table 8.—Average lifetimes of trees in different tropical forests

Average lifetime (calculated as the inverse of the average proportion of marked trees dying per year), number of deaths observed during the study, and duration of study, in different tropical forests. Baas Becking's data are based on a selection of trees marked for growth measurements; the other figures are based on all trees above a certain size in given forest plots.

Site (Authority)	*Lifetime (years)*	*Number of deaths observed*	*Years of watch*
Sandakan, Sabah (Nicholson, 1965)	93	78	6
S. Menyala, Malaya (Wyatt-Smith, 1966)	57	162	12
S. Menyala, secondary forest (Wyatt-Smith, 1966)	45	71	12
El Verde, Puerto Rico (Briscoe and Wadsworth, 1970)	87	166	20
Bt Lagong, Malaya, hill forest (Wyatt-Smith, 1966)	101	102	10
Gedeh, Java, montane forest (Baas Becking, 1948)	115*	99	22

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* Recalculated from raw data in paper.

Lowland tropical forests the world around probably do transpire at similar rates. When the soil is saturated, one can estimate the rate of water loss through evapotranspiration (the joint effects of evaporation and transpiration) from the BCI study watershed by the difference between monthly rainfall and runoff; presumably, transpiration causes most of the loss. The correspondence between rainfall and runoff is not precise, because of the time required for surplus water to run off. The 50 mm running off in December 1973 (Table 11), for example, presumably fell in November. The runoff is measured by a weir founded upon bedrock; groundwater flow is probably negligible. During and just after the dry season, the ground soaks up nearly all the rain that falls, but after the soil is saturated rainfall exceeds runoff by about 150 mm a month (Table 11). Evidence from other places also suggests that lowland tropical forests cannot use more than 150 mm of rain a month, and the rest runs off (Leigh, 1975). Rain forests generally receive 150 mm or more of rain most months of the year, so annual evapotranspiration should be similar in all lowland rain forests. Annual evapotranspiration lies between 1200 mm and 1600 mm for the three lowland tropical rain forests cited by Leigh (1975, Table 5).

One would expect transpiration to affect the structure and production of rain forests strongly because it is that which pulls nutrients to the tops of tall trees. Where foggy, breezy climate blocks transpiration, as atop the Luquillo mountains in Puerto Rico, the forest is stunted and appears starved of nutrients in spite of adequate soil (cf. review in Leigh, 1975). Tropical soils are poor in nutrients, so plants compete strongly for what is available. The more effective is transpiration, the taller a canopy tree can grow and the more competitors it can shade.

There is some vague evidence that transpiration is important to lowland rainforests (cf. Leigh, 1975). Brown and Mathews (1914) showed that dipterocarp growth in the Philippines slowed during the dry season and in the cloudy portion of the rainy season, when transpiration was presumably low, although some of this "growth" may merely be swelling from extra water in the trunk. Likewise for nutrients: the mass

Table 9.—Death rates for different sizes of trees

For each locality we give three columns of numbers. The first column represents the average number of trees in different size classes on the study plot during the period of observation. The second column, whose figures are in parentheses, represents the number of trees of each size class that would have died during the period of observation, were death rate the same for each size class. The third column represents the observed number of deaths in each size class during the period of observation. The data for Sabah are from Nicholson, 1965; the data for Malaya are from Wyatt-Smith, 1966.

Diameter	*Sandakan, Sabah*	*Bt Lagong, Malaya*	*S. Menyala, Malaya*	*S. Menyala (second.)*
10-20 cm	736 (47) 48	422 (50) 47	437 (92) 93	163 (43) 40
20-30 cm	242 (16) 18	195 (23) 20	151 (32) 35	53 (13) 23
30-40 cm	112 (7) 9	92 (11) 16	73 (15) 13	21 (7) 2
40-50 cm	41 (3) 1	68 (8) 8	43 (9) 9	15 (4) 3
50+ cm	80 (5) 2	85 (10) 11	64 (13) 12	13 (4) 3

Table 10.—Average growth rates for trees of different sizes

Average diameter increase, in cm per year (with number per hectare in parentheses) of trees of different size classes, in relation to altitude, climate and death rate. Data for La Selva from Hurtshorn, 1975; for Sabah, from Nicholson, 1965; for Mt Mariveles, from Brown and Mathews, 1914; for Malaya, from Wyatt-Smith, 1966; for Mt Maquiling, from Brown, 1919; for El Verde, from Wadsworth, 1947; for Vanikoro, from Whitmore, 1966; for the Côte d'Ivoire, from Muller and Nielsen, 1965; for Mt Banahao, from Brown, 1917. Growth rates for Gedeh, Java, are from Brown and Yates, 1917, while the size composition is from Meijer, 1959.

				Average annual diameter increase in (number per ha. of) trees with DBH				
Site	*Altitude*	*Annual rain, mm*	*Average life, yr*	*10–20 cm*	*20–40 cm*	*40+ cm*	*Years of measurement*	*Plot size (ha)*
La Selva, Costa Rica[a]	50 m	4000	29	.30	.37	.42	1	4.0
Sandakan, Sabah	40 m	3150	92	.11 (310)	.18 (198)	.34 (67)	6	1.8
Mt Mariveles, P.I.[b]	500 m			.18	.27	.30 (49)	9	
S. Menyala, Malaya	20 m	2270	57	.12 (279)	.17 (141)	.34 (66)	12	1.6
S. Menyala secondary forest	20 m	2270	45	.12 (408)	.22 (183)	.31 (70)	12	0.4
Bt Lagong, Malaya hill forest	550 m	2600	101	.11 (259)	.17 (183)	.29 (93)	10	1.6
Mt Maquiling, P.I.[c]	300 m	2150		.33 (204)	.51 (160)	.80 (64)	4	
Mt Maquiling, P.I. midmountain forest	700 m	2600		.13 (288)	.28 (192)	.43 (72)	4	
El Verde, Pto Rico[d]	450 m	4200	93	.30		.60	3	
Vanikoro, Fiji[e]		7000		.24 (860)	.24 (280)	.24 (110)	1	
Anguededou, Côte d'Ivoire		1960		.28 (244)	.32 (94)	.68 (26)	5	0.16
Gedeh, Java	1400 m	3400		— (121)	.29 (83)	.75 (80)	27	
Mt Banahao, P.I.[f]	2100 m	7500		.14	.15	.20	1	

[a] Data for *Pentaclethra macroloba*, the dominant tree in this forest.

[b] Selective cutting doubles growthrate of small trees but does not change that of remaining canopy trees.

[c] Size composition based on .25 ha plot at 450 m. Growth rates are calculated assuming that the ratio of overstory to understory trees in different size classes is the same at 300 m as on that plot.

In cleared areas, small dipterocarps of canopy species increase DBH as fast as big ones.

[d] Growth rates are calculated assuming that trees 10–20 cm DBH are 2/3 intermediate and 1/3 suppressed, while trees over 40 cm DBH are all dominant or codominant.

[e] Growth rates for *Agathis*, the forest dominant. These rates can be tripled by appropriate thinning.

[f] Growth rates for *Podocarpus imbricatus*, the dominant canopy tree on this mountain.

of leaves falling during the dry season only decompose and release their nutrients after the rains come (Smythe, 1970), and trees do grow best at the beginning of rainy season (Huttel and Bernhard-Reversat, 1975).

The primary fact to keep in mind is the similarity of leaf production and turnover in rainforests; blackwater swamp and mangrove wood production is far less uniform, and perhaps more sensitive to soil fertility. Why is leaf production in Malayan and Central American rain forests so similar, when roadside weeds and the vegetation of abandoned clearings grow so much faster in Central America than in Malaya (D. J. Janzen, personal communication)?

Consumption of Foliage

How much leaf is eaten in the trees? First consider the leaves that are eaten whole, so that no trace of them reaches the litter tubs. Considering the size of the mouths of most folivorous vertebrates, they may well eat most of their leaves whole. To simplify the matter, therefore, we assume that vertebrates eat *all* their leave whole. We also assume that the leaves which are eaten whole are all eaten by vertebrates: a much more dangerous assumption. Not every entomologist agrees that caterpillars only infrequently consume whole leaves, midrib and all.

Table 11.—Rainfall on a runoff from a 10-hectare watershed on Barro Colorado Island

Monthly rainfall on and runoff from the 10-hectare study watershed on Barro Colorado Island, in mm, and totals for the years. Rainfall is given in the upper row of each couplet. The rainfall records are from the Panama Canal Company, which maintains a rain gauge in the laboratory clearing of Barro Colorado, and runoff is measured by a standard 120° V-bladed recording weir, founded upon bedrock at the exit from the watershed.

1973

J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*TOTAL*
59	18	3	19	274	320	209	358	343	261	577	58	2513
3	0	0	0	4	62	52	184	224	160	411	50	1155

1974

J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*TOTAL*
6	14	41	12	100	271	330	279	249	452	396	119	2271
5	0	0	0	0	8	62	90	91	280	220	118	874

Leaf consumption by vertebrates

How much foliage do vertebrates eat? As there are rather few important species of vertebrate folivore, we will ask how much each species eats, and sum these for a total vertebrate feeding rate.

Consider, first, the howler monkey. The last published count (Chivers, 1969) listed 1000 howlers for BCI, an island of 1500 hectares: that is, two-thirds of a howler per hectare. C.M.Hladik and an experienced co-worker twice watched an individual animal all day, counting each mouthful of food it ate and estimating each mouthful's weight: he concluded that an 8-kg howler eats 400 g wet weight of leaves and 600 g of fruit each day (Hladik and Hladik, 1969). Thus, howlers eat 270 g wet weight, or about 60 g dry weight, of leaves per hectare per day, or about 22 kg dry weight of leaves per hectare per year. There may now be 1300 howlers on BCI (Milton, personal communication), so they may, in fact, eat nearly 30 kg dry weight of leaves per hectare per year.

Next, consider the sloths. There are about 10 sloths per hectare in the watershed area (Montgomery and Sunquist, 1975). Each sloth comes down to the base of a tree about once a week to defecate about 50 g dry weight of feces. They are largely folivorous. If they have a digestive efficiency near 50 percent, as some ruminants do, each sloth eats 100 g dry weight of leaves each week, and sloths in aggregate eat 1 kg dry weight of leaves per hectare per week, or 50 kg a year. Montgomery and Sunquist (1975) itemized the composition of sloth populations more carefully, and concluded that sloths eat 40 kg dry weight of leaves per hectare per year.

Eisenberg and Thorington (1973) quote figures suggesting that a 2.8-kg three-toed sloth's basal metabolism should account for 560 Kcal, or 140 g dry weight, of food a week—three times the assimilation Montgomery and Sunquist allow them. McNab (1978) estimates that *Bradypus* probably consumes about 360 g dry weight of leaves per week. Why the discrepancy? Montgomery (personal communication) assures us that the average metabolic demand of sloths is below the quoted basal rate because body temperature falls when the animals are inactive. McNab (1978) says that Bradypus almost appears to regulate its rate of metabolism by varying body temperature. These large discrepancies illustrate the perils of the indirect estimates of feeding rate we are so often compelled to use.

Finally, there are the iguanas. Probably thousands of iguanas live on BCI, but fewer than 10,000 if we exclude small young. A major egg-laying site on a small island, Slothia, just off BCI, is watched as part of the Environmental Monitoring Program (Rand, 1974), and hundreds of iguanas (but not thousands) come ashore to lay their eggs there each year. Iguanas which lay eggs there disperse afterwards over much of BCI (Montgomery, et, al., 1973). There appear to be only a few other nesting sites of comparable importance around BCI, so the iguanas nesting on Slothia presumably are a significant fraction of the iguana population of BCI. Iguanas are reptiles, and reptiles eat little compared to most mammals of the same size (Bakker, 1972). We would be surprised if iguanas ate more than 50 kg dry weight of leaves per hectare per year.

In sum, we believe vertebrates crop between 100 and 300 kg dry weight of leaves per hectare per year. In a semideciduous forest in Ceylon receiving 1700 mm of rain a year, which drops a shade over 3000 kg dry weight of leaves per hectar per year, leaf monkeys of the genus *Presbytis,* the major vertebrate folivores there, eat 480 kg wet weight of leaves per hectare per year (Hladik and Hladik, 1972). These leaves are 71.4 percent water (C. M. Hladik, personal communication), so these leaf monkeys eat 140 kg dry weight of leaves per hectare per year.

Why do vertebrates not eat more leaves? The answer occupies much of this symposium, and weaves many threads into a common pattern. Its evidence derives from bags of leaves put into the stomachs of sloths, the mineral budgets of cattle, and the diets of Australian possums in New Zealand. It explains why mouse lemurs eat insects while great Indris eat leaves, why a brushtailed possum readily eats *Melicytus* leaves yet would die if fed nothing else, why Malgache sifakas range widely over their thorn forest when fruit and new leaf abound and move much less when they have only mature leaves to eat, and why a koala's body temperature is more changeable than an ocelot's. It unites in a common theme the chemistry of leaves, the sacculation of colobine monkeys' stomachs, the sloth of sloths' stomachs, and the grand rhythm of leafing and fruiting in tropical forests.

In brief, leaves are full of poisons which make them difficult and unprofitable to digest. One route to folivory is to specialize in order to cope with the poisons of a particular species or genus of plant. In extreme cases, a plant's poisons are a necessary stimulus to the feeding of its specialist folivore (Ehrlich and Raven, 1965), which accordingly has become like Rappacini's daughter in Hawthorne's (1959) story who was brought up on poison and consequently found wholesome food poisonous. In a tropical forest, where most trees belong to rare and scattered species, this can only be the way of insects, which are so small that one tree is a world to them, and so short-lived that if need be they can adapt their life cycles to when their trees have leaves for feeding on.

The other route, the way of the vertebrate folivore, is to cope, necessarily indifferently, with a variety of poisons. The forest is full of mature leaves: there are always enough leaves to eat. The problem lies in finding food sufficiently digestible that enough energy can be extracted in a day to support that day's activities and save a bit for reproduction. Vertebrate folivores must economize in every way. They are large, so they need digest less per unit weight to stay alive. They move as little as possible. They control temperature at the minimum necessary to allow digestion. They are sparing of reproductive effort. Even so, they need elaborate digestive tracts; they must choose their leaves carefully, selecting the younger, less poisonous, more nutritious ones whenever possible, and they must not eat too many leaves of any one kind, for the same reason little boys should not eat too many strawberries.

Are vertebrate folivores so poorly adapted that the forest can rely on the indigestibility of its mature leaves and defend itself by "arranging for" periodic shortages in new leaves? On BCI there is a striking seasonal rhythm of leaf production (Table 12), with lows in late rainy and early dry season, and a gradual crescendo of leaf production starting in March and reaching its climax after the onset of the rains, when the forest is bursting with activity, full of insects and breeding birds. To document the rhythm, an experienced woodsman, Bonifacio de Leon, conducts a weekly census of the phenology of marked trees near the laboratory on BCI. Occasionally, a student of plant phenology, Carol Augspurger, conducts the census: her results accord with de Leon's. However, the census does involve subjective decisions (When do leaves cease being "new"? How many new leaves should a tree have to be worth recording?), the standards for which may drift with the lapse of time.

Sharp lows in new leaves may occur any time from August to March, and not all such lows can be explained by the imminence of the dry season. It is hard to say to what extent the trees "conspire" to produce these lows, that is to say, to what extent trees leafing "out of turn" must lay on extra poisons or suffer excessive herbivory, for these lows seem very sporadic and irregular, as if they were merely chance concatenations in the rhythms of this multitude of trees. For a week or two, however, the animals caught by such a low seem put out by their changed diet, and one would think extreme lows would work worse harm. Unfortunately, the seasonal rhythms of mortality in arboreal folivores is poorly known, although data of Montgomery (personal communication) do suggest that three-toed sloths die most frequently from October to December. New leaves are fairly rare then, and the weather is very cloudy and rainy, so it is difficult for sloths to maintain a body temperature high enough to assure adequate digestion (Montgomery and Sunquist, 1978): just the time when a shortage of new leaves would be most devastating.

There is a similar rhythm to fruit production on BCI (Table 13), which has an obvious effect on terrestrial frugivores (Smythe, 1970). When edible fruit abounds, most terrestrial mammals eat it, yet there is enough for all and to spare, and much of the fruit is left to rot or be consumed by insects. The biweekly trappings in the watershed catch few animals then, and few animals appear in the laboratory clearing. When fruit is in short supply, each of those species that earlier ate fruit so readily must now find a distinct

Table 12.—Rhythms of leaf flush at two levels of the forest on Barro Colorado Island

Number of individuals, and number of species equivalents, of canopy and subcanopy trees with a substantial number of new leaves, for 52 successive weeks of census in 1975 and 1976. These figures are based on 99 deciduous canopy trees representing 28 species, 95 evergreen canopy trees representing 39 species, and 46 subcanopy trees representing 32 species. Trees are counted as deciduous only if they are entirely leafless for at least one week of census before putting out new leaves. The number in parentheses in the deciduous tree columns are the numbers of individuals and species equivalents flushing for the first time after a period of leaflessness.

The number of species equivalents with new leaves is calculated by adding up the fractions of censused individuals of each species that carry new leaves. If only two trees have new leaves, one of a species with five censused individuals and the other from a species with four, the number of species equivalents with new leaves is 1/5 + 1/4 = 0.45.

Canopy deciduous trees		*Canopy evergreen trees*		*Subcanopy trees*		*Totals*	
N	*sp. eq.*	*N*	*sp. eq.*	*N*	*sp. eq.*	*N*	*sp. eq.*
August							
14 (3)	5.12 (0.67)	11	6.50	1	1.00	26	12.62
15	4.34	7	4.33	1	1.00	23	9.67
13 (1)	4.76 (0.17)	9	5.50	1	1.00	23	11.26
10 (1)	3.92 (0.17)	7	3.00	1	1.00	18	7.92
September							
10	3.68	6	3.11	0	0.00	16	6.79
8	3.04	7	2.83	0	0.00	15	5.87
12	3.95	15	7.08	0	0.00	27	11.03
8	2.79	16	7.69	3	2.25	27	12.73
October							
2	0.45	16	8.94	3	3.00	21	12.39
2 (1)	1.25 (1.00)	15	7.06	1	1.00	18	9.31
2 (1)	1.25 (0.25)	19	7.71	5	2.75	26	11.71
8	2.25	14	7.40	2	1.25	24	11.50
6	2.50	12	5.68	2	1.25	20	9.43
November							
7	2.50	11	5.18	3	3.00	21	12.39
3	1.50	8	4.58	0	0.00	11	6.08
2	0.50	7	4.25	3	3.00	12	7.75
6	2.25	7	4.50	1	1.00	14	7.75
December							
4 (1)	0.89 (0.14)	6	3.83	0	0.00	10	4.72
3	0.64	7	4.50	1	1.00	11	6.14
2	0.50	2	1.50	1	1.00	5	3.00
3	0.64	2	1.50	1	1.00	6	3.14
1	0.14	8	3.75	0	0.00	9	3.89
January							
2 (2)	0.29 (0.29)	4	2.50	3	2.25	9	5.04
3 (3)	0.54 (0.54)	19	8.65	6	4.50	28	13.69
5 (1)	0.99 (0.20)	24	9.18	6	4.67	35	14.84
3	0.60	22	6.93	9	6.33	34	13.86
February							
3 (2)	0.57 (0.37)	14	4.67	7	6.50	24	11.74
4	0.71	10	4.73	4	4.00	18	9.44
1	0.17	7	3.43	1	1.00	9	4.60
3 (2)	0.58 (0.33)	3	1.83	0	0.00	6	2.41

Table 12.—Rhythms of leaf flush at two levels of the forest on Barro Colorado Island (Continued).

Canopy deciduous trees		*Canopy evergreen trees*		*Subcanopy trees*		*Totals*	
N	*sp. eq.*	*N*	*sp. eq.*	*N*	*sp. eq.*	*N*	*sp. eq.*
March							
3 (1)	0.62 (0.20)	1	0.33	1	1.00	5	1.95
10 (6)	3.42 (1.80)	4	2.08	1	1.00	15	6.50
12 (3)	4.31 (0.59)	7	2.87	1	1.00	20	8.18
14 (4)	5.14 (1.25)	7	4.17	0	0.00	21	9.31
April							
15 (3)	4.64 (0.64)	4	1.67	0	0.00	19	6.31
17 (4)	5.56 (3.00)	5	2.45	0	0.00	22	8.21
18 (4)	6.70 (1.00)	4	2.33	0	0.00	22	9.03
28 (13)	9.55 (4.53)	11	6.42	5	3.58	44	19.55
37 (12)	11.92 (3.93)	12	7.70	16	10.08	65	29.70
May							
37 (5)	11.38 (1.25)	11	5.42	11	7.58	59	24.38
36 (11)	10.17 (2.50)	9	5.23	10	7.42	55	22.82
28 (3)	8.04 (0.43)	12	7.43	3	2.33	43	17.80
19 (2)	5.63 (0.18)	8	4.43	4	2.58	31	12.64
June							
11 (2)	2.82 (0.18)	5	4.50	1	1.00	17	8.32
7	2.41	7	5.20	1	1.00	15	8.61
13	4.32	8	5.40	1	1.00	22	10.72
17 (1)	6.52 (0.25)	10	5.01	1	1.00	28	12.53
July							
13 (3)	4.37 (0.75)	8	4.51	3	2.25	24	11.13
7 (1)	2.67 (0.25)	8	5.14	0	0.00	15	7.81
9 (1)	2.82 (0.25)	5	2.81	0	0.00	14	5.63
6	1.37	6	1.89	0	0.00	12	3.26
7	1.92	7	2.69	0	0.00	14	4.61

niche. As with the stream fish of Zaret and Rand (1971), niche differentation is more distinct and niche overlap less in the season of shortage. Moreover, these animals are easier to trap during the shortage. At its depth tapirs come into the laboratory clearing to eat the bread that is set out and on occasion the area resounds with the noise of pacas, coatis, and spider monkeys quarreling over the leftovers. One year, rains fell out of season, in late January, disrupting fruiting schedules and leading to mass starvation in the forest (Foster, 1973). Just as the fruiting cycle controls frugivore numbers, so surely must the cycle of new leaves control folivore numbers.

Leaf consumption by insects

How much foliage do insects eat? In the two years starting December 1, 1973, 0.65 ± 0.042 ha, or 8.6 ± 0.56 percent (mean ± standard error) of the 7.5 ha of leaves falling per hectare of ground per year consisted of holes and gaps. Holes and gaps comprised 11.7 ± 2.0 percent of the leaf area falling during the first dry season, 8.4 ± 1.2 percent of that falling during the first rainy season, 7.7 ± 0.7 percent of that falling during the second dry season, and 5.9 ± 0.4 percent of that falling during the second rainy season. A similar proportion, 7 percent, of the area of leaves falling at El Verde, Puerto Rico, consists of holes and gaps (Odum and Ruiz-Reyes, 1970).

Excluding holes and gaps, 13.7 hectares of leaves weighing 11,600 kg fell per hectare of ground during our two study years: one hectare of intact, dried, fallen leaves thus weighed about 850 kg. If trees resorb 19 percent of their leaves' dry matter before dropping them (Bray and Gorham, 1964), one hectare of intact leaves still on the trees contains 1050 kg of dry matter. Equating the weight represented by holes and gaps to insect consumption, the insects of BCI eat 680 kg dry

Table 13.—The seasonal rhythm of fruiting and trappability

The number of censused species of trees carrying mature fruit in the watershed area, based on the Environmental Sciences Program census and data from Carol Augspurger, and the numbers of agoutis (*Dasyprocta punctata*), pacas (*Cuniculus paca*), and coatis (*Nasua narica*), and totals for the three species, caught per trap-night each month from August 1974 to July 1975, in the watershed study area of Barro Colorado Island.

	Number of species carrying mature fruit dispersed by					*Number of animals caught per trap session*			
Month	*Mammals*	*Birds*	*Inanimate*	*Unknown*	*All means*	*Agoutis*	*Pacas*	*Coatis*	*Total*
August	10	5	1	0	16	6.5	2.5	1.5	10.5
September	11	6	0	1	17	7.5	3.5	5.5	16.5
October	8	6	0	1	14	3.5	2.0	2.5	8.0
November	7	6	0	1	13	4.0	5.5	0.5	10.0
December	6	7	1	0	12	7.0	7.0	5.0	19.0
January	10	10	0	1	17	8.5	5.0	8.0	21.5
February	12	12	2	1	23	4.5	4.0	0.0	8.5
March	19	14	5	1	32	2.0	1.0	1.0	4.0
April	18	13	7	2	35	4.0	1.5	1.0	6.5
May	31	13	11	2	50	1.0	0.0	1.0	2.0
June	20	10	3	0	30	0.0	0.0	0.0	0.0
July	15	9	0	0	22	3.0*	5.0*	0.0*	8.0*

* Trap session of August 1.

weight of foliage per hectare per year (1050 × 7.5 × 0.086).

It is exceedingly dangerous to take this number too seriously. To begin with, insects also generally prefer young leaves, and a hole made in a young leaf grows with the leaf. In one tulip poplar forest in Tennessee, holes triple in size, on the average, after they are made (Reichle, et al., 1973). On the other hand, there are many bugs and other insects with piercing mouthparts which presumably suck out juices without leaving visible holes, and there are also leaves which vanish without trace into caterpillar gullets. How these various errors balance, we cannot say.

Why do not the insects eat more? First, as we have remarked, leaves, particularly mature leaves, are full of chemicals which render them distasteful, indigestible, or poisonous to the insect that would eat them (Ehrlich and Raven, 1965). An insect can specialize to eat one kind of leaf, but only at the expense of having to pass up others. As most kinds of tropical tree are rather rare, it may be some time before they are found by insects suited to eat them.

Second, other animals eat the insects. The most conspicuous and best known insectivores are birds. How much do they eat? One can estimate a bird's "standard metabolic rate" from its weight (Lasiewski and Dawson, 1967). In a temperate zone forest, the birds' total energy demand is 2.5 times their standard metabolic rate, and digestive efficiency is 70 percent (Holmes and Sturges, 1975). We assume this is true for the tropics as well. To calculate the weight of folivorous insects eaten by birds on BCI, we total the feeding rates of primarily insectivorous birds, excluding ant-following antbirds and other feeders upon the litter fauna of the forest floor, and woodpeckers and barkgleaners which we shall assume eat woodborers. We also add half the feeding rate of birds which, like trogons, motmots, and many tanagers, eat both fruit and insects. Just what fraction of these birds' food is folivorous insects, we do not know. They also eat nectar-feeders, insects with woodboring or detritus-feeding larvae, predatory arthropods, and the like, as well (recall, however, that a high proportion of predatory arthropods in bird diets implies correspondingly high arthropod predation on folivorous insects). The excluded birds also eat some folivorous insects; we can only hope the errors cancel.

Accordingly, we find that the birds on BCI eat about 130,000 Kcal, or, rating a kg of insects as 5500 Kcal (Robin Andrews, personal communication), 24 kg dry weight of folivorous insects per hectare per year. It takes 7 or 8 calories of foliage to make a calorie of grasshopper (Wiegert, 1965). Rating a gram of foliage as 4000 calories (Odum, 1970: I-214), the insects that birds eat accordingly consume about 240 kg dry weight of foliage per hectare per year. This is an island-wide average; if birds feed at this rate in the watershed, a third of the holes and gaps in the fallen leaves were made by the insects that birds ate.

Applying the same technique, we find from data of Karr (1971) that birds in the moist forest of mainland Panama, 10 km east of BCI, eat 34 kg dry weight of folivorous insects per hectare per year. The total "existence metabolism" of birds in the Liberian moist forest at 500 m on the slopes of Mt. Nimba is an eighth higher than that at Karr's mainland Panama site (Karr, 1975). If the Liberian birds eat correspondingly more folivorous insects, they eat 38 kg dry weight of them per hectare per year. Both of Karr's study sites have rainfall regimes like that of BCI. Apparently, a substantial proportion of folivorous insects in tropical forests the world around are destined to be eaten by birds.

For comparison, the birds of the floodplain western hemlock-vine maple (*Tsuga heterophylla-Acer circinatum*) forest at 360 m on the western slope of the Oregon Cascades (stand Δ of Wiens and Nussbaum, 1975) and the forest birds of Hubbard Brook, New Hampshire (Holmes and Sturges, 1975) eat 11 and 5 kg dry weight of folivorous insects per hectare per year, respectively.

Other predators wreak comparable devastation on insect populations. Robinson and Robinson (1974) have calculated that in a coffee plantation near Wau, New Guinea, web-building spiders alone catch over 160 kg wet weight, or about 50 kg dry weight, of insects per hectare per year. True, this coffee plantation is in a sunny montane site in a volcanic valley, where one would expect exceptional productivity, but this calculation does suggest that those who neglect the ecological importance of a rain forest's spiders do so at their peril.

We have not even mentioned predatory insects, tree frogs, bats, and the like, nor such animals as white-faced monkeys (Hladik and Hladik, 1969), which spend a fair proportion of their time searching leaves for insects. Accordingly, it would appear that a very large proportion of folivorous insects live to be eaten. There is no reason to believe that these predators focus on senile individuals, postreproductives, or the starving. Dare we conclude that, without its birds and bats, its spiders and mantids, its monkeys and tree frogs, the forest could not prevent itself from being very badly eaten, in spite of its chemical defenses?

Regulation of Folivore Populations

The vertebrate folivores of BCI seem little affected by predators, and we believe their numbers are regulated by the seasonal shortage of new leaves, just as the great herds of the Serengeti are regulated by the seasonal shortage of fresh, protein-rich grass (Sinclair, 1975). It does not immediately concern us whether these vertebrates starve, or whether shortages of new leaves make them more susceptible to disease, parasites, etc. On the other hand, insect folivores are heavily preyed upon by animals larger and longer-lived than themselves. Does the cycle in leaf flush cause a similar cycle of insect abundance, thus inhibiting those predators which are dependent upon insects? Or are insects less affected by the cycle of new leaves, because they can cope better than vertebrates with leaf poisons? More generally, what does regulate insect numbers?

There is a striking rhythm to the numbers of insects caught in light traps on BCI (Smythe, 1974; Table 14). When the rains come in April or May, insects are caught in great numbers, and the birds celebrate by breeding (Willis, unpublished manuscript). As the rainy season wears on, catches decline and bird breeding slows down. Often there is a subsidiary peak in insect catches in December (Smythe, 1974), but catch size increases with insect mobility as well as with insect abundance, and insects may be rather more mobile at the end of the rainy season. After that, insect numbers stay low all through the dry season, in spite of the crescendo in leaf flush toward its end. It would appear that the prevalence of very old leaves and dry weather both depress insect levels.

Light traps, however, are not very precise estimators of insect levels, even apart from the great differences in the response of different insects to the light. They confuse changes in abundance with changes in mobility, and the figures we cite include all insects, not just folivores. Moreover, to understand insect dynamics it may be necessary to distinguish the different types of folivores. The great peak around May 1, 1975, of insects over 15 mm long consists almost entirely of adult june beetles (*Phyllophaga* spp.), which are generalist folivores (Henry Stockwell, personal communication) which emerged in great numbers just after the first rains. Such generalists undoubtedly obey very different rules from the specialists that can handle poisonous leaves.

We cannot, then, say with certainty what does regulate insect numbers. Surely birds do not; bird predation at Hubbard Brook did not even double during an outbreak of caterpillars, mostly *Heterocampa* spp., which in its peak year consumed 44 percent of the forest's leaf production (Holmes and Sturges, 1975). Such outbreaks usually seem to end by disease. If the more common trees on BCI were watched, each species might well show as fluctuating a history of

Table 14.—The relation between insect abundance and the number of trees with new leaves

Number of censused trees and shrubs with a substantial number of new leaves (out of 299), total weight (in grams) of insects under 5 mm long, and total numbers of medium-sized insects between 5 and 15 mm long, and of large insects over 15 mm long, caught in three light traps suspended at different levels of the forest in the watershed study area of Barro Colorado Island, during each week of census starting November 25, 1974.

The peak in numbers of large insects from May 5 through May 19 is due almost entirely to june beetles (*Phyllophaga spp.*), and the peak in medium-sized insects starting October 28, 1975, is comprised largely of ants.

Date	*Number of trees with new leaves*	*Weight of small insects*	*Number of medium insects*	*Number of large insects*
25 Nov.	16	0.56	57	17
3 Dec.	12	0.44	90	8
9 Dec.	17	0.62	98	7
16 Dec.	30	0.40	53	6
23 Dec.	27	0.65	49	5
30 Dec.	55	0.56	41	1
6 Jan.	78	0.49	36	14
13 Jan.	66	0.79	31	4
21 Jan.	47	0.69	21	11
27 Jan.	68	0.43	28	7
3 Feb.	54	0.63	25	11
10 Feb.	40	0.34	28	7
18 Feb.	33	0.54	38	23
25 Feb.	52	0.27	18	8
3 Mar.	88	0.33	19	15
10 Mar.	108	0.19	22	14
17 Mar.	114	0.28	15	7
24 Mar.	119	0.50	11	2
1 Apr.	97	0.12	15	0
7 Apr.	82	0.18	27	7
14 Apr.	108	0.18	31	7
21 Apr.	107	0.21	9	6
28 Apr.	100	0.18	26	20
5 May	118	2.06	24	156
12 May	156	0.79	48	235
19 May	174	2.05	19	268
27 May	189	1.36	83	28
2 June	185	1.38	50	61
9 June	188	1.33	89	66
16 June	173	0.37	65	20
23 June	187	0.50	56	9
30 June	181	0.85	117	19
7 July	109	0.61	78	14
14 July	109	0.39	39	4
21 July	68	0.22	30	19
28 July	41	0.19	25	15
6 Aug.	27	0.34	52	26
11 Aug.	24	0.36	22	12
18 Aug.	24	0.67	60	20
25 Aug.	23	0.21	23	4
2 Sept.	16	0.44	55	15
8 Sept.	19	0.57	90	10
15 Sept.	30	0.56	113	6
22 Sept.	34	0.15	36	5
29 Sept.	30	0.33	81	4
6 Oct.	28	0.19	75	0
14 Oct.	33	0.09	26	0
20 Oct.	32	0.24	49	0
28 Oct.	25	0.48	184	8
4 Nov.	24	0.74	305	5
10 Nov.	12	0.17	90	9

outbreaks as the forest at Hubbard Brook, and disease may well be what ends these outbreaks, too. Tropical trees, however, are islands, like the nettle patches planted by Davis (1975) in the middle of a field. Predator pressure may well slow the growth of insect populations already established on specific trees, and diminish dispersal to new trees. By rendering colonizations of trees less likely and extinctions more likely, the high predation pressure on BCI may greatly diminish insect folivory even if, strictly speaking, folivore populations are regulated by other means.

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Phenology of Leaf Production in Rain Forest of Gabon: Distribution and Composition of Food for Folivores

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Introduction

In an evergreen tropical forest, one might expect that food for leaf-eaters is available in large quantities throughout the year. However, not all leaves are suitable as food. Many folivores feed primarily on young leaves which contain a maximum of protein and a minimum of lignocellulose and toxic secondary compounds. To estimate the food actually available to folivores, it is necessary to study the leafing phenology and distribution of the many species of rain forest plants.

The evergreen forest of Ipassa (Figure 1) which is 10 km south of Makokou, Gabon, at an elevation of 500 m, was studied in 1971-1972 and in 1975 from a floristic and ecological point of view. Phenological data on tree and liana species were completed by a quantitative study of litter-fall. Leaves of all the species in the litter collected were identified, so as to obtain a quantitative and phenological analysis of the leafing characteristics of the different species. The climate at the Ipassa field station is characterized by a major dry season during which the sun rarely shines and the average temperature is at a minimum of about 21° C. Consequently, there is a minimum of evaporation in this dry season. The average yearly rainfall is 1700 mm. The four equatorial seasons are shown in Figure 2 with more detailed data concerning our main period of study:

Figure 1. A view inside the rain forest at Ipassa showing the importance of lianas in the forest structure.

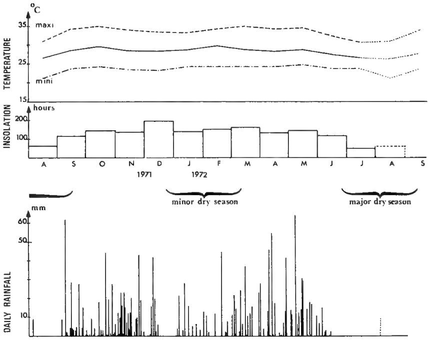

Figure 2. Data from the meteorological station of Makokou concerning the main period of phenological observations. Temperatures are monthly means (broken lines show maxima and minima). Insolation is the total time of bright sunshine per month. The records of daily rainfall show the different patterns of distribution during the rainy season and total absense of precipitation during the major dry season (also characterized by minimum insolation and minimum temperature).

(1) June-July-August (approximately): major dry season with no rain, minimum insolation, minimum temperature, and minimum evaporation.
(2) September-October-November: major rainy season with maximum rainfall and average insolation.
(3) December-January-February: minor dry season with low rainfall and maximum insolation.
(4) March-April-May: minor rainy season with important rainfall and tropical storms, and average insolation.

The temperatures shown (Figure 2) are from the Makokou meteorological station at the airport. In the forest, the vegetation has an important buffering effect. The maximum daily variation above the canopy is 10°C to 14°C while near the forest floor it is no more than 2°C to 6°C, with a gradient of vertical variation. Relative humidity may be less than 50 percent above the canopy but never less than 80 percent in the forest (Cachan and Duval, 1963, in Ivory Coast). The average relative humidity is 96 percent at the meteorological station and, thus, higher inside the forest.

In its structure and floristic composition, the Makokou forest does not differ from other rain forests of the Congo-Guinea block, though rainfall there often is considerably higher. The peculiar major dry season of the Makokou area, with its cool temperature and low evaporation, allows this "rain forest" to grow under relatively dry conditions.

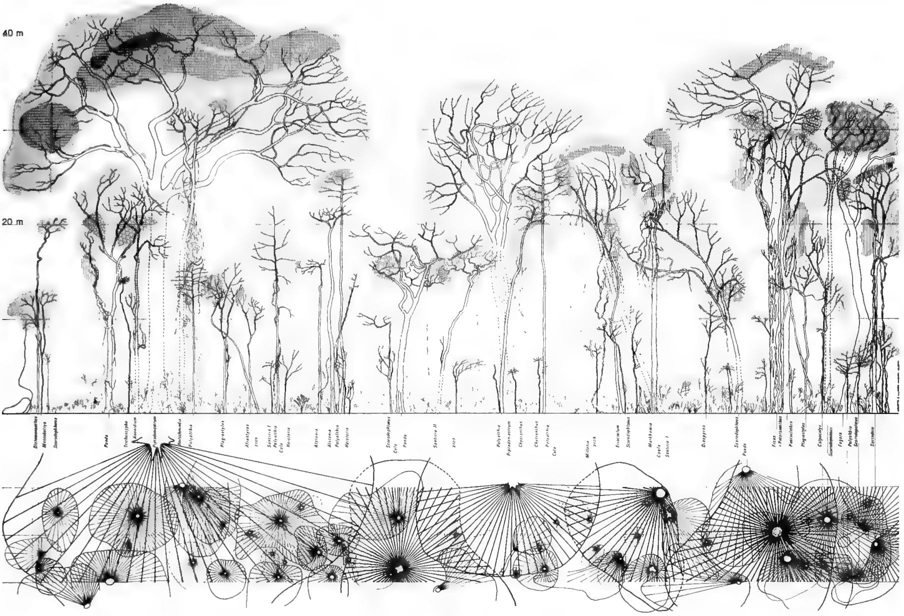

Figure 3. Vertical structure of the rain forest at Ipassa, near Makokou (Gabon), along a transect of 90 by 5 m. Some trunks outside the transect area but supporting a tree crown included in the section are shown in dotted lines. The horizontal structure is shown by the projection of the canopies and trunks in a larger sample area (90 by 10 m) including the strip of 5 m located behind that of the profile. Names of tree species: *Afrostyrax lepidophyllus, Alstonia congensis, Anonidium mannii, Beilschmiedia* sp. (= 1449), *Calpocalyx dinklagei, Chytranthus talbotii, Cola rostrata, Coula edulis, Diospyros hoyleana, Distemonanthus benthamianus, Eriocoelum macrocarpum, Fagara macrophylla, Ficus* sp. (= 1744), *Heisteria parvifolia, Maesobotrya* sp. (= 2111), *Markhamia sessilis, Milletia mannii, Panda oleosa, Pentaclethra eetveldeana, Petersianthus macrocarpus, Piptadeniastrum africanum, Plagiostyles africana, Polyalthia suaveolens, Santiria* sp. I, *Santiria* sp. II, *Scorodophloeus zenkeri, Sorindeia nitida, Trichoscypha* sp. (= 1447). Only generic names are written on the projection; canopies of lianas are represented by hatched areas on the profile.

Forest Structure

The study area is located in ecological quadrats (100 by 100 m) at Ipassa. No attempt was made to analyze either the riparian forest or the periodically flooded forest.

Vertical structure

A vertical profile along a 90 m transect, 5 m wide, in the Ipassa forest was constructed. Some trunks outside the transect area but supporting a tree crown included in the section are shown in dotted lines in Figure 3. We measured the height of trees, lianas, and limbs by using long poles placed on tree trunks. Some trees were climbed, and the main forks and parts of the canopy were accurately measured (optical instruments were useless in this type of forest).

Considering this small and detailed sample of the Ipassa forest alone, there is no obvious stratification (Figure 3). The crown of an emergent, *Piptadeniastrum africanum*, was between 25 and 45 m, two other dominant trees were lower: a *Piptadeniastrum africanum* of 20 to 35 m and a *Ficus* sp. (# 1744) 30 to 40 m, which grew on a *Petersianthus macrocarpus* tree which was reduced to a few branches and small crown. Under these three large crowns, there were many types of combinations, such as a *Beilschmiedia* sp. (# 1449) and *Scorodophloeus zenkeri* mixed with

Fagara macrophylla, all with crowns about 30 m high, and *Markhamia sessilis, Coula edulis,* and *Polyalthia suaveolens* with crowns 20 to 30 m high. In the middle of the profile, *Panda oleosa* covers some other crowns although all of its foliage lies between 20 and 30 m. There is a size-distribution among lower trees depending on the distribution of the dominant ones which capture the main part of the incident solar energy. The idea of well-defined strata has been recently refuted by different authors. Only in tropical forests, where one or more strongly limiting factors (such as flood, altitude, and temperature, or soil) reduces diversity to a small number of species, can consistent strata be demonstrated. Rollet (1974) made an extensive statistical study of Venezuelan-Guianese rain forest, and demonstrated that there are no height-frequency classes corresponding to strata.

To generalize as to the whole rain forest from that which has been briefly shown by the above example, we have to consider a dynamic point of view, clearly stated by Oldeman (1975). The trees can be divided into three sets:

(1) The "set of the future" including trees still possessing a potential for future development ("biologically young"), whose branching is mainly determined by an inherited pattern (one of the "architectural models" described by Halle and Oldeman, 1970). These trees are suppressed and their growth is very slow. We may suppose that they cannot produce much food for folivores.

(2) The "set of the present" including all trees which have attained their maximal dimensions intercepting a large part of solar energy, and showing a branching pattern that is mainly determined by prolific reiteration of the hereditary growth model, e.g., not from seeds but from buds. Trees of the present are often to be found at distinct levels, each of which is called a "structural ensemble" by Oldeman (1974). The highest structural ensemble forms the forest canopy. The growth of this set of trees is the fastest, thus we can expect these to have the largest mass of leaves available for folivores.

(3) The "set of the past" includes damaged or decaying trees without either future potential for development or competitive efficiency, destined to be eliminated from the forest. Nevertheless, many of these damaged trees are leafing out of season (for example, just after a large branch has been broken) and thus this set might represent a valuable complement for folivores.

The main ecological difference between the set of the future and the set of the present is an inversion of light and atmospheric moisture conditions. The set of the present intercepts the better part of the light and, under its cover, the high hygrometry and low light are the conditions of survival for the "trees of the future." As soon as the equilibrium is disrupted, e.g., by the fall of a tree, the surviving trees of the future start expanding their crowns by reiteration of the hereditary growth pattern from buds, in a phase of fierce competition. The winning trees become the new "trees of the present;" the losers reduce their volume by shedding branches and may survive again as trees of the future or may die.

Thus the fundamental pattern of the rain forest is not homogeneous but heterogeneous. Aubréville (1938) described the rain forest of the Ivory Coast as a "mosaic" determined by its regrowth, tree by tree. The basic idea seems to be correct, but the surfaces of simultaneous development are larger than the surfaces covered by a single tree. A falling tree most often clears rather extensive surfaces, where more than one other tree can grow. On such a surface, according to Oldeman (1975, manuscript), there is a succession of phases, including slow growth which is regulated by trees of the present. Old, well-structured phases, generally called "mature" forest, do not constitute more than an estimated 5 to 10 percent of the total forest (Oldeman, 1974).

Mixed in the canopy is the foliage of many species of lianas. They form a very important part of the total forest leaf biomass (at least 36 percent, A. Hladik, 1974), but their growth and population dynamics are still subject to study. They have the tendency to overgrow in any place where enough light is available. They seem to accompany the supporting trees during their growth upward, i.e., they generally do not climb toward the forest canopy along old trunks (Oldeman, 1974). They usually survive tree falls, and form the oldest and most diverse components of some forests (Montgomery, Sunquist, and Croat, in press).

In such a dynamic environment the classic notion of strata does not apply and the notion of ecotope has to be considered instead: it represents the plant, species or individual, and its feedback into its own environment. Ecotopes form various volumes distributed at different heights. Their places are related to the horizontal structure of the forest.

Horizontal structure.

In a plot of 900 m^2 (90 × 10), the projection of the canopy from a top view was drawn (Figure 3) with the help of a plumb line to determine the contours. The cross-sectional area of the crown of all trees over 10 cm diameter (35 individuals of 23 species) is 1640 m^2. In this sample, the large trees of the set of the present (4 individuals of 3 species) total 835 m^2. This is about half of the total of all trees. In an area of Barro Colorado Island used by radio-marked sloths, total cross section of trees over 15 cm diameter was about 35,000 m^2 per hectare and about 12 percent of the trees had crowns with cross-sectional areas greater than 20 m^2 (Montgomery and Sunquist, 1975, 1978). The leaf biomass of a tree is proportional to the cross-sectional area and to the height of the crown. Moreover, for each species it also depends on a factor of density of the foliage, and we noticed that many emergent trees have tiny leaflets (for example, many trees of the Leguminosae family, such as *Piptadeniastrum africanum*). With this restriction for a correct estimate of the leaf biomass, we can assume that few species account for a large part of the leaf biomass in a localized plot.

On a larger scale it is not possible to calculate the area of the crowns. The species diversity is better demonstrated by the number of tree boles (Table 1). The trees over 5 cm diameter on a plot of 0.4 ha belong to 95 different species. However, large trees (over 60 cm diameter) include few species. As the plot increases in size, the number of species of large trees becomes higher with 60 species for 20 ha following a rapid estimation over the total study area at Ipassa.

Considering only this increasing diversity of tree species as the plot increases in size, this African forest seems approximately as rich as the American rain forest (according to Rollet, 1969, there are 68 species over 60 cm diameter for 16 ha in Guiana and a total of 365 species of trees and lianas over 10 cm diameter in 64 ha). On the regional scale (northeast of Gabon), one might expect to find a total of perhaps 4,000 plant species.

There are few data concerning the distribution of lianas and the shapes of their crowns, owing to the difficulties of observation and field identification. The shape of the most obvious masses of liana foliage are roughly localized on the profile (Figure 3). Liana-leaf biomass is about one-third of the tree-leaf biomass and species diversity is unknown but obviously important. There are 33 identified species of lianas for 57 species of trees along two transects of 200 m each (A. Hladik, 1974). Montgomery and Sunquist (1978) identified a total of 28 liana species from 13 trees used by sloths on Barro Colorado Island. They examined 39 trees of which 11 had no lianas in their crowns. The remaining 28 trees contained a total of 55 liana species.

The distribution of one species of liana, *Entada gigas*, has been mapped at Ipassa (Charles-Dominique, 1977). A corresponding map of the unequal distribution of a nocturnal Prosimian, *Euoticus elegantulus*, shows that the animals are distributed exactly according to the unequal distribution of the lianas from whose stems they eat gum. It is exceptional though that the distribution of one vertebrate species can be related only to one plant species.

In the rain forest, the great diversity of tree and liana species, the low density of most of the species, and the many ways they can be distributed horizontally and vertically to form different ecotopes allow a great number of animal species to be specialized in particular niches. The distribution of the birds in the various ecotopes of the Ipassa forest is presently under investigation by Erard (personal communication). According to his field observations, the Muscicapidae spend most of their time in areas that vary from species to species. Such factors as branch density, which are not related to the notion of strata, determine species habitat preferences.

Five species of nocturnal Prosimians have been studied by Charles-Dominique (1971, 1977), who recorded on each occasion the types of branches and lianas on which the animals were first observed. The Angwantibo, *Arctocebus calabarensis*, uses the

Table 1.—Densities of tree species compared to number of individual trees in different plots at Ipassa (10 Km South of Makokou) and Bélinga (70 Km North of Makokou); data for Bélinga are taken from Le Thomas, in Aubréville, 1967.

	Diameter ≥ 5 cm		*Diameter ≥ 10 cm*		*Diameter ≥ 30 cm*		*Diameter ≥ 60 cm*	
Location and size of plot	*Species*	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*
Ipassa 0.4 ha	95	304	62	171	22	47	5	9
Ipassa estimate /ha		760		427		117		22
Bélinga 1.0 ha		789		495	50	119	14	22
Ipassa 0.9 ha					36	86	13	22

ecotope composed of thin lianas and thin branches developed around the decaying trees of the set of the past and in small clearings where vegetation is growing fast. Feeding essentially on caterpillars, this animal is a limiting factor on the population of folivorous insects of this particular ecotope. The potto, *Perodicticus potto*, lives in more open places and travels on the branches on top of trees of the set of the present. It feeds partly on folivorous insects. Allen's bushbaby, *Galago alleni*, also feeds partly on insects (and fruits), but this vertical leaper is found only on the vertical small trunks of the set of the future and on liana stems. This ecotope is characteristic of large areas near the ground of the rain forest and may also extend to some height near the tree tops. Demidoff's bushbaby, *Galago demidovii*, inhabits the volume of thick foliage and twigs enveloping large and small trees. It is also an insect feeder not competing with any of the previous species because it forages in a different ecotope. The fifth species of Prosimian of the Ipassa forest is the needle-clawed bushbaby, *Euoticus elegantulus*, which has the particular distribution described above. Because of its anatomy, *Euoticus* can move along the largest smooth trunks and branches and, thus, it is present in the most open volumes of the forest.

The zoological studies of P. Charles-Dominique introduced a practical aspect to the notion of ecotope which might slightly differ from a botanical point of view confined to studies of plant species. The forest structure is divided into different volumes for which height and localization are not correlated. The type of ecotope in each of these volumes is related to the dynamic structure of the forest (evolution of "sets" as proposed by Oldeman), but not to a theoretical notion of strata that have never been demonstrated in a rain forest. The colonization of different ecotopes by different vertebrates is the best demonstration of the validity of this view; but further botanical and zoological investigations are necessary to add precision and, eventually, to normalize the definitions.

The folivorous mammals at Ipassa are poorly known or absolutely unknown. The Colobidae and the Gorillas were only occasionally observed. Other primates show a tendency for folivory, especially *Cercopithecus nictitans* (Gautier-Hion and Gautier, 1974). To a lesser extent, chimpanzees also eat leaves (C. M. Hladik, 1973). The other arboreal folivores are Anomalurids (scaly-tailed flying squirrels) and the tree hyrax (*Dendrohyrax dorsalis*) of which we know very little.

Generally speaking, the folivorous mammals have small home ranges and a large part of their food is taken from a small number of tree species. For instance, the sloths of America (Montgomery and Sunquist, 1975, 1978) used "modal trees" on which they spent a large part of their activity.

In Asia and East Africa, the leaf monkeys living in a semideciduous forest feed on a limited number of tree species (Hladik and Hladik, 1972; Oates, 1974; Struhsaker and Oates, 1975). If folivorous species feed selectively on a small number of tree species in the rain forest, home ranges would necessarily be larger because of the dispersed distribution of the plant species. This seems corroborated by the observations on *Presbytis senex* in the Sinaradja forest in Sri Lanka (Hladik and Hladik, 1972). Superficial observations (location of the groups according to the calls) indicate that the group home range is about six times the size of that of the same species living in drier forests. In a species-rich forest, it is likely that different groups of the same folivorous species eat different species of leaves as staple food. Different folivorous arboreal species might be expected to be adapted to different ecotopes, as in the case of the other mammals.

Phenology of Leaf Production

Measures of litter fall

Total litter production at Ipassa between July 1971 and July 1972 was 13.3 T/ha/year, which is comparable to litter production in other rain forests (Table 2). We collected litter from 120 sampling baskets of corrugated sheet metal, each about 0.8 m^2 (total 95.4 m^2), placed 10 meters apart in line along two 600 m transects. Litter was collected from the baskets every 2 weeks (or 3 weeks during dry periods). It was dried to constant weight in an open electric dryer. The loss of litter weight due to the stay in the sampling baskets was calculated: 3 samples of litter were dried in an oven (90°C) and returned to 3 sampling baskets in the forest for 2 weeks during a period of heavy rain. They lost 6 percent of their weight. Considering that in the open dryer 5 percent of humidity is retained (by weight), our data can be considered as the correct dry weight ± 1 percent.

The litter was analyzed by sorting out leaves, fruits, flowers, wood, and "dust." The dust included decomposed wood and bark, pieces of leaves and flowers, and various unidentified materials. Large leaves were usually in good condition, except when eaten by insects. In the case of large compound leaves, we sometimes separated only the leaflets without petioles and petiolules. In the case of small leguminous leaflets, we did not take time to weigh them

Table 2.—Comparative litter production of different forests in the world.

Country	Types of forest	Litter production T/ha/year Leaves	Litter production T/ha/year Total	Reference
France	Temperate deciduous forest (*Fagus sylvatica*)	2.8	5.9	Lemée and Bichaut, et al. (1971)
France	Temperate evergreen forest (*Quercus ilex*)	1.6 to 3.4*	3.1 to 4.7	Rapp (1969) on 4-year study
Ivory Coast	Woodland savanna	1.8		Menaut (1974)
Sri Lanka	Semiarid semideciduous forest	—	3.9	Hladik (in prep.)
Sri Lanka	Dry semideciduous forest	2.4	4.6	
Ghana	Tropical semideciduous forest	7.4	9.7	John (1973)
Panama	Tropical semideciduous forest	6.0 to 7.0	11.4 to 12.6	Foster; Smythe (1974, unpublished manuscript) on 2-year study
Ivory Coast	Tropical evergreen forest-Banco	7.3 to 9.2	9.0 to 13.4	Bernhard-Reversat (1970) on 2-year study
Ivory Coast	Tropical evergreen forest-Yapo	5.7 to 7.6	8.3 to 10.1	
Gabon	Tropical evergreen forest	6.5	13.3	Hladik (present paper)
Malaya	Tropical evergreen forest	7.5	10.0	Lim (1974)
Sri Lanka	Montane evergreen forest	3.5	5.9	Hladik (in prep.)
India	Montane evergreen forest	2.4 to 5.0**	3.8 to 7.3	Blasco and Tassy (1975) on 3-year study

* There is a biannual variation of the leaf production: the average is 2.5 T /ha /year.

** This large annual variation might be due to the sampling method.

when they occurred in small quantities. Fruits and seeds were easy to recognize, but flowers sometimes were included in the "dust." Wood included all pieces of wood which fell into the sampling basket except for a huge mass of lianas and one small trunk which fell on a basket. The fall of trunk was statistically very rare and was not included here in the total litter fall. Quadrats larger than 100 m^2 are necessary for measuring total wood fall.

All macroscopic insects and other invertebrates were collected before each collection of litter. We obtained a total of 2.3 g/m^2/year (dry weight). A maximum of "insect production" occurred during the end of the major rainy season and the minor dry season. Charles-Dominique (1971), collecting insects in light traps at night, obtained a maximum of moths in April. This suggests that caterpillars were abundant at a period corresponding to our maximum of "litter insects." Many of these insects (caterpillars and grasshoppers) are folivores and grow during the period of leaf flushes.

Leaf-fall

Leaves from 40 of the 120 baskets (in a line of 400 m) were weighed with a minimum of manipulation. We obtained 6.5 T/ha/year of leaves for 13.9 T/ha/year of total litter fall (i.e., 47 percent). Leaves from 40 other baskets were identified to species before weighing (A. Hladik, 1974). Because identification involved frequent manipulations and some damage to leaves, a larger proportion of dust from the leaves was obtained.

Leaf-fall is more regular throughout the year than total litter fall (Figures 4 and 5). Leaf-fall reached a conspicuous low point of 1.2 g/m^2/day in June and July, during the major dry season. It reached a small peak of 2.0 g/m^2/day in September during the major rainy season, and a higher peak of 2.8 g/m^2/day in March and April during the minor rainy season. The total litter fall reached its annual maximum in the minor rainy season with 10.5 g/m^2/day because many twigs and decaying wood fell during storms.

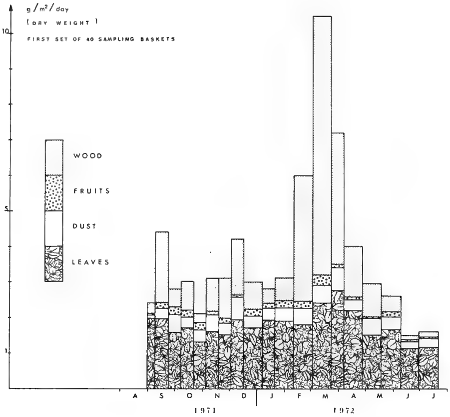

Figure 4. Seasonal litter-fall production is 40 sampling baskets (32 m^2) on a 400 m long transect at Ipassa (g/m^2/day).

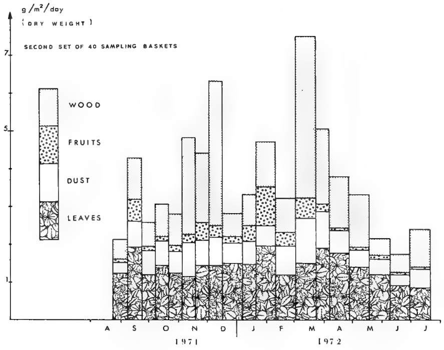

Figure 5. Season litter-fall production in the second transect at Ipassa. The "dust" fraction in these samples is more important compared to Figure 4 due to the method of analysis (see text).

The small peaks in our leaf-fall graphs correspond to the shedding of leaves by deciduous trees, e.g., two in March and April (*Berlinia bracteosa* and *Parkia bicolor*; Figure 4) and one in January and February (*Piptadeniastrum africanum*; Figure 5). These irregular peaks are related to the number of deciduous trees included in the transects.

Lianas contributed a large part of the leaf biomass (Hladik, 1974), and the relative leaf-fall from lianas and trees was: lianas, 36 percent; trees, 59 percent; unknown species, 5 percent, which probably included more lianas than trees. With the exception of one small peak between September 9 and 24 (Figure 6), the total leaf-fall of lianas was more regular than that of trees, but some individual liana species showed a seasonality in leaf-fall.

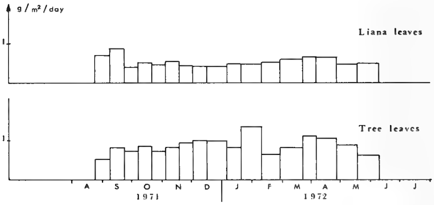

Figure 6. Comparative seasonal leaf litter-fall for trees and lianas at Ipassa (g/m^2/day).

Phenological sequences of trees

To complement the measures of litter-fall, direct observations of leaf-fall, leafing, flowering, and fruiting of 300 labeled trees along 4,000 m of trail were made at intervals of 2 to 3 weeks in 1971–1972 and 1975. The difficulty in quantifying new leaf production over these standing trees in the forest allows us to take notice of only peaks of production. Flushes[1] of numerous new leaves are obvious in the tropics because these leaves are very often bright or dark red (as previously mentioned by Richards, 1952) or at least light green.

The observations of phenological events have been combined with data on leaf-fall for a number of important species on the transects (Figures 7, 8, 9, and 10). There are three main types of phenological sequences with respect to leaf-fall. The first, illustrated by *Piptadeniastrum africanum* and others (Figure 7) occurs when the leaves fall during a fairly short period once each year (or without annual cycle) and the trees remain bare for a few days or more. These trees are called deciduous. The second type, illustrated by *Panda oleosa* and others (Figure 8), occurs when leaf-fall comes in peaks with concommitent flushes of new leaves. In the third type, leaf-fall is more or less continuous throughout the year, with a general

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[1] "Flushes" is used here as an expression of bunches of new leaf growth obvious from observations with binoculars. In fact, leaf flush might be related only to endogenous rhythmic growth which appears to be common for many tropical plant species, but not all (cf. work on the periodicity of tree growth by Koriba, 1958).

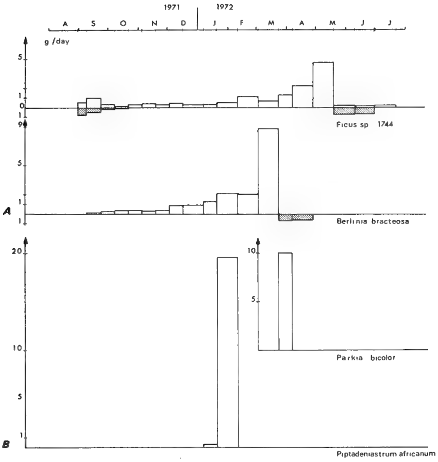

Figure 7. Phenology of deciduous trees. A = Quantitative estimate of the leaf production of two emergent trees at Ipassa as indicated by the dry weight of their deciduous stipules falling in 40 sampling baskets (shaded areas). The leaf-fall (clear areas) occurs in large quantities during a short period. B = The important and sudden leaf-fall of two leguminous trees (dry weight in g/day in the 40 sampling baskets).

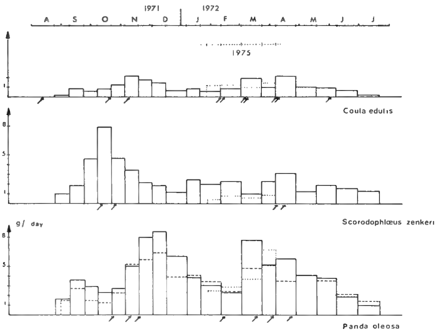

Figure 8. Seasonal leaf-fall in g/day in 40 sampling baskets and leafing times (arrows) of some important tree species of Ipassa. The dotted lines show the observations during 1975. For *Panda oleosa* leaf-fall production in the first set of baskets is compared to leaf-fall production in the second set analyzed (dashed lines).

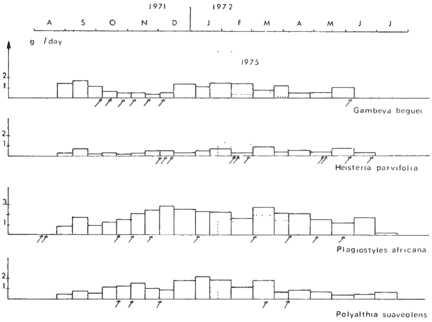

Figure 9. Seasonal leaf-fall in g/day in 40 sampling baskets and leafing times (arrows) of some common and one emergent tree species at Ipassa (dotted line is data taken in 1975).

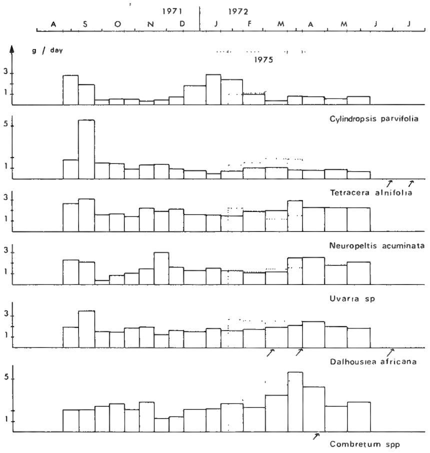

Figure 10. Leaf phenology of the most important liana species (leaf-fall over $10g/m^2/year$) in the analyzed leaf litter (40 sampling baskets). Dotted line is data taken in 1975. The most obvious leafing times (arrows) have been noted only for three species.

decrease in leaf-falling during the major dry season, and is illustrated by *Polyalthia suaveolens* and others (Figure 9). In these last two types of evergreen trees, leafing periods often correspond to rainy periods. A general survey is presented for the most important species (by weight in our baskets) including numerous individuals of a common species or one individual of a rare emergent species.

The emergent trees of our transect, which had large crowns, were responsible for a large part of the total leaf biomass. One huge strangling fig, *Ficus* sp. (1744), demonstrates the phenology of a deciduous tree in the tropics. Leaves start to fall in February with a peak at the beginning of March (Figure 7), then new leaves appear immediately and last for about a month. *Ficus* has deciduous stipules, and it was possible to measure the intensity of new leaf production by weighing the fallen stipules. The phenology of the genus *Ficus* is singular with two periods of fruiting (or even three) elsewhere in the world. It seems, however, to be different in Gabon where figs are not so abundant and a special study on *Ficus* sp. is in progress. *Berlinia bracteosa* (Figure 7) has deciduous stipules during the leafing period which follows leaf-fall in March. These trees with falling stipules are interesting because they allow the collection of quantitative phenometric data of new leaf production which are otherwise so difficult to estimate. Another species in our transect, *Piptadeniastrum africanum*, is deciduous (Figure 7). Leaves fell during a very short period which was followed immediately by several days of leaf production. For the tree shown (Figure 7), this occurred between January 7 and 21, but all the individuals were not synchronous with respect to leaf phenology (Figure 12). One *Parkia bicolor* tree showed the same rapid leaf-fall between March 24 and April 7 (Figure 7). New leaves appeared shortly after leaf-fall. Nevertheless, some other emergent large trees were not deciduous, e.g., *Gambeya beguei* (Figure 9) which had regular leafing and leaf-fall periods all the year.

The more common medium-size trees on our transect had a variety of leaf phenology patterns. The most common species were *Panda oleosa* with 10 trees (over 30 cm diameter) per ha, and *Scorodophloeus zenkeri* with 16 such trees per ha. Both are generally medium-size trees growing to 30 m high. The leaf-fall of *Panda oleosa* appears to be bimodal with peaks in November-December and March-April (Figure 8). New leaves appear before old leaves fall, and keep growing for some weeks during the rainy season. Leaf-fall of *Scorodophloeus zenkeri* (Figure 8) shows one peak earlier in the rainy season, in October. This species, however, has two leafing periods in October and April. *Coula edulis* with 4 trees per ha, is a medium-size tree whose leaf-fall seems bimodal, with perhaps additional leafing periods (Figure 8). The leaf-fall of *Coula* studied in the Ivory Coast (Bernhard-Reversat, 1970) also showed two peaks more or less distinguishable. *Polyalthia suaveolens* with 6 trees per ha, and *Plagiostyles africana* with 7 trees per ha are also medium-sized trees. Their leaf-fall appears more or less continuous (Figure 9) with two principal leafing periods for *Polyalthia*, contrasting with *Plagiostyles* which has new leaves many times during the year even including the dry season. *Heisteria parvifolia* with 2 trees per ha also has new leaves in the major dry season as well as the rainy season (Figure 9) although there is continuous leaf-fall.

Phenological sequences of lianas

The study of leaf litter-fall of lianas gave some interesting quantitative information although phenological events were directly observed for only a small number of species owing to the difficulty of recognizing individual lianas. The continuous total leaf-fall of lianas (Figure 6) is the result of varying seasonal production of different species (Figure 10).

Cylindropsis parvifolia and *Tetracera alnifolia* show a clear seasonality in leaf phenology. Other species like *Neuropeltis acuminata* and *Dalhousiea africana* show irregular leaf production without large peaks. The 1975 data indicate possible annual variations in leaf-fall production but probably with a similar seasonal pattern. The leafing periods precede the leaf-fall periods for *Dalhousiea*, but followed it for *Combretum*. For some lianas, such as for *Tetracera* and *Dalhousiea*, new leaves occurred during the major dry season.

Leaf Phenology and Food Availability

The total leaf-fall pattern of the Ipassa forest, examined by the method of weighing litter in several traps, shows only small annual variations (except a minimum during the major dry season). The specific leaf-fall cycles of some liana species, some common tree species and the emergent trees of our transect have been pointed out as partly complementary. Leaf flushes were recorded by direct observation, and in a few cases after precisely weighing the deciduous stipules. The sample on which species-by-species leaf analysis was carried out includes 18 common tree species, 2 deciduous emergent trees, and 1 evergreen emergent tree, corresponding to 70 percent

Table 3.—Estimate of the annual distribution of leaf production of some important tree species.

The total dry weight obtained on 31.8 m^2 of 40 sampling baskets has been partitioned into periodical production for each leafing period. The monthly numbers represent the future production of mature leaves (g by dry weight) in relation to the intensity of leafing. The young leaves available each month can be roughly considered as 1/10 of those weights. (During August new leaves were rare; in September we had no precise data).

	Monthly leaf production (by dry weight, on 31.8 m^2)									
Species	*O*	*N*	*D*	*J*	*F*	*M*	*A*	*M*	*J*	*J*
Panda oleosa		600			300	200	200			
Scorodophloeus zenkeri	450						300			
Plagiostyles africana	60	100		60	60	60	60	60	60	
Coula edulis	50	50			80	80	80	50		
Polyalthia suaveolens	70	70	70			70	70			
Macaranga barteri		50					200		50	
Santiria sp. II	30	30	10	40	30	10	50	60	30	
Santiria sp. I					30	30	10		30	
Petersianthus macrocarpus	40	100	30	20	30	20	10		30	10
Pentaclethra eetveldeana		75	75	30						
Pausinystalia macroceras			100				60			
Heisteria parvifolia			40		40			25	15	15
Ficus sp. 1744								250	80	
Piptadeniastrum africanum					400					
Gambeya beguei	100	100								
Total future production of mature leaves	800	1175	325	150	970	470	1040	445	295	25
Estimate of young leaves available	80	120	35	15	100	50	100	45	30	3

of the total tree leaf-fall (in dry weight, A. Hladik, 1974). We estimated the monthly available new leaves on this particular sample by dividing the annual dry weight of leaf-fall (for each species) in several fractions proportional to the importance of each leafing period. Thus, the monthly weight (Table 3) is the potential dry weight of mature leaves to be produced at each leafing period of each species. The dry weight of available young leaves during the period of production is about one-tenth of this number. This estimation gives the relative values of leaf production among various tree species, their variations throughout the year with peaks in November and April, and a rough estimate of food availability. Lianas are excluded, however, because we do not have enough data on their leafing periods and, to obtain an adequate figure, it will be necessary to make a general survey of the forest on a larger sample corresponding to the supplying area of folivorous animals.

As a different method of estimating food availability, we can use our phenological data of 300 labeled trees of about 150 species dispersed along 4,000 m of trails. This sample is not a plot and it does not give quantitative data on leaf production since it has not been related to crown size (and lianas are excluded). Nevertheless, it gives an idea of the variation in young leaves available in different seasons (Figure 11) and it can be compared to other studies on labeled trees. It is noticeable that the annual leafing pattern according to our study (Figure 11)

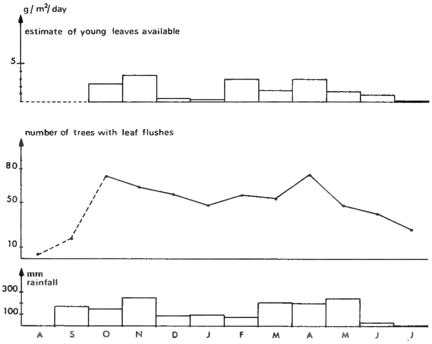

Figure 11. Monthly estimate of young leaves available (after data from Table 3) and number of trees with new leaves among 300 labeled trees at Ipassa. The maximum in October-November and February-March-April occurs when rainfall is maximum.

is similar to the one obtained by the leaf-fall method: most of the new leaves occur at the beginning of the rains that follow the dry seasons. Medway in Malaya (1972) and Leigh and Smythe in Panama (1978) obtained similar results. In Panama, leaf production shows a very high peak in June, after the dry season, and a sharp low in August. This pattern is probably due to the pronounced seasonality of this semideciduous forest, just as leaf-fall is more seasonal in Panama than in the rain forest of Ipassa. Distribution of rain in the tropics generally is quite variable from year to year, and monthly averages do not give enough precision to be correlated with phenological sequences. New leaves may occur just after thunderstorms during the dry season (Hladik and Hladik, 1972). Phenological studies have been conducted in wet and dry forests of Costa Rica (Frankie, et al., 1974). The results (in number of species) are surprising, especially for the wet forest and the riparian forest in the dry zone where most of the leaf flushes occur in the dry season. But what is a dry season? In that wet forest, February and March, the driest months, total each an average rainfall of 200 mm. Nevertheless, rainfall is only one among several climatic factors, and plant growth might be induced as well by temperature or saturation deficit or photoperiod (Catinot, 1970). Moreover, the factors controlling growth may not be the same for all species.

Beside the most common evergreen trees, the deciduous trees of a rain forest play a particular role in the food availability for folivores. Most of them are large emergent trees which suddenly produce a localized mass of young leaves. They may flush at different times of the year (Figure 12) according to the species, and even to different individuals of the same species, as in *Piptadeniastrum africanum*. The percentage of bare trees is only 1 percent at any time. Although the number of large deciduous trees is fairly small (about 2 to 3 per ha), they may be of great interest when growing in the supplying area of a folivore. Of the 21 deciduous species observed, 10 were Leguminosae, of which many species have a high protein level, especially in the young leaves (Table 4). Several times, when the *Piptadeniastrum* tree was leafing, many pieces of young leaves were found on the ground, indicating that folivorous animals had been foraging in the tree. Only 60 percent of the deciduous trees observed in 1971–1972 and in 1975 showed a similar leafless period. During a 6-year study in Malaya, Medway (1972) reported four annually deciduous species and four irregularly deciduous species. In the Cameroun, phenological observations of more than 2,000 trees (about 150 species) were carried out for up to six years under the supervision of Dr. R. Letouzey. These data are presently compiled for an overall study (A. Hladik, in prep.).

Leaf phenology should of course be considered as part of plant physiology and is probably related to the reproductive state of the plant (flowering and fruiting), a topic not discussed in this paper. When a tree is young, it may grow new leaves more or less regularly throughout the year and become deciduous when it is adult (e.g., phenological cycles of *Didymopanax morototoni* in Panama, A. Hladik, 1970). Changes in leaf phenology occur when a tree passes from the set of the future to the set of the present.

From comparative studies on cultivated trees in the tropics, rhythmic or continuous growth can be defined as either endogenous (genotypic) or related to the climate. The growth of some economically important tropical species is well known (for *Hevea brasiliensis*, Halle and Martin, 1968), but we have little knowledge of the growth habits of the various species mixed in a rain forest.

In conclusion, some folivorous mammals which depend mostly on young leaves will be necessarily distributed according to the leaf phenology of many or a few selected species. The deciduous trees offer a brief mass of leaf flushes at various places widely spread through the forest. The evergreen trees represent the remaining stock of young and mature leaves. The density of folivorous mammals might be generally low in relation to a crucial period when few new leaves are available. If folivores are able to utilize mature leaves at this time of restriction, their density may be very high. In the latter case, the problem for folivores is to use the most nutritious species.

Leaves as Nutrient Sources or Repellents

Nutrients

Folivores utilize more shoots than mature leaves, and preferentially eat the shoots and new leaves if, and when, available. This is clear at least among the leaf-eating forms of primates. The nutritional value of the shoots, buds, and young leaves of some trees in Gabon is higher than that of the mature leaves (Table 4). Similar nutritional differences have been shown for some species of Barro Colorado Island, Panama (Hladik, et al., 1971). Some comparative results concerning shoots and mature leaves of different species eaten by the Sri Lanka primates are shown in Table 5.

Primates make many food choices based on positive

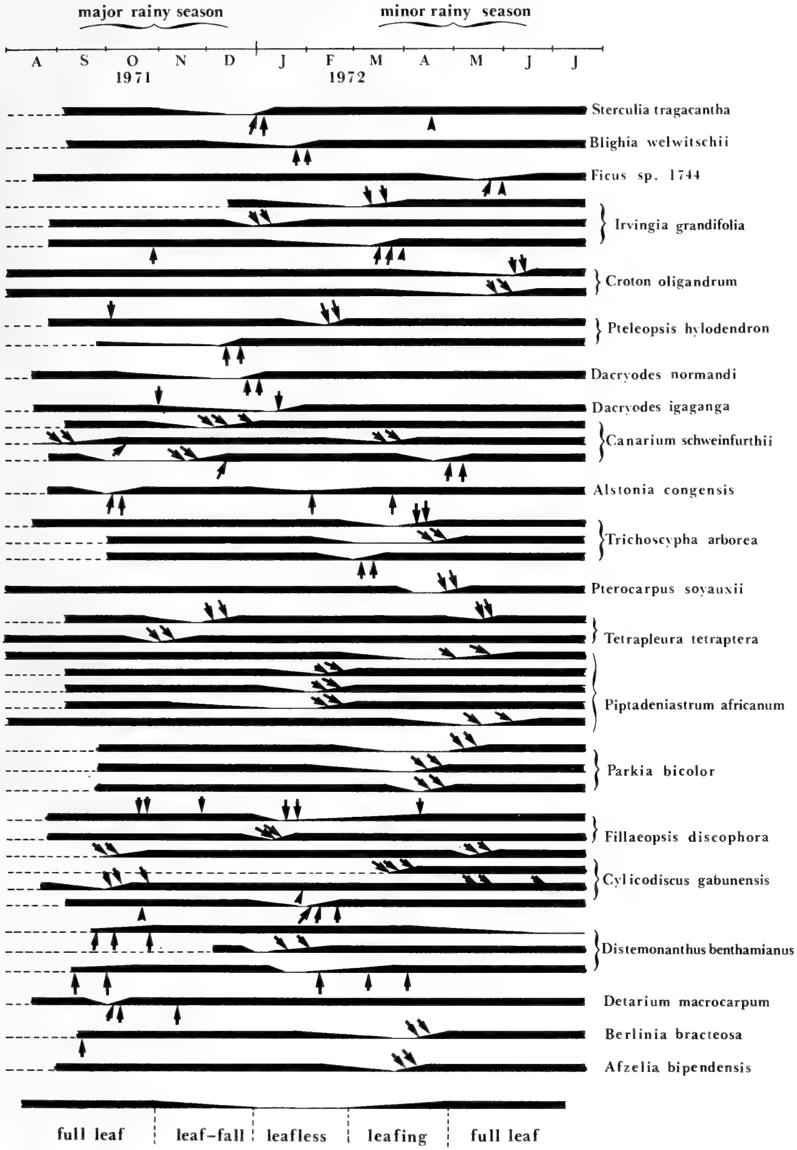

Figure 12. Leaf phenology of deciduous trees at Ipassa. The arrows show the leafing times which follow the period of leaf-fall, or may appear at different times of the year.

Table 4.—Composition of shoots, flushings, leaves, and stems eaten by primates in Gabon.

		Percent of the dry weight					*Parts per thousand*			
Species	*Food*	*Proteins*	*Lipids*	*Reducing glucids*	*Cellulose*	*Total minerals*	*P*	*Ca*	*K*	*Cl (NaCl)*
Baphia leptobotrys	shoots	55.0			12.3	6.4				
	young leaves	36.3	2.25	20.1	14.9	3.7	1.99	2.66	11.79	0.64
	mature leaves	26.1	1.3		36.6	8.9				
n° 1383 (leguminous tree)	young leaves	24.4	1.3	14.5	37.0	4.1	2.18	1.90	14.2	1.58
Newbouldia laevis	young leaves	21.7	4.1		13.8	5.4	2.83	2.21	19.1	
Ongokea gore	shoots	19.3	1.2	24.9	8.9	3.8	2.20	2.22	12.1	
n° 2335	leaves	17.9	1.6	13.3	37.6	5.8	3.66	2.73	21.9	1.94
Dinophora spenneroides (herbaceous plant)	leaves	16.7	10.7	31.1	11.0	3.6	2.03	4.64	17.2	1.50
Cryptosepalum congolanum	young leaves	13.1	0.92	21.3	25.8	3.6	1.97	1.10	11.2	0.97
Cissus dinklagei (liana)	young leaves	10.3	11.2	32.7	11.2	3.4	1.32	6.62	8.8	0.64
Gilbertiodendron dewevrei (not eaten by chimpanzee)	young leaves	10.2	0.7	13.5	46.7	3.9	3.17	4.38	14.1	0.58
Hypselodelphis violacea	stem	5.7	1.1	11.4	51.3	4.9	0.99	2.18	13.8	5.04
Musanga cecropioides	petiole	11.5	0.60	16.9	19.3	17.1	2.62	24.00	54.4	13.40
Pseudospondias microcarpa	petiole	4.8	0.33	28.0	21.3	10.0	0.81	8.0	33.4	3.24

Table 5.—Composition of some shoots, flushings, and young leaves eaten by primates in Sri Lanka.

		Percent of the dry weight					*Parts per thousand*			
Species	*Food*	*Proteins*	*Lipids*	*Reducing glucids*	*Cellulose*	*Total minerals*	*P*	*Ca*	*K*	*Na*
Drypetes sepiaria	shoots	14.74	0.91	9.0	12.7	7.5	3.27	2.7	3.30	0.065
	leaves	7.13	1.28	6.9	30.8	8.8	2.0	10.0	27.0	0.840
Walsura piscidia	shoots	17.79	1.45	5.2	14.8	6.6	2.58	2.29	32.06	0.087
	young leaves	19.52	1.47	8.3	13.6	7.3	3.40	1.65	32.50	0.075
	mature leaves	11.20	4.69	14.4	22.6	6.1	1.25	10.25	18.00	0.087
Manilkara hexandra	flushings	19.26	6.29	1.8	5.3	5.3				
	leaves	8.47	6.40	4.1	28.3	6.5	3.06	12.50	15.50	0.158
Sapindus emarginatus	flushings	16.92	1.46	2.7	13.3	5.4	3.57	3.22	24.40	0.117
	leaves	13.19	2.81	3.0	30.2	11.0	2.62	21.25	20.25	0.102
Alangium salvifolium	flushings	26.22	2.63	10.3	14.8	7.5	3.48	8.00	28.00	0.140
	leaves	16.98	7.68	6.7	21.0	11.6	2.10	24.50	24.00	0.245

motivation according to the chemical composition of the available material. The analysis of food samples selected by primates of Panama (Hladik and Hladik, 1969; Hladik and Hladik, et al., 1971), of Sri Lanka (Hladik and Hladik, 1972) and of Gabon (C. M. Hladik, 1973, 1974) show that all contain compounds of high nutritive value, at least in greater proportion than is found in natural products not selected as food by the monkeys.

Young leaves and shoots eaten by primates often contain more than 20 percent protein (Tables 4 and 5) which may reach 50 percent in leguminous shoots. Mature leaves have only between 7 and 15 percent protein. There is also an obvious difference in the cellulose and total mineral content. Shoots and young leaves contain more phosphorus than do mature leaves. The latter contain more calcium in a proportion higher than the animals need. Sodium chloride is generally not abundant. This may be the reason why some stems showing a high chloride content are eaten in large quantities by folivores, e.g., the petioles of *Musanga cecropioides* and stems of *Hypselodelphis violacea*, which are eaten by chimpanzees (C. M. Hladik, 1974b) and petioles of various *Cecropia* species eaten by howler monkeys (Hladik and Hladik, 1969).

When shoots and young leaves are eaten by folivores, even up to one-half of the locally available leaves, the plant species is not necessarily harmed since this early pruning may stimulate the growth of new shoots and leaf flushes. It costs the plant energy to replace these young leaves, but this is recovered as soon as the new leaves are functional. Conversely, use of the mature leaves by folivores may damage a plant by removing a large part of its photosynthetic and respiratory organs.

Alkaloids

Out of a total of 408 plant species tested, tests for alkaloids were made at first on fresh leaves of 154 species from 61 families of phanerogams and 2 Pteridophytes of Gabon, including the most common ones. The results of our tests show that only 44 species of the 154 tested were negative for alkaloids, and 18 were conspicuously positive. These proportions are very similar to those obtained by Webb (1949, 1952) in Australia. This screening for alkaloids, which was made with Mayer's and Dragendorff's reagents, after aqueous acid extraction, is not strictly selective. Other nonalkaloid substances, such as proteins, betaines, and tannins, may give precipitates, and Dragendorff's reagent also detects cardiotonic glycosides. Field tests made on fresh leaves are generally good guides to the presence of alkaloids, but further confirmation with a careful methodology needs to be conducted in the laboratory (see discussion by Farnworth, 1966).

We repeated these tests on dry herbarium specimens. Tests made on the same material, fresh and dry, sometimes do not yield the same results. Of 254 additional species which were tested using only dry specimens, the relative proportion of negative results is higher (121 species), but the conspicuous positive results are about the same (30 species). The variable results obtained for some species require more investigation.

Alkaloid screenings and chemical analyses have been made on many plant species in the world. Willaman and Schubert (1961) in a worldwide bibliographic survey reported 3,671 species to contain alkaloids, and Smolenski, et al. (1974) found 797 species to be positive out of 3,259 species tested. In a few countries, alkaloid surveys have been made on many of the living plants in various habitats; e.g., in New Guinea (Hartley, et al., 1973), in Congo-Brazzaville (Bouquet, 1972; Bouquet and Fournet, 1975). It appears that in the rain forest the percentage of positive species is not very high. Furthermore, the percentage of crude alkaloid weight is generally low in most of the species. In New Guinea where chemical analyses were conducted (after species were screened in the field for the presence of alkaloids), the results for the characteristic plants of the lowland rain forest were: 18 positive species of a total of 93 tested species (20 percent) with 13 species with less than 0.5 percent (dry weight) and only 5 species between 0.5 to 6.5 percent (dry weight) (Hartley, et al., 1973).

It seems more important, however, to discuss the total biomass of species which contain alkaloids rather than merely species numbers. A preliminary estimate of alkaloid content and its relation to leaf production in a rain forest (Table 6) is given according to our species-by-species leaf-litter analysis. Tree and liana species are listed in decreasing amounts of leaf production by dry weight. The results of the tests concern fresh or dry mature leaves, or both. To complement these data, we added an index of insect folivory for herbarium specimens (there is a bias because the best available plant material has been chosen for herbarium specimens; nevertheless, comparison between species is possible). Comparative data are given from Bouquet's work in the Congo and the Ivory Coast. Alkaloids are distributed without any outstanding difference between tree and liana species; between rare and common species, or between emergent and medium species. Neither is

Table 6.—Alkaloids and other secondary compounds in leaves related to leaf production in the Ipassa forest.

The production shows the relative importance of the different species (by dry weight) collected in 40 sampling baskets (31.8 m^2) during 11 months. Alkaloid tests (Mayer (M) and Dragendorff (D)) were made on fresh material and on herbarium specimens (in parentheses).

Tree species	*Leaf production (g dry weight)*	*Alkaloids tests*		*Insect folivory*	*Comparative data (mostly from Bouquet, et al., 1972, 1974, and 1975)*
		M	*D*		
Panda oleosa	1272	+ + (−)	+ + − (−)	0	Alkaloids in bark and roots
Scorodophloeus zenkeri	742	− (+?)	+? (+)	0	
Plagiostyles africana	543	+ (+)	+ (+)	0	
Piptadeniastrum africanum	476	− (−)	− (−)	2	Saponins in leaves; alkaloids in bark and roots
Pentaclethra eetveldeana	152	− (−)	+? (−)	0	Saponins in leaves; alkaloids in bark and roots
Coula edulis	371	− (−)	− (−)	1	Tannins in bark
Polyalthia suaveolens	367	+ + + + + + (+)	+ + + + + + (+ +)	2	Alkaloids in bark and roots
Santiria sp. II	332	− (+?)	− (+ +)		Tannins in bark and roots of *Santiria trimera* s.l.
Santiria sp. I	92	+? (−)	+? (−)	2	
Ficus sp. 1744	332	(−)	(−)	0	
Macaranga barteri	313	(−)	(+)	2	
Celtis tessmannii	285	(+ +)	(+ + +)	1	No alkaloids in leaves, but in bark
Petersianthus macrocarpus	274	− (+)	− (+)	0	Tannins in leaves
Dialium sp. 2142	269	(−)	(−)	3	
Strombosiopsis tetrandra	229	(−)	(−)	2	No secondary compounds
Gambeya beguei	181	+ (−)	+ (−)	0	No alkaloids
Pausinystalia macroceras	166	+ + + (+ +)	+ + + (+)	0	
Heisteria parvifolia	134	+ + (+)	+ + + (+)	0	Tannins in bark and roots
Sorindeia nitidula	123	(−)	(−)	1	
Coelocaryon preussii	129	(−)	(−)	2	Saponins and tannins in bark and roots
Ongokea gore	127	(+)	(+)	0	Saponins in leaves
Baphia pubescens	103	(−) (−)	(+) (−)	2	
Blighia welwitschii	103	(−)	(−)	0	Saponins in leaves
Eriocoelum macrocarpum	100	(−)	(−)	2	
Anonidium mannii	99	+ (+)	+ (+)	2	Alkaloids in leaves

Table 6.—Alkaloids and other secondary compounds in leaves related to leaf production in the Ipassa forest. (Continued)

Tree species	*Leaf production (g dry weight)*	*Alkaloids tests*		*Insect folivory*	*Comparative data (mostly from Bouquet, et al., 1972, 1974 and 1975)*
		M	*D*		
Dialium sp. 1462	88	(−)	(−)	2	
Pycnanthus angolensis	66	(−)	(±?)		No secondary compounds
Alstonia congensis	63	+	+	0	Alkaloids in bark
		(−?)	(−?)		
		(+)	(++)		
Markhamia sessilis	63	(−)	(−)	1	Saponins in leaves; alkaloids in roots
Irvingia gabonensis	58	(+?)	(+)	0	Tannins in bark and roots
Drypetes gossweileri	57	(−)	(+)	2	
Cola rostrata	50	−	−	3	
		(−?)	(−?)		
Lianas species					
Combretum spp.	872	−	−	1	Tannins in leaves of some *Combretum* species
		(−)	(−)		
		(−?)	++		
Neuropeltis acuminata	576	−	+	2	
		(+?)	(++)		
Entada scelerata		(+)	(−?)	0	
Dalhousiea africana	548	(+?)	(+?)	2	
Uvaria sp. 2075	494	(−)	(−)	2	
Tetracera alnifolia	356	(−)	(−)		Flavones in leaves
Cylindropsis parvifolia	343	(−)	(−)	0	
Pycnobotrya nitida	225	−	+?	0	No secondary compounds in bark
		(+?)	(+?)		
Entada gigas	187	+	+?		Saponins in leaves and bark
		(−)	(−)		
Salacia sp. 2589	183	+++	+++		
		(+)	(++)		
Urera cameroonensis	163	−	+		
		(−)	(−)		
Castanola paradoxa	117	(−)	(−)	3	
Dictyophleba stipulosa	107	(−)	(−)	3	
Dichapetalum mombuttense	77	(−)	(−)	0	Alkaloids in roots of other species
Cissus dinklagei	57	−	−		
		(−)	(−)		

there a clear relation between our estimation of insect feeding damage and that of alkaloids in the leaves.

In addition, for a few species, both young and mature leaves were tested. On the fresh material, we obtained more precipitate in the mature leaves than in young ones, but too few species have been tested in this respect. When testing a similar dry weight, the amount of precipitate was either similar or higher in the young leaves. It is difficult to formulate a firm conclusion since proteins are very abundant in young leaves, and may contain precipitate instead of the alkaloids. In any case, in terms of fresh weight, young leaves have more diluted alkaloids and it is likely that they have a low toxicity for most folivorous species.

The presence of alkaloids and other secondary compounds perhaps has been selected for by the pressure of animals which feed on plants. For example, insects feeding on leguminous seeds may exert selection pressure for the presence of alkaloids (Janzen, 1969, 1971, 1973). The presence of tannins in mature oak leaves may be related to a similar evolutionary process of the plant such as chemical bonding with proteins to prevent digestion by caterpillars (Feeny, 1969, 1970). Other work is currently in progress concerning insect feeding on shoots of Meliaceous trees (Grijpma, 1976). Freeland and Janzen (1974) recently reviewed herbivory in mammals. Unfortunately, data concerning arboreal mammal folivory and leaf toxicity in a rain forest are scarce. It is important, however, to note that most tropical trees which have been tested have larger amounts of alkaloids in bark, roots, or seeds than in leaves (according to the preliminary screenings for alkaloids by Bouquet, 1972, Bouquet and Fournet, 1975). Whittaker and Feeny (1971) defined allelochemics according to their ecological functions, one of which is plant interspecific competition. It is not surprising to find larger concentrations of allelochemics in roots than in leaves where eventual precursors might not be toxic. In temperate regions toxicity by root exudates as well as leaf exudates has been demonstrated (e.g., leachate of *Adenostoma fasciculatum* foliage, Muller and Chou, 1972). In any case, various patterns in alkaloid physiology might exist as suggested by McKey (1974).

Conclusion

In a rain forest, little is known about the specificity of insect leaf folivory. What is known is that the impact of insect folivory on leaf production may reach 10 percent of the total litter-fall (Leigh and Smythe, 1978). For primates and for many other vertebrates, the diet of folivorous species may include a small number of plant species; but two groups of the same folivorous species living in nearby areas may feed on a different set of plant species (Hladik and Hladik, 1972; C. M. Hladik, 1978; Richard, 1973, 1978; Rudran, 1978). Different individual sloths may also have different species of "modal tree" (Montgomery and Sunquist, 1975, 1978). In any case, the impact of the folivorous vertebrate populations is low; they do not eat more than 1 percent of the total leaf production of a rain forest (C. M. Hladik, 1978; Montgomery and Sunquist, 1975; Leigh and Smythe, 1978). Because they utilize only a limited set of plant species, their distribution is mainly determined by the complementarity of the various leaf phenological patterns of lianas and trees in their various co-existing phases of development and growth activity. The plants chosen as food by vertebrates can be related to the composition of the leaves in terms of primary compounds. By contrast, secondary compounds have less influence on vertebrate food choice (see C. M. Hladik, 1978). For invertebrates which are in fact the main consumers (see Leigh and Smythe, 1978), the process of food selection might be different owing to a long history of co-evolution, but further data are still necessary to support the hypothesis concerning insects and leaf co-evolution in rain forests.

Summary

An evergreen tropical forest of Gabon has been studied in terms of its ecology. Profile and projection maps contributed to an analysis of this heterogeneous, species-rich forest. Different ecotopes are described and related to the ecology of the resident vertebrate fauna.

The total leaf litter-fall (6.5 T/ha/year) in the Ipassa forest is similar to other observations in the tropics. It varies throughout the year with a minimum during the major dry season. A climatic pecularity of Ipassa is the lack of direct sunshine in the dry season. Various leaf phenological patterns are shown by different types of tree and liana species. New leaves generally grow at the beginning of each rainy period. Deciduous trees play an important role in the availability of food for leaf-eaters, because they give a localized mass of young leaves at different times of the year. A quantitative estimate of the young leaves available as food is presented.

The toxicity of leaves of tree and liana species in the tropics is still subject to discussion because not enough data are presently available. According to our biochemical analysis of food plants (in different

primate diets of various countries), plant species are chosen according to their richness in nutrients, the young leaves especially showing a greater amount of proteins and soluble sugars than mature leaves.

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Complications in Interpreting the Chemical Defenses of Trees Against Tropical Arboreal Plant-eating Vertebrates

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Introduction

At first glance, the interaction between tropical trees and arboreal plant-eating vertebrates seems relatively straightforward: the animals eat what they can according to their detoxification abilities, and this selects for further or different chemical defenses in the tree population, provided that appropriate mutations occur, and if the fitness of the average tree of that species is reduced more by the herbivory than by the cost of the defense. Considerable publicity has been given to this topic in the recent past. It is a philosophy familiar to all at this conference. The plant world is not colored green; it is colored morphine, caffeine, tannin, phenol, terpene, canavanine, latex, phytohaemagglutinin, oxalic acid, saponin, L-dopa, etc. We now hunger for the details so that we can anticipate their application to our particular case studies. The details are slow to come, because it is hard to know what is in a tree from the viewpoint of a monkey, sloth, or koala, because it is hard to know how much a given amount of herbivory depresses the fitness of a plant, and because it is hard to know what a defense costs a plant. Having never worked on arboreal vertebrates myself, I will here attempt to glean from the studies of others factual or conceptual information that, in my opinion, threatens the above conceptual scheme with far more complexity than it appears to have on the surface.

"One Monkey's Poison Is Another . . . "

Strychnine is a well-known alkaloid that is very poisonous to carnivorous animals. Eight ounces of the powdered bark of *Strychnos nux-vomica* (Loganiaceae) sewn into the abdomen of a fish is lethal to a large crocodile a few hours after the fish is eaten. Furthermore, the strychnine moves up the food chain; the flesh of the crocodile is then toxic to dogs and humans (Zobairi, 1948). Such concentration in the consumer's flesh is not universal, however, since "in the Yangtsze estuary it is the practice of wild-fowlers to incorporate the seeds of strychnine fruits with small garlic bulbs as a bait for wild birds" (Herklots, 1933).

The other side of the coin is displayed in a doctor's battle with Kenyan fruit bats (*Epomophorus wahlbergi*) that were stealing his *Passiflora* fruits (Jex-Blake, 1931). He injected the fruits with drugs and estimated that 1 to 2 dozen bats consumed 67 grains of strychnine, 12 grains of KCN, 6-7 grains of perchloride of mercury, and 20 grains of white arsenic, but apparently with no deaths (one grain equals 0.0648 gm). He estimated this to be enough strychnine to kill 35 to 40 persons (12 grains kills a lion, 6 a tiger or leopard). In corresponding with an Australian, he learned that strychnine put in apples or in honey on fruit surfaces kills *Pteropus* fruit bats immediately. *Epomophorous* lives in and around African forests where juicy yellow strychnine-rich fruits occur. One might predict that *Strychnos* does not occur in Australia. However, there are two species of *Strychnos* there (Bentham, 1869). One can predict with some safety that *Pteropus* does not eat their fruits. It has been rumored that the fruit flesh is harmless and that only the seeds are poisonous (Dixon, 1894; Willis, 1966). In 1894, Prebble mixed the pulp of a large fruit with half an ounce of water; this dose taken orally killed a cat in 10 minutes. A 2-month old dog was killed in 18 minutes after ingesting 5.6 grams of fresh pulp of a *Strychnos nux-vomica* fruit. Something less than 1 gram of pulp had no effect on a pigeon, but 2 grams killed it. Dixon (1894) says that in India only the pied hornbill (*Buceros malabaricus*) eats the fruit.

Given this confusing background, let me note that Dixon (1894) also stated that "among monkeys, the only creature that is extremely fond of the fruit of *Strychnos nux-vomica* is the dark-faced monkey, *Semnopithecus entellus*, the langur or hanuman of Western India. Blanford says certain vegetable poisons are said to be taken by *Semnopithecus entellus* with impunity, doses of five and even ten grains of strychnine having been given to one without effect, although the same drug killed *Macacus rhesus* quickly." Dixon then goes on to note that *Macacus sinicus, M. pileatus*, and village cattle do not eat the fruits when available.

What if we accept Dr. Powell's conclusion (Mitchell, 1910) that "as a whole carnivorous are more sensitive than herbivorous animals to the common poisons . . . monkeys and fowls are unaffected by doses of strychnine that would kill a pack of hounds?" Most of the toxicological tests of naturally occurring secondary compounds have been carried out on animals that never encounter the putative toxins in nature, and we may well discover that our understanding of toxicity to wild herbivores is not only minimal, it is misleading. Let us assume for the moment that most strongly herbivorous mammals are in fact highly resistant to strychnine taken orally. One is immediately forced to the conclusion that the evolution or elaboration of strychnine as a chemical defense by certain plants was probably driven by insects, fungi, or other types of herbivores. Alternatively, its presence in fruits may be adaptive in deterring species of animals whose gut would destroy the seeds or animals whose defecatory behavior places the seeds in the wrong place. Such compounds may also prevent an animal from eating too many of the fruits at a time. It would be a clever mechanism indeed that forced the frugivore to eat only a couple of fruits before becoming ill, thereby maximizing the spread of the seeds among the appropriate frugivore population. All tropical field biologists have probably had the experience of eating wild fruits, only to have a violent sore throat after the second or third fruit.

But then what do we do with the knowledge that something over 60 kinds of alkaloids have been isolated from the South American *Strychnos toxifera* (Leonard and Sherratt, 1967), and it seems probable that similar numbers of alkaloids occur in the Old World members of the genus? Since many of the anecdotes mentioned above are based on feeding fruit pulp, it is possible that secondary compounds other than strychnine are producing the variable effect. Perhaps it is comforting to know that strychnine poisoning only leads to death through violent muscle tetanus—the mind is perfectly clear until death (Kirtikar, 1894).

Filtering Out Apparent Dispersal Agents

In pollination biology, one has to distinguish carefully between pollinators and visitors (though the distinction is often poorly made). It is equally important in examining the impact of vertebrates on tree fruits and seeds to distinguish between those that disperse the seeds to sites optimal for the plant and those that merely disperse the seeds (or perhaps worse, prey on them). Just as pollination biologists have not dealt with the relative merits of different actual pollinators (but have recognized that many flower traits are adaptive not in attracting pollinators but in keeping out visitors), dispersal biologists have not dealt with the adaptive significance of the various kinds of seed shadows generated by various combinations of vertebrates that move tree seeds. In the previous section, I mentioned that village cattle and macaques avoid the fruits of *Strychnos nux-vomica* in India, while langur monkeys are very fond of them. These differences presumably are due to the differential effect of strychnine on these different potential dispersal agents, and should generate quite different seed shadows than if the fruits were innocuous. Several other examples come to mind.

A substantial portion of the tannin-rich natural products exported from India are, or were, in the form of myrobalans, which are the dried fruits of the combretaceous tree, *Terminalia chebula* (Combretaceae), and other related species (Hathway, 1959). The fruits look just like those of the closely related *Terminalia catappa* or "almendro" of neotropical beaches. There are two somewhat surprising statements available. First, the fruits of *T. chebula* are highly sought after as food by rats, squirrels, pigs, deer, monkeys, and porcupines (Hathway, 1959; Howes, 1953). Second, the fruits contain 25 to 53 percent dry weight hydrolyzable tannin (Hathway, 1959). To give the reader some feeling for what this means, the flesh (endocarp) of a green banana contains about 8 percent tannin. One's first reaction is that this high tannin concentration in the ripe chebula fruit, around an apparently mammal-dispersed seed, is probably to repel certain vertebrates in favor of those that are relatively insensitive to tannin, or even to insure that no one animal eats large numbers of the peachlike fruits. That may be all there is to it, but consider the following.

Howes (1953) and others have stressed that tannins are very potent inhibitors of fungal spore germination; a juicy fruit lying on the forest floor is an obvious candidate for fungal attack, especially since the skin is likely to have been broken in falling and the ground beneath the tree should be covered with the spores of those fungi that regularly grow on the rotting fruit of the species. Fungi (as well as bacteria) and vertebrates are conspicuously competing for the fruit (Janzen, 1976). There should have been very strong selection in the past for fungi and other microbes that render the fruit inedible or unattractive to the mammal as rapidly as possible, thereby placing intense selection on the tree to produce a fruit resistant to fungal attack. In short, the tannins may be there to *increase* uptake of the fruit by mammals.

The conclusion that tannins are functional in selectively eliminating fruit-eating vertebrates is supported in part by a conclusion that may be derived from Howes' (1953) survey of the sources of high concentrations of vegetable tannins. There are two kinds of tannins, nonhydrolyzable and hydrolyzable, with the latter type potentially much more easily degradable by the gut of animals than the former. While both kinds are known from most parts of woody plants (with nonhydrolyzable types by far the more common), all the commercial sources of hydrolyzable tannins are ripe fruits (e.g., *Terminalia* spp., *Acacia* sp., *Caesalpinia coriaria*) or galls (the association of hydrolyzable tannins with galls is due to other causes not under discussion here). No ripe fruits are commercial sources of nonhydrolyzable tannins. One can conclude from this that, whereas the adaptive value of nonhydrolyzable tannins may be purely defensive, hydrolyzable tannins may be adaptive in eliminating certain organisms while encouraging or at least not severely deterring others.

The previous paragraph leads me to argue that certain tropical mammal-dispersed fruits should be a major source of antibiotics of all kinds, not just hydrolyzable tannins. For example, I have found that the ripe fruit of *Andira inermis* in Costa Rica is very resistant to mold and bacterial growth, even when diced with dirty field tools. However, if the diced fruit is then heated in an oven at 200–300° F. for 30 minutes, many kinds of fungi and bacteria immediately grow copiously on the flesh. It appears that there is a heat-labile antibiotic in the flesh of these bat-dispersed fruits. While bats avidly feed on these fruits, they are ignored by semiferal pigs and cattle. Is it possible that this aversion is not due to directly toxic secondary compounds, but rather to the effects of the postulated antibiotic on the microflora of the vertebrate? Here there may well be a balance between putting enough antibiotic in the fruit to greatly slow fruit decomposition, but not enough to seriously damage the gut microflora of the appropriate dispersal agent. It is of interest here that antibiotics as feed additives increase nutrient utilization by poultry, swine, lambs, and calves, but only slightly or even negatively influence the same parameter for adult ruminants (Hungate, 1966). In short, the plant with ruminant dispersal agents should have severe constraints put on the ways it can protect its fruits from microbes, and the ruminant may have to be more careful about the ripe fruits it eats than would be required of a nonruminant. If a vertebrate has a gut flora finely tuned to the leaves of the particular plants locally available to it, the antibiotics in a stomach full of fruit could cause a highly detrimental disruption. This may explain why animals that eat a lot of leaves often pass up trees full of seemingly innocuous ripe fruit.

In case anyone should feel that it is of little importance which particular microbe community a ruminant has in its gut, and thus the dangers of antibiotics in food are little, let me cite Pienaar's (1968) advice for moving the smaller antelopes from place to place in South Africa. He says, "If the quality and composition of the vegetation of the new habitat varies much from that of the area of capture, it is essential to dose the animals orally with a few ccs. of rumenal fluid of some local ruminant or the fresh dung of local ruminants shaken up in water, in order to prevent fatal digestive disturbances."

It is often difficult to know if a fruit is highly desirable to all of the vertebrates in the habitat, since all the fruits may be quickly eaten from the tree or immediately after falling. In Africa, however, certain large vertebrates are selectively removed by hunting, and the resulting experiment can be instructive. For example, in the central part of Kibale Forest, Kanyawara (near Fort Portal, Uganda), elephants have been eliminated. Other mammals have been reduced but not eliminated. There are several large *Balanites wilsoniana* trees that drop bushels of large juicy fruits in late October. The fruits carpet the ground, a ground that has hundreds of fresh tracks of pigs and other ungulates. The forest overhead contains at least 5 species of monkeys, all of which eat fruit on some occasion. There are arboreal squirrels and terrestrial rodents in the forest. I could find no evidence that any animal was feeding on the fallen *Balanites* fruits. (Tom Struhsaker and Doyle McKey inform me that pigs and squirrels eventually consume the seeds over many months, but they are not after the fruits.)

Bill Freeland then took me to several *Balanites* trees in the Kibale Forest Nature Reserve (where elephants still occur in moderate abundance). The ground beneath these trees was beaten flat by elephant feet, there were heavy trails converging on the *Balanites* trees, and there was not a seed or fruit left in the area. There is a record of a wild African elephant with 1000 *Balanites aegyptica* in its gut (Buss, 1961; earlier, I erroneously referred to these as "date palm seeds," Janzen, 1971a).

So why should most animals ignore *Balanites* fruits and elephants eat them in great numbers and so avidly? I cannot answer this question from the tree's viewpoint, but the physiological reason must involve incredible resistance by elephants to diosgenin (a sapogenin), a generally toxic plant steroid and the precursor molecule for the manufacture of cortisone, sex hormones, and antibiotics. The ripe fleshy fruit of at least 4 species of African *Balanites* contain 4 to 8 percent diosgenin on a dry weight basis (Hardman, 1969). This is the same concentration as is found in the tubers of various wild species of *Dioscorea* (Hardman, 1969), the tubers of which are not dug out and eaten by the same species of pigs (and others) that are largely ignoring the *Balanites* fruits on the ground in Kibale forest. When one understands what cortisone and sex hormones do to humans, it is not surprising that the ripe fruits of *Balanites* are not eaten by the monkeys in Kibale Forest.

It should be added that the apparent high resistance of elephants to a steroid sapogenin is probably not part of a generally exceptionally high resistance to secondary compounds by elephants. For example, Pienaar (1968) points out that in drugging for live capture, elephants are much more sensitive to the action of neuroleptic-analgesic drugs than are most other large animals. While it takes 2 to 4 micrograms per pound of Etorphine to immobilize most ruminants, 0.47 to 0.67 micrograms per pound brings down an elephant. Of course, the brain/body weight ratio of an elephant is much smaller than that of ruminants, and that may be the whole story. On the other hand, it is simultaneously likely that there is strong interspecific physiological heterogeneity that should be reflected in feeding preferences.

In closing this section, a balanced presentation requires me to note that the variations in preference shown by vertebrates toward tropical fruits could be a purely capricious outcome of secondary compound content selected for by herbivorous insects and microbes. This possibility cannot be eliminated until we understand something of the adaptive value to trees of the various seed shadows generated (or potentially generated) by various combinations and intensities of fruit eaters.

What Is Toxicity?

In almost all cases an animal expends energy and resources in converting what is eaten into usable materials. "Toxicity" can only be operationally defined as that case where the energy and resources expended are greater than the return in usable materials, or worse, adequate energy and resources are not available to counter or nullify the biological activity of something eaten. Toxicity thus becomes defined as an outcome and is not an inherent property of any chemical. This is, of course, not to ignore the fact that certain chemicals are commonly easily dealt with (e.g., starch) and certain ones are commonly very toxic (e.g., caffeine). Bearing this definition of toxicity in mind, it immediately becomes obvious that toxicity is a measure of the difference between the gain by the animal and the loss, and therefore as the nutrient content of a food item increases, its toxicity may decrease even though the absolute or percent content of the secondary compound stays constant. In short, a vertebrate may elect to pay a few grams of liver for a large amount of nutrient (see Freeland and Janzen, 1974). Such trade-offs might be expected to be most frequent where the liver damage can be recovered at a later time of year, or where the liver damage allows the intake of nutrients that will get the animal through a particularly stressful period such as a dry season, even though continuous intake of such food would be lethal. In other words, the vertebrate may starve at a slower rate by eating food containing harmful secondary compounds than by not eating at all.

While the phenomenon may be common, Doyle McKey (1978) has begun the elaboration of what is probably going to be the best case on record. McKey argues that a monkey (e.g., black colobus in Cameroun) may consume seeds with high levels of potentially dangerous secondary compounds in them, while ignoring mature leaves with similar concentrations of secondary compounds, because the reward of nutrients is much higher from a gram of seed than a gram of mature leaves. Thus, the seed is not toxic, but the leaf is, and yet they have the same secondary compound concentration. In like manner, mangabey monkeys in Kibale forest near Fort Portal, Uganda, may feed on a nearly pure diet of nearly ripe but incredibly foul-tasting *Diospyros* seeds for weeks at a time (William Freeland and Peter Waser, personal communication). While it may be that the animals are simply immune to compounds that have strong physiological effects on other animals, herbivore-plant studies have simply ignored the possibility that the animal trades considerable damage for high-nutrient intake.

There may be a strategic complication for arboreal mammals that promotes the consumption of foliage and other plant parts that are very rich in potentially toxic compounds. Virtually all plant-eating vertebrates are periodically confronted with very large amounts of high-quality food that potentially can be converted to fat and muscle reserves to be used in lean times (though vertebrates inhabiting the forest crown perhaps least frequently have this opportunity). The tropical ground-inhabiting vertebrates do build up fat reserves, as carried to the extreme in pigs, human steatopygia, fat-tailed sheep, camel humps, Zebu cattle humps, etc. "The East African investigators reported that Zebus which were cut off from water completely, stopped eating and metabolized fat. Both fecal and urinary losses were drastically reduced and the animals were stated to live comfortably without water for two months at 22°C or until their supplies of fat were depleted" (Ferguson, 1971). Such a terrestrial animal might rarely be in a circumstance where it was forced to trade damage for food, such as by eating evergreen foliage during a tropical dry season.

For an arboreal mammal, however, accumulation of fat reserves means lowered distances that can be jumped, harder impact in a fall (and Old World monkeys fall amazingly frequently), more work in sustained suspension, lesser agility in negotiating difficult climbs, reduced volume of the canopy that can be entered, and greater chance of branch breakage anywhere in the tree crown. Thus, one might expect the most sedentary arboreal mammals to be those with the most fluctuating weights; ironically, the most sedentary arboreal mammals—sloths, koalas, and proboscis monkeys—are all specialists on a diet made up largely of mature leaves and poor in species, probably the most difficult diet on which to build up a large fat reserve (though likewise the one on which a fat reserve is least useful owing to the seasonal omnipresence of the food). In short, one would expect grass- or seed-feeding ground-inhabiting vertebrates to be the most likely to build up fat reserves and use those to pass times of food shortage, and arboreal leaf-eating vertebrates to be the most likely to have few reserves and shift onto food sources that were rich in both nutrients and defensive compounds in times of food shortage.

What About Fatty, the Monkey?

In the previous section, I briefly suggest that the extra weight of fat deposits might make life acrobatically difficult for an arboreal vertebrate, and that the lack of fat might at times force feeding on foods rich in secondary compounds. Here I would like to suggest that lacking fat deposits may further complicate the life of an arboreal leaf-eater when she is reproducing. When a fetus is developing, the herbivorous parent is expected to become more discriminating for two reasons. First, secondary compounds that might circulate in the mother's system with little harm might be lethal to the growing fetus. Second, a large number of secondary compounds induce vomiting and other forms of contraction of the muscles in the abdomen; many naturally occurring human abortants affect the gut in exactly the same way. As Kirtikar put it in 1893, "it has ever been held a golden rule in pregnancy not to give acrid or powerful purgatives at any time during pregnancy," as peristalsis of the lower abdomen is "contagious." Obviously, it is easier to be discriminating in food choice if one has a large fat reserve than if one has to live on one's daily intake, and I may note that the mother not only has to provide food for the growing fetus but do it with some regularity. A fat body could be all-important in providing the regularity. Of course, the mother may elevate her physiological defenses at the time of pregnancy (at a cost, however). For example, Pienaar (1968) noted that pregnant female gemsbuck were particularly resistant to the drug Etorphine.

Once the baby is born, the problem gets worse, not better. First, secondary compounds taken in food can still find their way into the milk. We have all experienced this with cows raised on different pastures. Second, the period of lactation is generally regarded as a larger strain on the mother's resource budget than is pregnancy (Pond, 1977). To keep herself alive and to provide a flow of milk in the absence of a fat body, the mother must either greatly attenuate the juvenile's development, trade a lot of her own defense system for high rates of nutrient input from very damaging plant tissues, or belong to a species sufficiently specialized on a set of leaf species that the juvenile can begin to eat leaves at an early age.

Vertebrates as Doctors

To this point I have been considering secondary compounds as neutral or damaging in some way to the vertebrate; however, the leaf-eater is a whole system, not just a gut. If a mammal can evolutionarily or contemporarily learn to avoid certain plant parts because they lower its fitness, it may also learn to seek out certain plant parts because they raise its fitness when searching for nutrients. This point is unquestioned, but I would like to ask if plant-eating vertebrates may do it on occasion as a way of writing their own prescriptions.

My question can perhaps be best answered by giving a few of the many examples sprinkled in the older literature. "I have often noticed, when following solitary elephants, that, when they fed extensively on a certain creeper known to Malays as *akar beluru* and to Science as *Entada schefferi* (leguminosae), they invariably traveled far after such a meal. Possibly that creeper has some sustaining effect on the elephant which acts as an incentive to greater and unusual effort" (Hubback, 1941). Or perhaps it acts as a pain killer, when the elephant has made a decision to take a long walk. Freeland has noted that the feces of black and white colobus and red colobus monkeys in Kibale forest are relatively free of protozoan parasites while those of more omnivorous primates have many. It is tempting to postulate that this is due to the steady flow of secondary compounds from the foliage that they eat. Ogilvie noted in 1929 that Indian bison regularly eat the bark of *Holarrhena antidysenterica* (Apocynaceae); while this may of course be in search of trace minerals, it may also be related to the specific epithet of the plant.

Through some rather gruesome trial and error, McCann (1932) devised a cure for tapeworms that involved drinking a concentrated extract of pomegranate (*Punicum granatum,* Punicaceae) roots. In 1940, Caius noted that pomegranate root bark contains an alkaloid that is highly toxic to tapeworms. Mexican folklore has it that pigs are very fond of pomegranate roots. An extract of *Boerhavia diffusa* (Nyctaginaceae) plants has traditionally been used in India as an antihelminthic, its common name is pigweed, and Indian wild boars have been recorded selectively digging out the roots and eating them (Dharmakumarsinhji, 1960). Since pigs customarily carry large internal populations of nematodes, it seems quite reasonable that they could learn or inherit the habit of seeking out antihelminthic plants. A number of large carnivores eat the stomach and intestinal contents of herbivores they kill. McCann noted in 1959 that civets and jackals are avid fruit-eaters, and some of the fruits act as purges. Burton (1952) comments that Indian tigers and wild dogs avidly seek out the fruits of *Careya arborea* (Barringtoneaceae), while bears and wild dogs are very fond of the fruits of *Dalbergia latifolia* (Leguminosae).

All of these preferences may be nothing more than nutritionally based, but it is also possible that they are based on the elimination of intestinal parasites. Enterovioform, a common antidysentery formulation, is about 50 percent dry weight tannin, which does not differ much from the *Terminalia* fruits mentioned earlier. The nonruminant Asiatic two-horned rhinoceros has been recorded as eating so much of the tannin-rich bark of the mangrove, *Ceriops candoleana* (Rhizophoraceae), that the urine was stained bright orange (Hubback, 1939). Such a concentration of tannin could easily affect parasitic organisms in the bladder or urinary tract.

One of the most effective chemoprophylactics for schistosomiasis is extracted from the fruits of the Brazilian *Pterodon pubescens* (Leguminosae) (Mors, et al., 1967), and it would seem to require little coevolution for such a fruit to be eaten by wild animals for its medicinal properties rather than for its food value. It is of interest in this context that the antihelminthic seeds of *Citrullus vulgaris* and *Cucurbita maxima* (both Curcurbitaceae) have been eaten for that purpose in China since ancient times (Crook, 1935; Aikman, 1974); in India, the southern mole rat (*Gunomys kok*) seeks out *C. maxima* fruits and eats the seeds, and the Indian desert gerbil (*Meriones hurrianae*) does the same with the seeds of *Citrullus colocynthis* (Ayyar, 1931; Prakash, 1972). Finally, I might note that there may be many cases where the plants eaten are taken in as an antidote for toxins in other plants eaten earlier. Indian elephants are occasionally killed by the large amount of cyanide in green Koda millet (when raiding crops) (Morris, 1934; Pillai, 1954). Pillai (1954) lists tamarind fruit, plantain stems, and astringent guava juice as antidotes, plants which could easily be eaten at the same time and simply construed as part of the elephant's search for nutrient.

Carried perhaps to an extreme, it is even possible that primates and other arboreal herbivorous vertebrates use various combinations of foods to regulate the rate of passage of foods through the gut. Vomiting and diarrhea are clearly adaptive in ridding the intestinal tract of toxins. It seems quite plausible that, for example, a leaf-eating monkey might mix fruits with the leaves in various proportions in order to keep the entire intestinal charge moving at a desirable rate. Furthermore, I suspect a monkey that is overdosed on leaf toxins would seek out and consume large amounts of fruits that would flush out the system.

Comparison of Vertebrates and Insects as Arboreal Folivores

To this point I have been dealing with some of the reasons why vertebrates may or may not feed on leaves and fruits, but this presupposes that they are there to be fed on. Although no measurements have ever been made of the amount of leaf material actually eaten by insects from the overall canopy of a mainland tropical forest (see Leigh and Smythe, 1978 for some estimates), it is obvious that there are a lot of them there feeding on leaves, seeds, and fruits. The kinds of damage they do range all the way from complete defoliation of a crown and removal of an entire seed crop, to the selective elimination of a very few shoot tips. Additionally, we have no idea what fraction of what they eat could have been eaten by a vertebrate had it not been eaten by an insect. Even before such data are available, however, we can outline several quite different ways that plant-eating insects can influence what is available to vertebrates. I mention them here simply because they seem to be generally ignored in attempts to reconstruct overall herbivore communities. In one sentence, plant-eating insects will undoubtedly influence plant-eating vertebrates in the same sorts of ways that they influence other plant-eating insects.

Tropical insects do defoliate, at times totally, their host plants. I have numerous examples of this recorded in Costa Rica, and there are many cases in the older literature. Many of the examples are from trees growing in pastures, roadsides, villages, etc., but there is total or severe defoliation of trees in natural forest as well. It is of course less conspicuous in a mixed forest than in a monoculture, but nevertheless occurs there. The question is, does this result in less food for the vertebrates in the area? Of course it does in some absolute overall sense, but there may be a more explicit sense.

Several authors (Miles, 1968; Green and Ryan, 1972; Sumway, et al., 1972) have emphasized in recent years that a standard response to having part of a leaf fed on is for the plant to increase the concentrations of secondary compounds in the area of the wound and even in the other leaves on the same branch. They have worked with crop plants, but I suspect the same process in wild tree leaves as well. If it does occur in tree leaves, the tree could well respond to defoliation by making the remaining leaves less edible or the new crop of leaves less edible. For example, when the rainy season begins in lowland Guanacaste Province, Costa Rica, the large deciduous tree, *Bombacopsis quinata* (Bombacaceae), produces a crop of tender new leaves. If the tree is growing within the foraging range of a leaf-cutter ant nest, it is guaranteed to have the entire leaf crop eaten or cut off. The tree responds by producing a second crop of leaves which invariably is not touched by the leaf-cutters. There are two interpretations. First, the leaf-cutter ant may be a prudent harvester and, if it is, it is without doubt one of the brightest herbivores in the community (see the following section). Second, the second crop of new leaves may be chemically quite different from the first. These leaf-cutter ants are very sensitive to the defenses of their hosts, as demonstrated by their strong host preferences, and commonly cut but one age of leaves from a tree (Rockwood, 1973).

In short, it is quite possible that the feeding by herbivorous insects on the leaves of a tree changes the chemical content of the remaining and new leaves. Such a facultative response of secondary compound production is most expected in habitats where the herbivores are highly territorial but many of the members of a tree population are not included in at least one territory of the herbivore population in a particular year. It should be noted that this kind of competition among herbivores may work in the opposite direction when a vertebrate defoliates a tree, resulting in foliage less suitable for the insects that usually feed on that tree.

Insects and vertebrates may compete directly by simply eating those parts wanted by the other. I know of no documented cases of this with foliage. However, I can see it easily occuring with fruit-eaters and seed-predators. For example, an unidentified moth larva eats the molasseslike fruit pulp around the seeds of *Cassia grandis* (Leguminosae) in the lowlands of Costa Rica (Janzen, 1971b) and presumably lowers the food value of the pods to the mammalian seed-dispersal agents, as well as causing them to ignore the pods. When *Amblycerus cistelinus* larvae have eaten the seeds out of a *Guazuma ulmifolia* fruit (Janzen, 1975), there is no more food there for the mice, squirrels, deer, monkeys, or other vertebrates that eat the fruit for its seeds (although in some cases it appears that they are seeking only the fruit rather than the seed). Even this kind of interaction is ambiguous, however. For example, when bruchids attack the hard (and indigestible) seeds of various species of *Acacia* in Africa, they eat part but not necessarily all of the contents before a mammal consumes the indehiscent pod. Any seed fragments in the pod are now available to the mammal, whereas the unattacked seeds would have passed intact through the mammal (see Lamprey, et al., 1974).

Most important, insects and vertebrates may compete through the medium of the contemporary and evolutionary fitness of the host plant (Janzen, 1973).

On a contemporary time scale, one of the easiest ways to get a tree to abort its seed crop is to defoliate it (by insects, clippers, or other means) (e.g., Rockwood, 1973). This means that an insect outbreak in December may well result in a shortage of seeds for monkeys in August. This shortage may, in turn, result in very heavy seed predation on the trees that do fruit, with an eventual lowering of the density of adult tree crowns in which the insects can have their outbreaks, so to speak. Such interactions are undoubtedly numerous in tropical forests, but almost totally undocumented. They have the outstanding characteristic that the insects or the vertebrates may be having a huge influence on each other yet never come in contact. Furthermore, even if the vertebrate community is harvesting only 5 percent of the net productivity of the plant and the insect community harvesting another 5 percent, they may be competing very strongly, as the sum of 10 percent may well be the total loss that can be tolerated without the plant dropping out of the community, or grossly changing its density.

On an evolutionary time scale, arboreal vertebrates and insects may of course compete equally, as mediated through the defense repertoire of the plant. As insects select for certain chemical or behavioral defenses in a plant species, the vertebrates which obtain only a very small fraction of their total food from the plant may become innocent victims, much as are the fishes in the pesticide-polluted streams in Midwest cornfields. By relaxing their feeding pressure on a plant involved in a co-evolutionary arms race with insects (and virtually all are involved in such a race), such vertebrates do not gain a relaxation of defenses in evolutionary time. The vertebrates may well be confined in great part to making their living through fortuitously picking up what they can handle in a battlefield whose microstructure is determined by the insects and the plants. Obviously the truth to such a statement varies from habitat to habitat, with it being most true in most neotropical mangrove swamps (where there are virtually no arboreal vertebrate leaf-eaters) and perhaps least true in a medium-aged successional stand, such as the vegetation in the central part of Kibale forest near Fort Portal, Uganda, when it had its original complement of big herbivores as well as the primates still present (e.g., Struhsaker, 1978). At the extreme end, it is tempting to view the big mammals as the driving force behind the co-evolution of the grasses' predator-satiation escape behavior at the leaf level in the mammal-rich African grassland, with the insects being the innocent benefactors. Vertebrates can, of course, be major selective agents for chemical defenses in broad-leafed plants, but to do so they must have an impact on many individuals in the population, parasitize the plant with fair regularity, and lower the fitness of the plant more than does the average insect.

The Prudent Leaf-Eater

When should herbivorous arboreal vertebrates harvest less plant matter than they are physiologically capable of handling? This is a very difficult question because it skirts dangerously close to the precipice of deciding that vertebrates do things "for the good of the species," which is nonsense. However, it is not nonsense to expect a vertebrate to do things for the "good" of its offspring or other closely related individuals since it is thereby doing things for its own genes. Thus, there is a gradient from the case where the arboreal herbivorous vertebrate should be totally selfish to where it appears to be highly prudent in harvesting plant parts.

One would expect the most selfish herbivorous arboreal vertebrates to be the solitary species without territories (or even home ranges). Such an animal (and its offspring) is least likely to suffer the long-range consequences of having eaten plant parts so severely that plant species composition changes, or on the other hand if it was prudent, some other animal would merely move in and eat the unharvested resource. In short, if nothing is to be expended on defense of a site, the best strategy would appear to be to consume its resources as rapidly as possible and move on. Such a frontier behavior is rather familiar to *Homo sapiens*. As the population density increases (in evolutionary or contemporary time) to where there is no place to move on to, one would expect selection to favor home ranges and territories. The more erratically the plant parts are produced in space and time, the more likely that the population density will never increase to where it is advantageous to defend a territory.

At the other end of the spectrum, I would expect to find the most prudent arboreal herbivores in those cases where the food is regularly available and harvesting to physiological satiation has the chance of altering the availability of food for later years, and for later generations of closely related individuals. Animals that eat tree parts have a particularly good chance to do this kind of damage, as the turnover rate of tree populations is very slow when feeding pressure is relaxed.

There is a major dichotomy at this point. A seed-eating vertebrate and its offspring may harvest from adult trees for hundreds of years without substantially altering the species composition of the trees in their territory or home range. However, the more successional the site and the shorter the average life span of the tree providing the seeds, the less this should be true. It should be more true the more sporadically the seeds are produced and the more the tree species is involved in predator satiation. For example, it seems unlikely that seed-eating arboreal vertebrates could badly alter the species composition of Dipterocarpaceae in Malaysian dipterocarp forests, since the seeds are produced at long intervals, predator satiation is the escape mode practiced by these trees, and species composition is probably in large part set by seedling competition rather than host-specific seed-eating (Janzen, 1974).

On the other hand, arboreal folivores have a great chance of quickly altering the species composition of the tree species in their territory or home range. By repeated defoliation they will not only kill the tree (or reduce later seed and flower crops which may be of importance if eaten) but even lesser defoliations can result in tree removal through raising the chance that its crown will be crowded out by neighboring crowns. Defoliation by primates can also alter crown structure (Oppenheimer and Lang, 1969) and thus influence competitive outcomes among tree species. As mentioned earlier, these consequences of defoliation may be the selective pressure operating against arboreal social primates that might otherwise strip a tree of its edible new foliage and repeatedly return to that tree or branch to eat the new leaves as they appear. A territorial solitary arboreal vertebrate might only avoid this behavior if the consequences would be felt within its lifetime (which is progressively more doubtful the lower the species richness of the forest and the diet). On the other hand, a highly social unit that might hold a site for many consecutive generations could be expected to frequently avoid thorough defoliation of those edible tree species that, when damaged, are particularly likely to lose in competition with other tree species bearing less edible foliage.

Discussion

The complications described in this paper have severe implications for the field worker attempting to understand why an arboreal mammal eats a particular plant part and ignores many others on the same and different plants. Simply measuring the secondary compound content of the foliage of 2 tree species, for example, may only result in the observation that the foliage of both is rich in potentially toxic compounds. If a mammal eats one and ignores the other, one cannot then conclude that the secondary compounds are unimportant. One may even find that the one with the apparently less defended leaf is ignored while the better defended leaf is eaten. Whether a given secondary compound can be ingested without overall negative effects depends on the condition of the animal, the dose, the past experience of its inducible enzyme systems with the compound or related compounds, the past experience of its gut microflora with that compound, the simultaneous ingestion of nutrients, the simultaneous ingestion of synergists or antagonists of the secondary compound, the tasks to be asked of the animal's detoxification system and of the animal in the immediate future, the expectations of the animal for the later use of the habitat, the use of the secondary compound as a medicine, and the use of the secondary compound as a scent mark or pheromone. From studies on other animals in other circumstances, there is absolutely no way, other than very generally predicting, to know whether a given secondary compound will be detrimental if ingested. Carefully controlled and organized feeding trials are essential for understanding the impact of secondary compounds on feeding behavior of a particular species of animal.

The obvious experiments are easy with small and abundant animals, such as arthropods and molluscs (e.g., Cates, 1975; Cates and Orians, 1975; Rehr, et al., 1973a, 1973b), but it is going to hurt when we have to start experimenting with vertebrates, and especially the rarer arboreal ones, with poisoned food to understand the role of secondary compounds in their feeding choices. Perhaps the answer is to start with the more abundant pest species, such as the Australian opossums introduced into New Zealand (e.g., Fitzgerald, 1978), and work opportunistically with animals like sloths and primates when a habitat is slated for destruction anyway. We may never be able to determine which secondary compounds are severely detrimental to orangutans and gorillas, but if we can show to what degree secondary compounds are the cause of the dietary fingerprints for other primates, then it would seem safe to assume that the same processes underly feeding patterns for these rarer primates.

Now it is obvious that the kinds and concentrations of nutrients and secondary compounds in leaves greatly influence whether an arboreal leaf-eater eats them at all, as well as when and in what quantities and proportions. To elaborate the actual patterns and processes for specific animals and habitats, one needs to know what is in the leaves eaten and rejected. The logistic problem is exactly the same as that faced by the botanist who wishes to know what insects are eating a plant, the mammalogist who wishes to know what plants are being eaten by a mouse, the agronomist who wishes to know what ions are being eaten by a plant, etc. In all cases, once the insect, plant, or ion is in hand, a specialist is called upon to identify it. If entomologists, ornithologists, primatologists, ecologists, evolutionary biologists, etc., are to give secondary compounds the attention that they have long deserved in understanding the interactions of animals and plants, an identification service is essential. The time is right for such a service and it would pay handsome rewards in understanding the interactions of animals and plants, interactions that are hardly trivial in the manipulation of nature, and in the examination of nature for esoteric enjoyment.

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Nutritive Value as a Factor in Plant-Insect Interactions with an Emphasis on Field Studies

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Introduction

The immense variety and often specificity of plant-insect interactions and their economic importance when they affect agricultural and forest products have stimulated considerable study. Beck (1972) has succinctly described the history of the field as beginning in the early twentieth century with the postulate that both sensory and nutritional factors operated to delimit feeding specificity. The implication of vitamins in human nutrition then prompted an emphasis on nutritional factors. In reaction to the general similarity of requirements so established, Fraenkel (1959) asserted that all green plants fulfill these requirements, and that responses to secondary plant substances were entirely responsible for specificity. Now we have come full circle with Waldbauer's (1962) demonstrations that differences in growth persisted even after oligophagous insects were induced to feed by the removal of the sensory structures that normally were responsible for rejecting nonhost plants. House (1967) further resuscitated consideration of nutritional factors by demonstrating with artificial diets differing only in the amounts of amino acids and glucose not only that the diet with the highest amino acids to glucose ratio yielded best survival, but that it was strongly preferred. Further complications have been added as factors influencing plant-insect interactions: age of vegetation (de Wilde,

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et al., 1969, as one example of many) and distribution of susceptible stages in space (Tahvanainen and Root, 1972) and time (Janzen, 1972), all of which may have different consequences depending on the developmental stage of the insect (Anonymous, 1969).

It is obvious from the above that plant-insect interactions are an analytical nightmare. I have chosen to sidestep most of the problems by concentrating on the influence of nutritional quality of the plant, specifically as measured by percent nitrogen, carbon to nitrogen ratio, amino acid composition, or any other indicator of the abundance of protein building materials, and using as a criterion of importance their expression under field conditions. This will be accomplished by collecting and organizing results of laboratory studies in order to interpret the fewer results of field studies. The studies are of two sorts: (1) chemical analyses of varieties of plants that have been bred for resistance to pests and (2) alteration of the nutrient chemistry of plants by culturing procedures, usually by fertilizing or by fertilizing with one essential nutrient deleted. Wherever information on effects of nutritional value and plant secondary substances are available for the same combination of host and consumer, an attempt will be made to evaluate relative contributions. Finally a more general speculation about insects compared to vertebrates as arboreal folivores will be offered.

Resistant Varieties

Solanaceous plants—Colorado potato beetles.

Cibula, et al. (1967) raised Colorado potato beetles (*Leptinotarsa decemlineata*) on 11 categories of solanaceous plants (different ages and varieties of 4 species), determined amino acid constitution of alcoholic extracts of the plants, and the survival and weight at emergence as adults of the beetles on the different plants. Combining their measures of survival to and weight at emergence as the best indication of the net effect of the diets, the 3 categories of plants that yielded best growth of beetles were also highest in unbound amino acids: young and blooming potato plants and blooming Rutgers tomatoes. Within groups the same pattern held. Senescent leaves were with one exception lower in amino acids and without exception less suitable for beetle growth than younger leaves. For tomato leaves of the same age, growth was better on the varieties that were higher in amino acids.

The chemical basis of host selection by the Colorado potato beetle has been extensively studied (reviewed in Hsiao, 1969). In one set of experiments, the addition of small amounts of leaf powder of 84 species of plants to an artificial diet that initially supported moderate feeding and growth caused from over 100 percent decreases (mainly nonsolanaceous plants) to almost 100 percent increases (mainly solanaceous plants) in growth compared to the basal diet (Hsiao and Fraenkel, 1968). The responses to the leaf powders of the species analyzed by Cibula, et al. (1967) generally agreed with the correlation of suitability of diet with the quantity of unbound amino acids; however, the large differences depending on age and variety make this interpretation speculative. Secondary plant substances were probably responsible for the stimulation, because different species were stimulated by different kinds of extracts (Hsiao and Fraenkel, 1968). Presumably, if improved growth due to leaf powder arose from fortifying the basal diet with amino acids, then the same kind of extract would always enhance growth. Apparently, secondary plant substances operate to exclude *L. decemlineata* from nonsolanaceous plants, many of which otherwise could support growth and development, but within the solanaceous group secondary plant substances may provide cues to the best nutritional sources, which also tend to be the richest sources of amino acids.

Wheat—pale western cutworm

Kasting and McGinnis (1961) related the growth and development of the pale western cutworm (*Agrotis orthogonia*) on hollow- and solid-stemmed spring wheats to nitrogen concentration. Solid-stemmed wheats had been bred for resistance to the wheat stem sawfly (*Cephus cinctus*). Three patterns emerged: (1) Differences in growth and survival on different plant parts were correlated with nitrogen concentration. (2) Growth and survival on the same plant parts declined with age, as did nitrogen. (3) Growth but possibly not survival on similar parts was greater on the susceptible than on the resistant strain, as was nitrogen. Diet-supplementing experiments further implicated nitrogen metabolism in the susceptibility of wheat to attack by insects. Additions of amino acids, yeast extracts, casein, and extracts of hollow-stemmed sprouts, in ascending order, all improved pith as a nutritional source for the pale western cutworm. Pith was the worst fraction of solid-stemmed wheat for the maintenance of *A. orthogonia* and does not even occur in hollow-stemmed varieties (McGinnis and Kasting, 1962). Even the best supplemented diet of pith, however, only supported half the growth of the supplement alone or diluted with metabolically neutral powdered cellulose, suggesting the operation of a toxic factor. The presence of a toxic factor was demonstrated by the reduction of growth and survival of *A. orthogonia* upon the addition of ether extracts of piths from two resistant strains to diets of sprouts and sprouts-cellulose powder. Conversely, the residual pith after ether extraction no longer inhibited growth and survival when mixed with extracts of sprouts. The relative importance of nutritional and toxic factors in determining the suitability of wheat as a diet for *A. orthogonia* can be roughly evaluated from Table 1, although results from different experiments were not always consistent. Apparently supplementing pith with extracts of sprouts increased survival from zero to one-half of survival on the best diet (sprouts). Adding in metabolically neutral carbohydrates in the form of cellulose powder reduced this improvement by around one-half (Table 1C). It is curious that in Table 1A pith plus sprout extract yielded smaller third instars, but not in Table 1C, while the opposite was true for cellulose powder plus sprout extract. To the extent that combinations of cellulose powder, extracts of sprouts, and ether extracts of pith resemble natural pith, toxic and nutritional factors contribute about equally to making pith unsuitable for the development of the pale western cut-worm.

Peas—pea aphids

Maltais and Auclair (1957) reported analyses of total nitrogen, soluble nitrogen, and total sugars for three resistant and three susceptible strains of peas. Population counts of aphids (*Acyrthosiphon pisum*) over a 13-year period in field plots were 2-3 times higher per plant on the susceptible varieties of peas. Resistant strains were 11.5 to 37.1 percent lower in soluble and total nitrogen and 23.4 to 63.7 percent higher in sugar to nitrogen ratios than susceptible strains. The concentration of nitrogen was 38.4 percent lower in older (toward base of plant) than in young (terminal) growth. Analyses of amino acids indicated that the consistent difference between resistant and susceptible varieties was about 70 percent more glutamine, asparagine, and homoserine in susceptible strains. When pea leaf petioles of resistant varieties were immersed in solutions of these substances, increases in their concentrations could be

Table 1.—*Survival and weight attained by* Agrotis orthogonia *on different diets*.
The entries are adapted from McGinnis and Kasting (1962), A. from Table IV; B. from Table V; C. from Table VII.

Diet	*Number of larvae*	*Percent surviving 2 molts*	*Weight (mg) 2 days after molt 2*
A. Golden Ball pith	35	0	—
Golden Ball pith: sprout extract	37	32	4.1
Cellulose: sprout extract	40	48	8.0
Sprouts	39	59	9.7
B. Golden Ball pith	19	0	—
Cellulose: sprout extract	20	30	6.4
Cellulose: sprout extract: ether extract (GB pith)	18	11	6.2
Sprouts	19	68	12.8
C. Sprouts: ether extract (GB pith)	19	37	13.3
Cellulose: sprout extract: ether extract (Thatcher)	16	21	7.5
Cellulose: sprout extract: ether extract (GB wall)	19	5	3.7
Cellulose: sprout extract: ether extract (GB pith)	20	15	8.4
Cellulose: sprout extract	18	67	8.3
	19	74	6.7
Sprouts	19	79	14.3
	19	74	13.3

identified in the leaves and in the haemolymph and honeydew of feeding aphids. Resistant leaves supplemented with other amino acids yielded 9 percent greater growth compared to 22 percent when they were supplemented with glutamine, asparagine, and homoserine (calculated from Maltais and Auclair, 1962, Tables 1 and 2). In other tests, aphids feeding on a resistant compared to a susceptible variety of peas grew and survived only half as well. The saps being sucked contained 2 and 3.75 percent nitrogen, respectively. The same concentrations of nitrogen in artificial diets yielded the same relative difference in growth and survival (Auclair, 1969). Tests of preference and success of development on a series of artificial diets that differed only in percent nitrogen demonstrated that aphids aggregated on the diets that permitted best development (Auclair, 1965). I am not aware of any work that has implicated secondary plant substances as influences on this plant-insect interaction.

Strawberries—strawberry mites

Rodriguez, et al. (1970) rated the amount of injury by strawberry mites (*Tetranychus urticae*) and determined the nitrogen concentration of leaves for 5 varieties of strawberry. The amount of damage was highly correlated with the nitrogen content of the different clones. The application of different fertilizer treatments to a relatively resistant strain produced plants with a wide range of leaf nitrogen. Number of mites, number of eggs laid, and damage to leaves were all correlated with leaf nitrogen.

Corn—corn earworms

Knapp, et al. (1966) made genetic crosses to produce corn plants that were susceptible, intermediate, or resistant to attack by the corn earworm (*Heliothis zea*). Samples of corn silk were then analyzed for amino acids. The concentration of free amino acids but not total protein increased from resistant to intermediate to susceptible crosses.

Fertilizer Treatments

Brussels sprout plants—aphids

Van Emden and Bashford (1969) produced a wide range in the soluble nitrogen content of Brussels sprout plants by applying different fertilizer treatments. Two species of aphids (*Myzus persicae* and *Brevicoryne brassicae*) were raised on old, intermediate, and young leaves of plants raised under the different fertilizer treatments. Both aphids responded with higher fecundities on the treatments that yielded higher levels of soluble nitrogen in leaves. *M. persicae* produced more young when fed on older leaves, while *B. brassicae* did not respond to age. This result is surprising. In view of the strong response to the fertilizer treatment, the aphids should have produced more offspring on the young leaves: they were as much higher in soluble nitrogen compared to old leaves as the extremes of the fertilizer treatments. A possible explanation for this anomaly is the presence of mustard oils at higher concentrations in younger leaves. Another indication of the importance of soluble nitrogen was the much higher fecundities of both aphids in a similar, earlier experiment, using a variety of Brussels sprout plants that was almost twice as rich in soluble nitrogen.

Apple rootstocks—mites

Storms (1969) cultured apple rootstocks on different combinations of mineral nutrients. Mites (*Tetranychus urticae*) produce more young on leaves that were higher in nitrogen both within and between treatments. In one trial with bean plants, the normal host, the pattern held but at higher levels of fecundity for a given concentration of leaf nitrogen, suggesting that responses to secondary plant substances may also be involved.

Wheat—grasshoppers

Smith and Northcott (1951) produced differences in the nitrogen content of the same variety of wheat by fertilizer treatments. Grasshoppers (*Melanoplus mexicanus*) survived better to adulthood and then laid more eggs per female when raised on wheat plants with 6 percent compared to 4 percent nitrogen. No grasshoppers completed development on plants containing 3 percent nitrogen.

Other studies

Where the mineral nitrogen content of soils has been altered by fertilizer treatments without accompanying analyses of the plants, higher soil nitrogen has usually been associated with (1) more severe damage to plants: spotted alfalfa aphids (*Therioaphis maculata*) on alfalfa (Kindler and Staples, 1970), chinch bugs (*Blissus leucopterus*) on sorghum (Dahms and Fenton, 1940); (2) larger numbers of insects: corn leaf aphids (*Rhopalosiphum maidis*) on sorghum (Branson and Simpson, 1966), aphids (*R. fitchii*) on oats (Coon, 1959), greenbugs (*Schizaphis graminum*) on winter wheat (Daniels, 1957); or (3) greater fecundity of insects: pea aphids (*Acyrthosiphon* *pisum*) on peas (Barker and Tauber, 1951a). In two reports that I have seen, no response in fecundity to soil nitrogen was detected: aphids (*Myzus persicae*) on nasturtiums (Barker and Tauber, 1951b), potato aphids (*Macrosiphum euphorbiae*) on potatoes (Taylor et al., 1952), and in one instance insect populations responded inversely to nitrogenous fertilizers: greenbugs (*Schizaphis graminum*) on oats (Arant and Jones, 1951).

Conclusions Based on Laboratory Studies

There is a preponderance of evidence from a variety of sources of a correlation between the susceptibility of plants to insect attack and the concentration of nitrogenous compounds in plant tissues, suggesting that the phenomenon may be rather general in significance. Response to nitrogen content has been shown for: (1) insects of four different orders (Orthoptera, Homoptera, Lepidoptera, and Coleoptera) plus mites; (2) both chewing and sucking habits of feeding; (3) feeding on different structures (leaves, stems, and reproductive structures); (4) feeding in the presence of secondary plant substances; (5) the same kind of insect feeding on different species or varieties; (6) the same kind of insect feeding on different ages of the same structure; and (7) the same kind of insect feeding on the same ages of the same structure, differing in percent nitrogen. A conscious effort was made to find counter examples. As noted in the preceding section, only 2 cases of no effect and 1 of opposite effect were seen, and these were not supported by analyses of the plants.

All of the plant-insect interactions considered above involve plants used in agriculture. The plants have been subjected to intense selection for thousands of years to improve their palatability and yield for human beings. The important influences on such highly modified plants grown under such artificial conditions will not necessarily apply to plants in general. This is certainly true for the cited correlations of plant nitrogen and insect damage. Almost every author concluded that nutritional factors alone were not sufficient to account for observed differences in plant resistance or susceptibility to insect attack. On the other hand, the great value of the analyses of the effect of nutritive value in these grossly simplified interactions is that they permitted unequivocal demonstration of cause and effect even when other powerful factors operated (see sections *Wheat—pale western cutworms* and *Peas—pea aphids,* above). The properties of these "simple" interactions can then be used to identify and to a degree corroborate similar responses in more natural situations.

Field Studies

Balsam fir trees—spruce budworms

Shaw and Little (1972) got significant increases in foliar crude fat, total sugar, nitrogen, and caloric content by applying high urea fertilizer to 6-year-old fir trees in a nursery lot. Second instar spruce budworms (*Choristoneura fumiferana*) were introduced to the new foliage of fertilized and unfertilized trees. They survived better to pupation and were bigger as pupae and adults on fertilized than on unfertilized trees.

Oak trees—winter moth larvae

Infestation of the English common oak (*Quercus robur*) by the winter moth (*Operophtera brumata*) is limited to a short period in the spring. Feeny (1970) has shown that the termination of the infestation by mid-June was associated with poorer growth on older leaves. During the critical period from late April to mid-June, leaf proteins decreased by one-half, tannins doubled, and toughness increased sevenfold for similar sizes of leaves. The restoration of good growth on June 1 compared to May 13 leaves by preparing leaf powder-agar diets demonstrated that toughness influenced growth (Feeny, 1970). Additional experiments, however, showed that the combination of decreasing protein and increasing tannins in leaves had important consequences. The addition of as little as 1 percent tannins to an artificial diet that supported as good growth as young oak leaves significantly decreased size of pupae (Feeny, 1968). Tannins in oak leaves exceeded 1 percent by mid-June and increased to 5.5 percent by September (Feeny, 1970). The proposed mechanism for the deleterious effect of high levels of tannins was that they formed complexes with proteins that could not be assimilated. Histological studies on larvae showed that the complexed proteins did not get out of the gut. At what point the additional protein deprivation caused by tannins would decrease growth under natural conditions is not clear. Judging from Feeny's studies (1970, Fig. 7), tannins were approximately 1 percent of dry weight in leaves by June 1. At that date, growth equal to that on young leaves could be restored by eliminating the effect of toughness. Unfortunately, the more direct tests of adding tannins to diets based on young oak leaves were not performed.

Grass—mirid bugs

McNeill (1973) noted a change in the feeding site of mirid bugs (*Leptoterna dolabrata*) from leaves to flowers of the grass (*Holcus mollis*) coincident with a drop from 3 to 1 percent nitrogen in leaves. Newly developed seeds contained 10 to 13 percent nitrogen. When the bugs were reared in the laboratory exclusively on leaves, they all died before adulthood, whereas 25 percent became adults when flower heads were added.

Prickly pears—Cactoblastis

Prickly pears that grew on poor compared to rich soils in Australia were yellow, contained half as much nitrogen, and did not support good survival of larvae of the moth (*Cactoblastis cactorum*). Application of fertilizer restored normal color to the cacti and caused increases in the abundance of moth larvae (Dodd, 1936, summarized in Dahms, 1940).

Calabash trees—flea beetles

Damage to leaves of calabash trees by flea beetles (*Oedionychus sp.*) is usually limited to the early part of the rainy season in northwestern Costa Rica, when new leaves were being produced; however, when Rockwood (1974) hand-defoliated trees during the middle of the rainy season, the crop of new leaves that the trees produced was severely attacked, 3 of 8 trees losing all leaves. No leaves were eaten on the control trees. No chemical analyses were performed.

Salt marsh plants—various insects

Applications of fertilizer to salt-marsh plots over a 5-year period have increased nitrogen concentrations in the common plants (*Spartina alterniflora, S. patens*, and *Distichlis spicata*) compared to control plots from 30 to 80 percent. The biomass of herbivorous insects in sweep-net samples was approximately 7 times greater on fertilized plots, while the biomass of plants produced in a year was approximately 3 times greater. Sucking insects dominated by mirid bugs accounted for most of the increase (Valiela, et al., 1975; S. Vince, personal communication).

Red mangroves—various insects

My research in collaboration with John Teal and Ivan Valiela is reported elsewhere (Onuf et al., 1977). However, I shall present the necessary documentation for the conclusions drawn.

Small islands along the coast of the Florida peninsula are usually covered with mangroves. Often one or a few of these islands in a particular locality are sites of nesting colonies of birds while nearby islands remain vacant. We have capitalized on just such a situation at Fort Pierce, Florida, to study the effects of nutrient enrichment on a red mangrove (*Rhizophora mangle*) ecosystem. The rookery consisted of brown pelicans (*Pelecanus occidentalis*); common (*Casmerodius albus*), snowy (*Leucophoyx thula*), and cattle (*Ardeola ibis*) egrets; double-crested cormorants (*Phalocrocorax auritus*); and great blue herons (*Ardea herodias*). During the period of maximum growth of mangroves from March through September, the birds added each day approximately 1 and 0.1 grams/m^2 dissolved nitrogen as ammonium and phosphorus as phosphate respectively, based on analyses of guano caught in containers of water set out beneath the trees. The guano was a source of nutrient enrichment to the mangroves of the bird island because concentrations of ammonium and phosphate ions in sedimentary pore water samples were respectively 25 and 2.5 times higher on the bird island than on an island without birds a kilometer away (control island hereafter). The enrichment by guano stimulated primary production (Table 2) and caused increases in the nitrogen concentration of some structures (Table 3); however, the greater proportionate increases in woody and reproductive tissues than in leaves seems anomalous.

Table 2.—Primary production on the bird island compared to the control island as measured by the growth of initially equal cohorts of labeled red mangrove branches from March to September, 1974.

Biomass (grams dry weight) produced	*Bird*	*Control*	Bird / Control
Leaves:			
dropping off	139.2	126.0	1.10
increase of attached	198.3	168.7	1.18
Reproductive parts:			
stems	10.9	5.4	2.02
buds and flowers	61.8	30.5	2.03
fruits and hypocotyls	30.4	18.1	1.68
Woody tissue:			
increase of existing stems	83.2	46.7	1.78
new internodes	74.7	34.4	2.17
Total	598.5	429.8	1.39

The proportionate response to the nutrient enrichment was much greater by herbivorous insects than

Table 3.—Percent nitrogen of parts of red mangrove trees from the bird island compared to the control island.

	Percent N (mean ± SE)	
Tree parts	*Bird*	*Control*
New leaves	1.60 ± 0.10	1.29 ± 0.04
Old leaves	0.48 ± 0.03	0.36 ± 0.02
Fruits	1.01 ± 0.17	0.61 ± 0.02

Stems, prop roots, subterranean roots, flowers, and whole seedlings were not different in percent N between sites, based on small numbers of determinations.

Table 4.—Production of plant biomass and biomass lost to herbivores on labeled branches of the bird and control islands between March and September, 1974.

Biomass	*Bird*	*Control*	*Bird/Control*
Added	598.5	429.8	1.39
Aborted—*Ecdytolopha*	101.2	26.9	3.76
Eaten—*Phocides*	14.6	1.9	7.68
Alarodia	3.5	0	—
Total lost to herbivores	119.3	28.8	4.14

Mangrove skippers (*Phocides pigmalion*) are nest-builders during their larval development. They were never observed at either study site to move far from their nests. Generally they fed on mature leaves, apparently indiscriminately scalloping the edges.

The limacodid moth (*Alarodia slossoniae*) was much more active than the skipper, never being seen on the same branch on successive days. They fed transversely across mature leaves, beginning at the tip.

Two other lepidopteran consumers were seen on the bird island but never during similar searches on the control island. They were not included in the quantitative evaluation of damage (Table 4) because they did not appear on the labeled branches used to estimate production; however, one of them caused the most severe local damage. All io moth larvae (*Automeris io*) were seen within a meter of one another, as many as 13 at one observation, for over a month. They stripped whole branches of leaves by the plants themselves (Table 4), and this trend held for all the obvious herbivores, regardless of their mode or object of attack.

Ecdytolopha sp. is an olethreutid moth that undergoes its larval development inside leaf buds. In this study, its feeding on developing leaf primordia frequently caused the loss of the pair of leaves that was due to appear next. Leaves that survived were always mutilated and sometimes were dropped soon after unfolding from the bud. Occasionally, damage extended to 2 more pairs of leaves, since buds always consisted of 3 pairs of leaf primordia (Gill and Tomlinson, 1971). Rarely a whole apical meristem was destroyed. The estimated 17 percent compared to 6 percent loss of biomass due to *Ecdytolopha* on the bird and control islands was based only on leaves aborted straight from the bud and therefore is an underestimate.

during this period. The other, (*Megalopyge opercularis*) was seen individually 3 or 4 times.

Damage to the viviparous seedlings of red mangroves by scolytid beetles (*Poecilips rhizophorae*) was evaluated independently because the tagged branches included so few seedlings. Infested seedlings could always be identified by the presence of entrance holes, often made obvious by protruding plugs of rust-colored frass. Infestations began earlier and reached higher proportions on the bird island (Table 5). In turn, the tunneling of the beetles reduced establishment of seedlings (Table 6).

To this point only the effects on the plants have been described. The sedentary habits of the mangrove skipper (*Phocides pigmalion*) suit it well for analysis of the reciprocal effects of plant on insect under field conditions. The hypothesis under consideration is that the nitrogen-rich vegetation (Table 3) grown under conditions of nutrient enrichment provides better nutrition for insects. In so doing, the relatively small difference in numbers of skipper larvae between bird and control islands (Table 7) can be reconciled with the relatively much larger difference in damage done (Table 4).

Survival and increase in size were both shown to be greater for *P. pigmalion* on the bird island than on the control island by making repeated observations on the same individuals (Table 8). Amount consumed by these same caterpillars was measured at every observation by clamping partially consumed leaves between sheets of cardboard and transparent plastic, tracing their outlines with a felt-tip pen, and later determining the areas of missing portions. The resulting schedule of amount eaten by animals at different sizes (Fig. 1) permitted a test of nutritional value of bird- compared to control-island vegetation. If guano-enriched vegetation is higher in quality, less should be required to grow an equivalent amount.

Table 5.—The number of red mangrove seedlings still attached to the parent plant per 100 examined that were infested by the scolytid beetle Poecilips rhizophorae.

Island	*20 June 74*	*13 July 74*	*25 July 74*	*10 Aug 74*	*24 Aug 74*	*13 Sep 74*
Bird	4		28	69	All bored (~ 300)	All bored (~ 150)
	0		32	74		
	3		70	100		
	22		78	90		
	8		56			
	5					
Control		6		17	35	64
		0		12	5	13
		0		5	0	19
		0		0	3	56
		6		14	28	45
		3		7	24	62

Table 6.—Establishment (defined as leafing) of bored compared to unbored seedlings planted in December, February and August. Seedlings were obtained from the mainland shore.

Dates		*Leaves*	*No leaves*	*Number planted*	*Percent established*
11 Dec 73	Bored	17	81	98	17.3
to					
23 Feb 74	Unbored	34	64	98	34.7
		$\chi^2 = 6.785$	$0.001 < p < 0.005$		
8 Feb 74	Bored	2	16	73	2.7
to					
10 Dec 74	Unbored	17	16	64	26.6
		$\chi^2 = 6.497$	$0.005 < p < 0.01$		
25 Aug 74*	Bored	33(0)	67(100)	100(100)	33(0)
to					
17 Oct 74	Unbored	54	46	100	54
		$\chi^2 = 8.138$	$0.001 < p < 0.005$		

*Seedlings collected from control island, without parentheses, bird island, with parentheses. No unbored seedlings were available on the bird island at the time of the planting.

Therefore, a greater proportion of bird- than control-island points should lie below than above the joint regression in Figure 1, as is the case (Table 9). The greater damage to bird- than control-island vegetation by *Phocides* (Table 4) was compounded of greater abundance (Table 7), survival to bigger size (Table 8), and the almost cubic relationship between amount eaten and length of caterpillar (Fig. 1) and these differences were at least in part caused by differences in nutritive value of the vegetation, correlated with nitrogen content (Table 3).

Other studies

Stark (1965) has reviewed work on the effects of fertilization on forest insects. For 15 host tree-insect combinations application of nitrogenous fertilizers reduced insect survival. Only 3 cases of no effect and 1 of greater effect were mentioned. There was no

Table 7.—Number of nest-building caterpillars of the mangrove skipper Phocides pigmalion seen during general searches of the study areas on different dates.

Date	*Time of search Min:Sec*	*Number of caterpillars of* Phocides pygmalion *Bird*	*Control*
3 September 74	67:15	33	30
26 September 74	31:15	24	17
28 October 74	38:17	7	2
5 December 74	16:57	2	1
20 February 75	24:56	6	1
21 April 75	24:57	7	2
Total		79	53

Table 8.—Survival and growth of the mangrove skipper Phocides pigmalion.

A. Number of larvae that survived the indicated number of days.

	Days until death or disappearance		
	0–15	*16–30*	*31–45*
Bird Island	4	2	7
Control Island	9	7	1

$\chi^2 = 8.81$ df = 2

$0.01 < p < 0.025$

B. Number of larvae that grew the indicated lengths.

	Increment in length (mm)		
	0–5	*6–15*	*16–26*
Bird Island	5	1	7
Control Island	10	6	1

$\chi^2 = 9.35$ df = 2

$0.005 < p < 0.01$

agreement on possible mechanisms by which the increased resistance was achieved nor reports of nitrogen concentrations of the vegetation. Without knowing more about the basis of the reported responses, the differences between these results and almost all the others discussed in this paper must remain perplexing.

Discussion

This review has been a polemic in support of nutritive value, specifically as indicated by the nitrogen

Table 9.—A test of the hypothesis that caterpillars of the mangrove skipper Phocides pigmalion grow more efficiently on the nutrient-enriched vegetation of the bird island. A higher proportion of bird than control points must lie below the joint regression line of area of leaf consumed vs. length of caterpillar (Fig. 1) to be consistent with the hypothesis of nutritional improvement.

Island	*Number of points* *Above regression*	*Below regression*	
Bird	20	31	Caterpillars ≤ 13 mm long
Control	18	10	$\chi^2 = 4.551 \quad .01 < p < .025$
Bird	21	17	Caterpillars > 13 mm long
Control	29	19	$\chi^2 = 0.0681 \quad .35 < p < .4$
Bird	41	48	All lengths of caterpillars
Control	47	29	$\chi^2 = 4.099 \; .01 < p < .025$

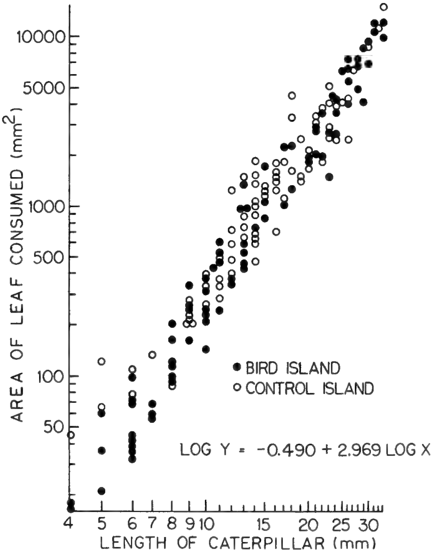

Figure 1. Total amount eaten by the mangrove skipper (*Phocides pigmalion*) at different sizes.

content of plant tissues, as a factor affecting plant-insect interactions. The guiding principle has been that a factor must be important if it can be demonstrated to operate under field conditions. There, all other factors are free to operate and completely overwhelm expression of influences that may seem important in isolation. When the factor still emerges, then it is important. The effect of nutritive value meets this criterion and as well may be quite general, as suggested by the variety of plants and insects already implicated in the few studies performed.

In no way does imputing importance to nutritive value eliminate other factors. The few cases where more than one factor has been studied in the same system suggest that either a complementarity exists: secondary plant substances limit Colorado potato beetles to solanaceous plants (Hsiao and Fraenkel, 1968), amino acid composition influences susceptibility among solanaceous plants (Cibula, et al., 1967), or that different factors are mutually reinforcing: increasing leaf toughness and tannins and decreasing nitrogen content with age limit infestations of winter moth larvae on oak trees to a short period in the spring (Feeny, 1968, 1970). Where only one factor has been considered, it is almost certain that others are also involved: leaves of red mangroves, for instance, contain tannins, toughen and decrease in nitrogen as they grow older. It would be surprising if all these factors, perhaps in combination with others, did not influence the distribution of attack by the different herbivores among different tissues or ages of tissues.

It is suggested, then, that good protection against herbivory requires the simultaneous operation of different factors. Unfortunately for plants, most of the modes of protection must be set aside in order to grow. Thus, amino acids and proteins must be provided in abundance to build the regulatory machinery and some of the structure of growth; toughness must be sacrificed to permit elongation of newly divided cells, and chemicals that confer protection because they interfere with animal metabolism must be reduced because they usually interfere with the metabolism of plant cells as well. (The greater concentration of mustard oils in young leaves of Brussels sprout plants [van Emden and Bashford, 1969] is a counter example.) Only when growth has been superseded by differentiation can the protective features be restored. Then the concentrations of amino acids and proteins will be reduced—directly, because they are no longer needed for growth, and indirectly, by increasing the carbohydrates of energy reserves and building the structural components that make for toughness. In addition, defensive chemicals can be synthesized and sequestered where they will not interfere with the functioning of the plant but will be released by the feeding of animals.

It is likely that these constraints tending to concentrate herbivory on meristematic tissues and periods of rapid growth apply to vertebrates and insects alike. Overall improvement in the nutritive value of vegetation probably acts either to aggravate vulnerability at this stage or to extend it to other stages or structures. Size and developmental period account in large measure for the much more general occurrence of insects than vertebrates as arboreal folivores. Thus, *Ecdytolopha* is able to feed on the youngest growing shoots of red mangroves by undergoing its larval development entirely inside the protective bud covers. Winter moth larvae on oak trees can complete their development during the few weeks of new growth in spring (Feeny, 1970). Arbivorous moth larvae with long developmental periods grow best on low carbohydrate to nitrogen diets in early instars, higher carbohydrate to nitrogen diets in later instars, just as the vegetation changes (Edel'man, 1963). When feeding conditions are unsuitable, most insects just wait it out in a resistant, resting stage. None of these strategies are available to vertebrate arboreal folivores. They must depend instead on the year-round occurrence of new growth, resort to a variety of sources in addition to leaves, or make a large investment in the physiological machinery necessary to detoxify and process large volumes of low-quality food.

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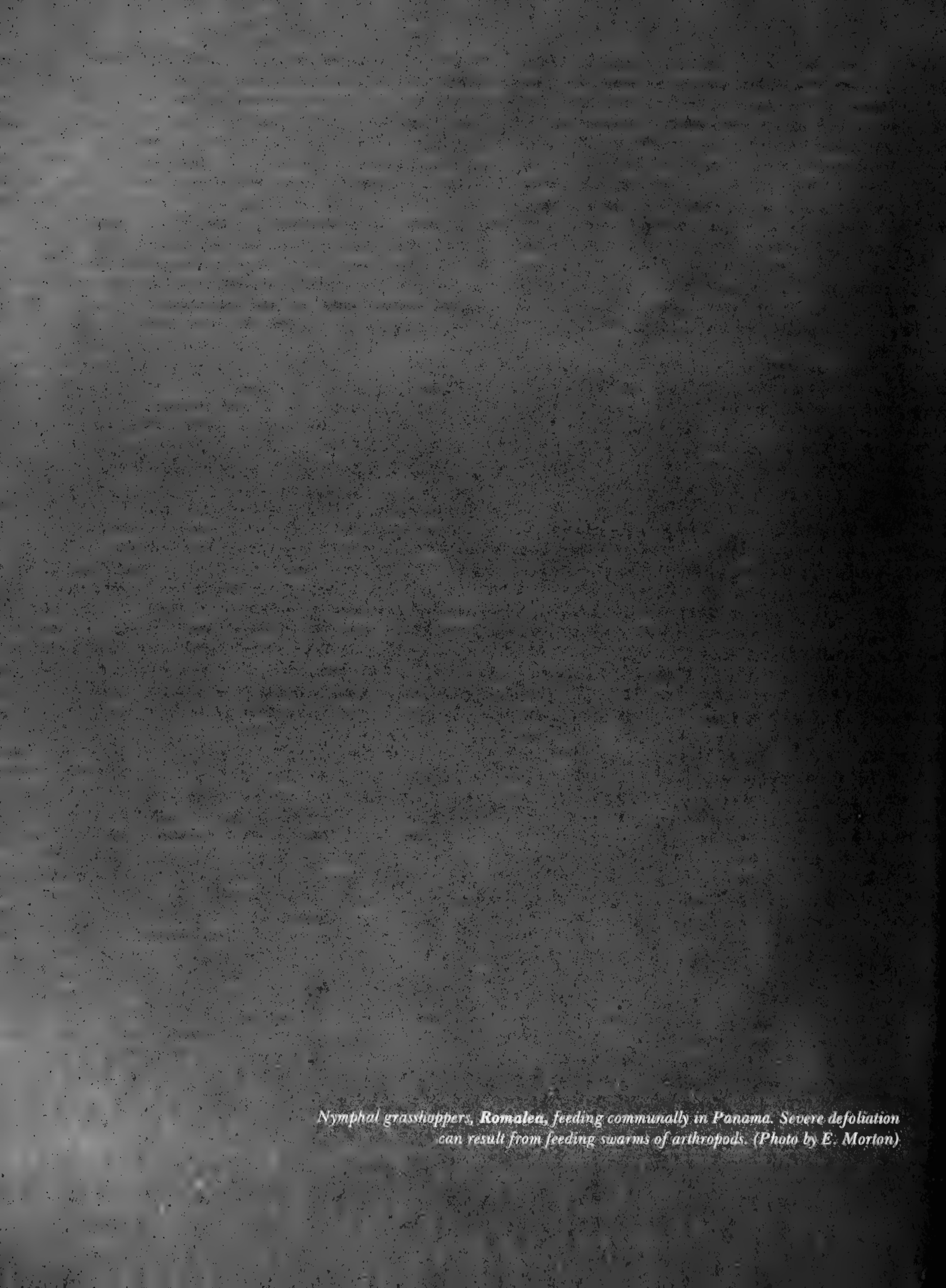

Nymphal grasshoppers, ***Romalea,*** *feeding communally in Panama. Severe defoliation can result from feeding swarms of arthropods. (Photo by E. Morton)*

NONMAMMALIAN ARBOREAL FOLIVORES

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The Feeding Activities of Tropical Insect Herbivores on Some Deciduous Forest Legumes

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Introduction

The following study examines the composition of insect herbivore communities associated with a group of woody, herbaceous and vining plant species in the Leguminosae in a highly seasonal tropical habitat. Both leaf- and sap-feeding insects are examined. Emphasis is directed toward the degree of insect specificity for particular host plants, the time and location of feeding on the host, and the seasonal changes in herbivore abundance and species composition. Qualitative descriptions of defoliating insect outbreaks are given for several plant species in the study area.

Early characterizations have suggested that insect outbreaks in tropical forests should tend to be rare because of the stability of checks and buffers acting to prevent any one species from becoming overly ıbundant. Although large-scale outbreaks of foliage-feeding insects in Temperate Zone forests are well documented in the literature of economic entomology and forestry (Kulman, 1971, Mattson and Addy, 1975), little is known of their frequency in tropical forests. Rockwood (1974) reported nearly complete defoliation of leaf crops produced after experimental hand defoliations of *Crescentia alata* H., B. & K. trees in Costa Rica by alticid beetles. Smith (1972) reviewed reports of the spectacular irruptions of the migratory day-flying moths, *Urania fulgens* Walker and *U. leila* L. in Central and South America. Large within-and between-year differences in larval densities on the host plant are suggested for these species. Other records of outbreaks of defoliating insects exist but generally deal with defoliators on plants grown in horticulturally or agriculturally simplified ecosystems in the tropics.

Further indications that tropical insect herbivore populations are anything but stable come from the sequential sampling of insects by a variety of trapping techniques, each revealing conspicuous differences in seasonal abundance. Fogden (1972) has shown that the abundance of 2 largely folivorous groups of insects, the Lepidoptera (larvae) and Orthoptera, fluctuate widely depending upon time of year in Sarawak—one of the least seasonal climates in the tropics. He suggests that peaks in insect abundance are related primarily to the times of peak leaf production which come with the rains associated with the northeast monsoons. Confidence in the causal basis of this relationship is enhanced by observations that habitats with greater seasonal differences in amounts of leaves flushed had the larger fluctuations in seasonal herbivore abundance. Other collections of insects from tropical sites, most with more seasonal climates than Sarawak, reveal even larger seasonal fluctuations in foliage feeding insects (Duviard and Pollet, 1973; Bigger, 1976; Robinson and Robinson, 1970, 1973; Orians 1973; Charles-Dominique, 1971).

The following study examines the broadest aspects of community structure among insects exploiting food plants subject to extreme seasonal differences in rainfall. The sudden arrival of heavy rains following 4 dry-season months should act to some degree as a factor synchronizing the chemical and structural qualities of leaves available to herbivorous insects. Many of the chemical changes which can be expected under these circumstances have been reviewed by McKey (1974). Alkaloids are expected to be genrally highest in newly expanded leaves and to decrease with leaf age. Tannins which bind up available protein are generally lowest in young foliage and tend to increase in quantity with age (Feeny, 1970). The sheer abundance of new leaf material should be greatest in the first 2 months following the arrival of the rains. These and other differences in leaf resources are expected to affect the composition and change of consumer populations through the wet season.

Site Description and Census Methods

Observations were taken from a study site in the Parque Nacional Santa Rosa, northwestern Costa Rica (10° 40′ N., 85° 37′ W.), Guanacaste Province, 37 km northwest of the town of Liberia. Censuses were conducted in a 10 ha area between the "Casa Historica" and the administrative compound, both roughly 7 km west of the park's entrance on the Interamerican Highway.

The park is a vegetational mosaic of derived savanna dominated by the African grass, *Hyparrhenia rufa* Stapf., deciduous forest dissected by riparian and mesic evergreen forest along major drainage courses, and evergreen oak forest (*Quercus oleoides* Schlecht and Cham.) on well-drained upland sites. According to the life-zone terminology of Holdridge, the park is mainly "tropical dry forest, moist forest transition." The study site itself is at an elevation of 290 m. Much of the area was formerly heavily grazed savanna with interspersed patches of mature shade trees (*Enterolobium, Pithecellobium, Bursera* and *Cedrela*). The modest protection from fire and grazing which the study area had received since the park was established had allowed a thorough invasion by herbaceous and woody successional vegetation including the seedlings of many deciduous forest tree species. Twelve of these species in the Leguminosae were chosen as the principal host plants to be censused for associated herbivorous insects. Two of the species were herbaceous annuals, *Sesbania emerus* (Aubl.) Urban and *Indigofera sp.* Four species, *Bauhinia ungulata* L., *Cassia biflora* L., *Mimosa albida* Humb. and Bonpl., and *M. pigra* L. are woody shrubs of low stature. *Acacia farnesiana* (L.) Willd. and *A. collinsii* Safford become small trees, while the remaining 4 species in the census, *Enterolobium cyclocarpum* (Jacq.) Griseb., *Pithecellobium saman* (Jacq.) Bentham, *Gliricidia sepium* (Jacq.) Stend., and *Lonchocarpus minimiflora* Donn. Smith become large trees of the deciduous forest. All plants in the census, however, were chosen for roughly equal size and foliage volume. Most individuals were 1.5 to 2 m in height allowing complete inspection for associated insects.

Twenty individual plants of each species were tagged and visited on each census. Two censuses—1 near midday and 1 starting at least 1 hour after sunset—were conducted for each census date. No attempts were made to quantify missing foliage although qualitative notes were kept on all insect infestations noticed in the study area.

All potentially herbivorous insects were counted and listed by species for each plant census. Notations were made for each insect indicating whether inactive, feeding, or moving. If feeding was observed, then the site was classified as either stem, leaf rachis, or leaf blade for sucking insects. Foliage was classified for all feeding insects in one of the following catgories: (1) terminal foliage within at least 10 cm of the shoot tip, leaves unfolding or recently unfolded, texture soft, and color usually a lighter green than older foliage and (2) subterminal foliage, leaves generally fully expanded and hardened, and of the same color as the obviously older vegetation on the plant. These criteria were applied in a subjective manner and are useful for only very general questions concerning the type of foliage consumed by insects.

A reference collection of insects was carried on most censuses to aid with species notation. Leaf-mining and leaf-rolling insects were not tallied nor were other extremely small insects smaller than 1 mm in length. Censusing began in August and September 1972 for most of the 12 legumes. Censuses were repeated at irregular intervals until the beginning of the dry season in December. Sufficient foliage was found on only 4 species to allow censusing during the dry season. Censusing resumed on most of the legumes as the first vegetation appeared at the beginning of the following wet season.

Comparison of Herbivore Activity, Day Versus Night

Activity data recorded on censuses within the period of the first week in August to the second week in December are analyzed in Tables 1, 2, and 3[1]. Table 1 indicates that herbivorous insects are two and one-half times more abundant on nighttime censuses Evening censuses spotted 4 times the number of leaf-feeding herbivores found during the day. Sap-feeders, similarily, were significantly more abundant during evening hours. Leaf-feeding insects, however, showed significantly greater tendency toward nocturnality in numbers than the sap-feeding insects. The Cicadellidae, unlike the other 2 sap-feeding families, showed a high degree of nocturnality. Of the sap-feeders located during the day, more than four-fifths were feeding. Of the leaf-feeders located during the day, less than one-fifth of the total were feeding. Most leaf-feeding insects spent the day off of the food plant; those that remained—chrysomelid and curculionid beetles—were usually hiding under leaves.

Table 1.—The total number of herbivorous insects observed on their host plants and the total number of herbivorous insects actually observed feeding on their host plants are broken down by (1) time of feeding, day versus night and by (2) taxonomic categories.

Major herbivore groups	*Total numbers observed Day:Night*	*Numbers observed actually feeding Day:Night*
LEPIDOPTERA	52:199	
COLEOPTERA		
Acrididae	16:54	
Gryllidae	1:19	
Phasmatidae	5:191	
Tettigoniidae	10:232	
Chrysomelidae	75:86	
Curculionidae	146:138	
Scarabeidae	5:238	
Subtotal for leaf-feeders	310:1324	59:476
HOMOPTERA		
Cicadellidae	18:110	
Membracidae	95:106	
HEMIPTERA		
Coreidae	417:542	
Subtotal for sap-feeders	530:764	455:604
TOTALS	840:2088	514:1080

Of the 12 legumes listed in Table 2, only *A. collinsii* and *Enterolobium* do not have significantly greater herbivore loads on night censuses. In the case of *Enterolobium*, this difference is due to the very large percentage (90 percent) of the herbivore community composed of sap-feeders. Evening numbers of feeding insects were higher on 11 of 12 legumes, although significant day-night differences were not present for *Bauhinia*, *A. collinsii*, or *Lonchocarpus*. Legumes taken as a group, then, tend to have significantly larger herbivore loads in the evening hours.

Location of Consumers on Host Plants

The feeding sites of all insects observed feeding, both day and night censuses combined, are dichotomized

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[1] All comparisons noted in this and the following section have been checked for statistical significance and all are significant at the 0.05 level based on chi-square tests for homogeneity.

in Table 3. Sap-feeding insects prefer to feed on apical foliage—light green, growing or unfolding shoots within at least 10 cm of the terminal bud. In most cases stylets are inserted in stems or petioles although some species were observed feeding from the midribs of leaves. The coreid bugs on *Enterolobium*, *A. collinsii*, and *A. farnesiana* caused wilting and necrosis of shoot tips. This loss of foliage by sap-feeding was substantial on several plant species and should not be overlooked in studies which attempt to quantitatively assess the impact of herbivores on host plants. Most other sap-feeding insects left little obvious effect of their feeding on the health of existing foliage.

Foliage-feeders likewise show a significant preference for apical foliage over subapical foliage although statistically they do so to a lesser degree than sap-feeders.

Foliage Harvest by Leaf-cutting Ants

Leaf-cutting ants were observed removing leaves of only 4 of the 12 legume species in the study; 1 time each on *Mimosa albida* and *Sesbania*, 3 times on *Cassia*, and 7 times on *Bauhinia*. All but one of these observations occurred on nighttime censuses. The occurrence of only 11 observations of *Atta* activity on the nearly 4000 individually censused plants indicates the general rarity of their activities on this suite of species in this particular habitat. The foraging behavior of leaf-cutting ants in a slightly more mesic habitat less than 1 km from my study site has been the subject of a recent intensive study by Rockwood (1975, 1976). The results above indicate that leaf-cutter activity may occasionally penetrate completely deciduous forest habitats but that such areas are almost certainly on the extreme boundary of exploitable habitat for these ants. The fact that the activity I observed was limited to the evening hours, even though all observations came during the late or early wet seasons, corroborates Rockwood's observations that physical factors depress foraging activity in savanna and deciduous forest.

One finding from Rockwood's study is especially relevant to this paper. Although he found that mature leaves were occasionally harvested by leaf-cutters, distinct preferences existed for new leaves and certain tree species. A large peak in foraging activity coincided with the leaf flush at the beginning of the rainy season in April and May followed by a second lesser peak coinciding with a smaller flushing of leaves at the beginning of the dry season in January and February. The increased foraging activity was directed toward the harvesting of new leaves. Thus, the accumulating evidence for *Atta* supports the

Table 2.—The total number of observed herbivores and the total number of herbivores observed eating their food plants are broken down by (1) time of feeding, day versus night, and by (2) host-plant species.

Legume species	*Total numbers Day:Night*	*Actual numbers feeding Day:Night*
CAESALPINACEAE		
Bauhinia ungulata	38:73	28:38
Cassia biflora	15:180	11:52
MIMOSACEAE		
Acacia collinsii	55:42	26:34
Acacia farnesiana	96:311	38:104
Enterolobium cyclocarpum	287:352	239:308
Mimosa albida	6:34	1:15
Mimosa pigra	34:166	34:72
Pithecellobium saman	13:76	5:49
PAPILLIONACEAE		
Gliricidia sepium	159:274	35:96
Indigofera sp.	8:86	4:52
Lonchocarpus minimiflora	93:247	79:77
Sesbania emerus	41:267	23:183
TOTALS	845:2108	523:1080

Table 3.—The total number of herbivores observed feeding on their host plants is broken down by (1) herbivore guild, sap- versus foliage-feeders and by (2) feeding site on the host plant.

Feeding site	*Sap*	*Foliage*	*Totals*
APICAL	839	368	1207
Stem	776	15	791
Leaf	63	351	414
blade	32	349	381
rachis	31	2	33
SUBAPICAL	239	190	429
Stem	202	6	208
Leaf	37	184	221
blade	4	173	177
rachis	33	11	44
TOTALS	1078	558	1636

hypothesis that attine ants choose leaves nutritionally superior for the growth of their fungus gardens and that in most cases such leaves are the newest leaves of a limited set of tree species.

Herbivore Populations Associated with Legumes

(1) *Gliricidia sepium*

This legume begins losing leaves in December and January and is largely leafless through the dry season until May. During the last 4 months of the 1972 wet season it had a fairly complex herbivore fauna. Eight censuses over this period recorded 18 different herbivore species. Five of these species, however, contained 90 percent of all herbivores recorded. The most abundant herbivore was a small (less than 2 mm) curculionid (Otiorrhynchinae) leaf-eating beetle, *Promecops* sp. (nr. *P. leucothyreus* Fahreus). This species was abundant on all censuses, chewing characteristic notches into the margins of leaflets. Promecops reappeared in high numbers on the foliage during the early 1973 wet season. Populations were apparently highest on the young vegetation in June but remained high through most of the wet season. *Promecops* was never observed feeding on any other plant species in the area and it is likely that is has but a single host species in this region.

A second beetle, the scarab (Rutelinae), *Leucothyreus femoratus*, was numerically roughly only half as abundant on *Gliricidia* during the late wet season as *Promecops*, yet inflicted at least as much leaf damage as the latter species. Numbers remained high until the end of the 1972 wet season. The population reappeared in the habitat the following wet season in mid-June and became very abundant in August. *Leucothyreus* was abundant on 4 of the other legumes in the census—*A. farnesiana, Cassia, M. pigra*, and *Sesbania*—and was occasionally encountered on all but 2 of the censused legumes.

Three major species of Orthoptera were commonly found on *Gliricidia* in numbers diminishing until the end of the wet season; *Ancistrocercus, Scudderia*, and *Calynda*. These 3 species were rarely sighted during the first 4 months of the next wet season. All 3 had broad lists of preferred plant species.

Two other major herbivorous insects of *Gliricidia* appeared during June and July 1973. *Talurus*, a chrysomelid beetle (Eumolpinae), appeared in enormous numbers on the first of June and had largely disappeared by the end of the month. Leaf damage was heavy, up to 50 percent of new leaf surfaces maturing in early June were removed by this species. *Talurus* had a broad host list including *A. farnesiana, Bauhinia*, and *Lonchocarpus* and probably several other plant species in the habitat not included in the censuses. The host-specific Lepidoptera, *Azeta versicolor* (Noctuidae), became an important defoliator during late June and early July. Neither of these 2 important herbivores on *Gliricidia* were noticed in the late wet season of 1972.

(2) *Lonchocarpus minimiflora*

Seven censuses of this legume in the wet season 1972 produced an herbivore list of 30 species, 278 individuals. The most abundant herbivore was a coreid bug, *Leptoglossus* sp., present on all censuses through 1972. It was, however, rarely encountered on early wet-season censuses in 1973. The insect fed on young terminal stems, leaf rachises, and the midribs of leaflets of *Lonchocarpus* and was never observed feeding on other plant species in the study area. Apparently, it had one of the heaviest assemblages of orthopteran grazers. More important were the phasmid, *Calynda bicuspis*, and the tettigoniid, *Ancistrocercus inficitus*. The only other legume in the census on which these 2 grazers were as abundant was *Cassia biflora*. As with *Leptoglossus*, populations of these 2 important late wet-season herbivores were very low following the dry season and were showing recovery to pre-dry season levels by mid-July and August.

The early wet season herbivore populations were marked by the appearance of the polyphagous chrysomelid beetle, *Talurus rugosus*, which fed on newly unfolding leaflets for the first 3 weeks of June. The removal of the new leaf crop developing during this time by this beetle was in the range of 25 to 50 percent. New foliage was produced after the disappearance of *Talurus*, thus reducing the impact visually with time.

(3) *Acacia farnesiana*

Twenty-two herbivorous insect species and 199 individuals were recorded on 8 *A. farnesiana* censuses in the late wet season of 1972. The principal Orthoptera present in only moderate abundance was the tettigoniid, *Insara bolivari*. The almost complete absence of the important grazers, *Calynda* and *Ancistrocercus*, is notable. Both of these Orthoptera had broad host preferences yet avoided feeding on *A. farnesiana*. *Mozena lunata* (Coreidae) was an important sap-feeding herbivore present in the habitat in relatively equal numbers throughout the year. This insect fed from the newest growing shoots causing wilting and cessation of further apical growth. Small numbers of Lepidoptera larvae were regularly found on late wet-season censuses.

Since *A. farnesiana* retains a leaf crop through the dry season it was possible to conduct censuses on it for most of these months. Populations were severely depressed through this period until shortly before the first heavy rains in the last week of April. The census on April 16 recorded comparatively large numbers of Lepidoptera larvae, the first brood of the geometrid moth, *Semiothisa diffusata*. By June extremely large populations of both *Semiothisa* and the noctuid, *Panula scindens*, were feeding on *A. farnesiana* in greater numbers than at any other time of year. Throughout the rest of the year moth larvae of these 2 species were present but in greatly reduced numbers. This legume was the only one censused which supported continuous substantial populations of lepidoptera larvae through the entire year.

Two unidentified species of scarab beetles in the genus *Phyllophaga* appeared on the foliage in mid-May and early June. Moderate numbers of chrysomelid beetles (*Talurus rugosus*) fed on foliage through most of the month of June. July and August censuses showed fewer cases of species outbreaks and an increasing importance of orthopteran herbivores.

(4) *Enterolobium cyclocarpum*

The primary herbivores on the 7 late wet season censuses were the coreid bugs, *Pachylis laticornis* and *Savius diversicornis*; these 2 sap-feeding species composed 283 (78 percent) of the 363 censused herbivores (19 species) on this legume. Both species caused the wilting and subsequent death of apical shoots. The abundance of the 2 species was greatest at the beginning of the censuses in the mid-wet season and became rare by the end of the wet season. While sap-feeders on this legume were more abundant than on any other legume in the census, foliage feeding Orthoptera, Coleoptera, and Lepidoptera were virtually absent in the late wet season. *Enterolobium* was deciduous through the dry season and unfortunately was not formally censused during the following wet season. Casual observations of *Enterolobium* during May and June 1973 and 1974 indicated that, as with most of the legumes in this study, it also had important foliage-feeding insects on the foliage produced after the beginning of the rains. Lepidoptera larvae of a single species were noticed in large numbers during late May and early June. In mid-June 1974 I witnessed a virtually complete defoliation of *Enterolobium* saplings and large trees by an, as yet, unidentified meloid bettle. This outbreak species was observed to feed exclusively on *Enterclobium*.

(5) *Sesbania emerus*

This was the only annual herbaceous legume in the study. All plants of this species germinate from seed during the first month of the wet season. They continue to grow until flowering in September and October. A height of 2 to 3 m is common at this time. Observations of hundreds of these plants during the early growing seasons in 1972 and 1973 indicated that this legume is virtually herbivore free for the first 5 to 6 months of growth. This appeared to be the only one of the 12 legumes in the study which had no discernible damage to its early leaf crop. The situation is dramatically different during the last 2 weeks of November as the seed crop is maturing and turning brown. Large numbers of herbivores appear for the first time on the foliage of this plant. Thirteen herbivore species and 240 individuals were recorded on 7 nighttime censuses of this legume. Over 70 percent of these individuals were recorded on the last 2 censuses on November 16 and 25. The noctuid caterpillar, *Ephyrodes cacata,* and the chrysomelid beetle, *Myochrous melancholicus,* strip most of the foliage from the plants within a week after their appearance in the habitat. The coreid bug, *Burtinus notatipennis*, and the pentatomid bug, *Euschistus bifibulus*, fed from maturing seedpods and stems. These abundant herbivores on *Sesbania* were not found on any of the other legumes in the study.

While most *Sesbania* plants were being defoliated in late November, other plants were noticed in adjacent areas without obvious herbivore infestation. Inspection of these plants revealed them to be 1 to 2 weeks behind in seed crop development. Eventually these plants too were defoliated by the same set of herbivores. These observations suggest that important changes occur within *Sesbania* plants near the time of seed maturation which makes foliage and sap highly attractive to herbivores. Since the plant is unusually free of herbivores over the first 5 or more months of growth, it seems probable that chemical defenses are lowered during the final stage of seed maturation. Indeed, for an annual the maturation of a seed crop is its final objective, and it would not be surprising if a rather costly investment in defensive compounds is not passed on in some form to the propagules of the next generation. Further studies of this plant and other annuals, their herbivore loads, and changes in biochemistry should be highly rewarding.

(6) *Bauhinia ungulata*

During the late wet season of 1972 *Bauhinia* had one of the smallest associated herbivore loads of the 12 censused legumes: 61 individuals, 15 species. The more common foliage consumers were the tettigoniid grasshopper, *Ancistrocercus inficitus*; the chrysomelid beetle, *Typophorus variabilis*; and the scarab beetle, *Leucothyreus femoratus*. *Bauhinia* apparently lacks any important sap-feeding insects other than occasional Membracidae. March and April censuses revealed practically no herbivores. Immediately following the rains, however, the first flush of large tender leaves was accompanied by the presence of significant numbers of leaf-eating Scarabeidae, *Phyllophaga* sp., in mid-May and early June. Throughout late May and early June, larvae of the hesperid moth, *Aguna asander*, were common on the newest leaves. Both of these herbivores were gone by the end of June, coincident with a decreasing production of large fast-growing terminal leaves. No more such outbreaks were noticed through the end of August.

(7) *Indigofera* sp.

This legume grows either from seed or perennial root stocks at the beginning of the rains. *Indigofera* had a relatively light herbivore load: 91 individuals recorded in 17 species from 7 nighttime censuses. Of all recorded herbivores in the late wet season 76 percent were Orthoptera; 46 percent of the individuals belonged to the phasmid species, *Calynda bicuspis*; and 11 percent were *Ancistrocercus inficitus*. This legume was essentially free of other orders of herbivores through the end of the wet season. Censuses were resumed in late June when new growth had reached at least 1 meter in height. Important herbivores on early to mid wet-season foliage included *Calynda;* the acridid grasshopper, *Schistocerca crocotaria*; an unidentified species of noctuid caterpillar (*Glympis* sp.); and nymphal spittlebugs (Cercopidae). During this period of observation, Orthoptera constituted a smaller percentage of total individuals than for the preceding late wet-season censuses.

(8) *Mimosa pigra*

This legume is a short, stout briar common in certain early second-growth situations. The principal defoliators were *Calynda* and the scarab, *Leucothyreus femoratus*, and to a lesser extent the tettigoniid, *Ancistrocercus inficitus*. These 3 herbivores accounted for 61 percent of all individuals counted. The total herbivore load consisted of 30 species and 186 individuals recorded on 7 wet-season censuses.

(9) *Mimosa albida*

This vining briar was censused from August 21 until December 1, 1972. The list of herbivore species for this legume accumulating on 8 censuses was shorter than that for any of the other legumes in the study—8 species and 36 individuals. The Orthoptera, *Ancistrocercus*, *Calynda*, and *Rhammatocerus* composed 88 percent of the entire herbivore load. No censusing of this legume was carried out after the first wet season.

(10) *Pithecellobium saman*

This legume was censused 6 times in the late wet season between September 25 and December 4, 1972. Five censuses recorded 19 herbivore species and 67 individuals. The only herbivore regularly found on this legume was a single unidentified Homoptera (Cicadellidae) which constituted 38 percent of all herbivores tallied. The remaining species were a small but diverse assemblage of Orthoptera and Homoptera. Censusing was not resumed after the first wet season.

(11) *Acacia collinsii*

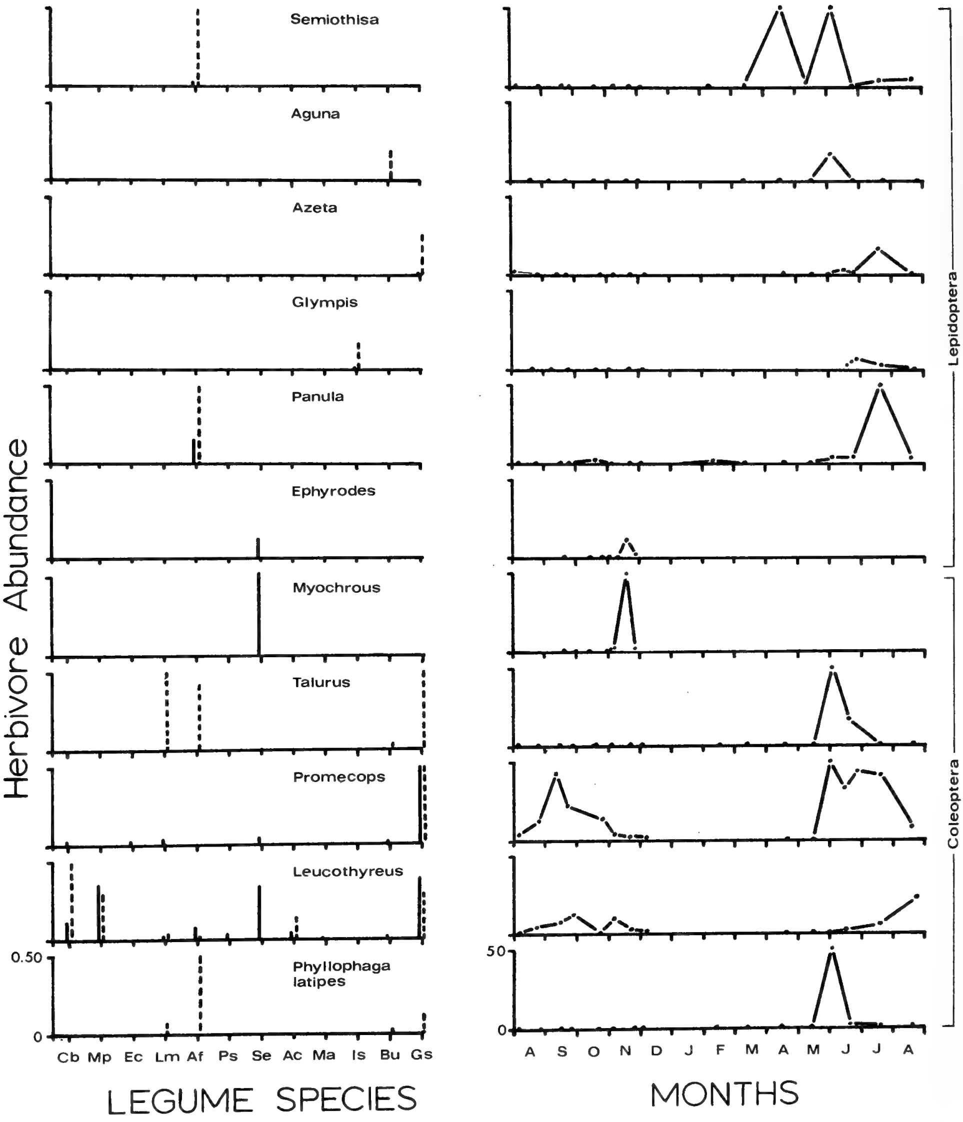
The well-documented mutualistic association between this legume and *Pseudomyrmex* ants (Janzen, 1966) had undoubtedly relieved this legume of many potentially herbivorous insects. Those censused plants with healthy ant colonies had only 3 regular host-specific herbivores: a small (1 mm) and highly agile chrysomelid beetle, *Pachybrachys* sp.; a coreid bug, *Capaneus achilles*; and the larvae of the moth *Coxina hadenoides* (Noctuidae). Seven late wet-season censuses yielded only 56 herbivores in 9 species, an herbivore load smaller than on 10 of the other legumes.

(12) *Cassia biflora*

This small woody legume had the heaviest load of orthopteran defoliators of all the legume species in the study. The principal species were the phasmid *Calynda* and the tettigoniid *Ancistrocercus*. Relatively small numbers of the beetle *Leucothyreus* were also recorded. The herbivore load on *Cassia* was extremely similar to that on *Lonchocarpus* in species composition. *Cassia* lacked any important sap-feeding insects. A total of 207 herbivores in 24 species were recorded from the 8 late wet-season censuses.

Herbivore Outbreaks Noticed on Other Plants

Pisonia macranthocarpa D. Sm. (Nyctaginaceae) is a common woody plant species which attains small tree size in the understory of deciduous and evergreen forests. *Pisonia* was a common plant in the study area. It was conspicuous because it retained its leaves through the dry season. Old leaves are dropped and a new leaf flush produced in mid-April, generally in advance of the first rains. During the first week in May 1973, many of the trees in the study area were 80 to 100 percent defoliated by a spectacular irruption of meloid beetles. At precisely the same time 1 year


Herbivore Abundance
Semiothisa
Aguna
Azeta
Glympis
Panula
Ephyrodes
Myochrous
Talurus
Promecops
Leucothyreus
Phyllophaga latipes
0.50
0
Cb Mp Ec Lm Af Ps Se Ac Ma Is Bu Gs
LEGUME SPECIES
50
0
A S O N D J F M A M J J A
MONTHS
Lepidoptera
Coleoptera

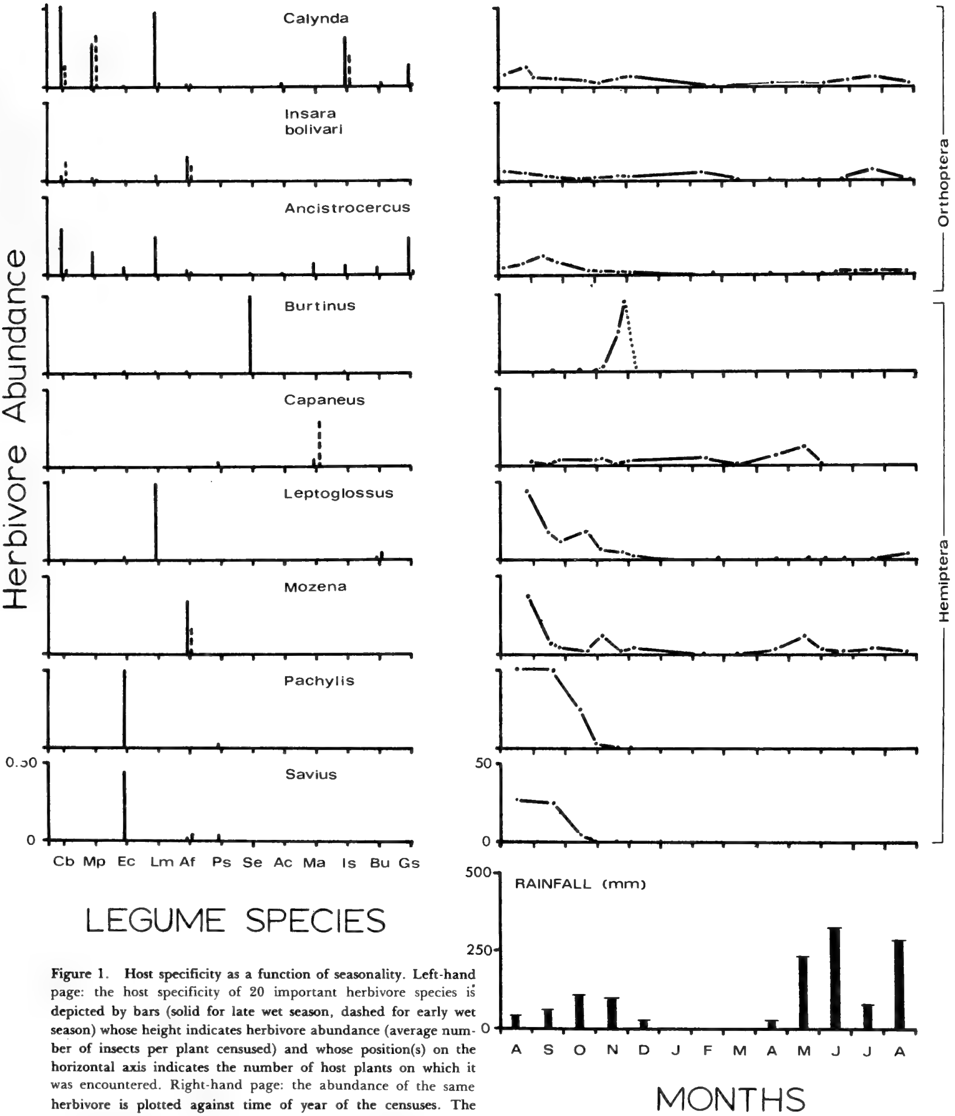


Figure 1. Host specificity as a function of seasonality. Left-hand page: the host specificity of 20 important herbivore species is depicted by bars (solid for late wet season, dashed for early wet season) whose height indicates herbivore abundance (average number of insects per plant censused) and whose position(s) on the horizontal axis indicates the number of host plants on which it was encountered. Right-hand page: the abundance of the same herbivore is plotted against time of year of the censuses. The abundance figure in this case is calculated by averaging the numbers of individuals of that species found on all of the host plants on which it fed for any one date. At the bottom of the right-hand column is a depiction of the rainfall regime for the same time period in the study area.

later, the same phenomenon recurred. The irruptions were largely limited to an area of 3 to 4 ha, an area with a high density of *Pisonia* in a patch of savanna bordering mature dry forest. Relatively more isolated plants, scattered throughout the rest of the study area, were untouched. *Pisonia* had other insect herbivores common especially in the early months of the dry season, none of which caused defoliation as severe as that inflicted by the Meloidae. In spite of the heavy loss of foliage to meloid beetles, all of the trees apparently survived.

Two other outbreaks of meloid beetles were observed within or in the near vicinity of the study area. A second unidentified meloid beetle emerged in large numbers in the mid wet season (July and August) removing the entire foliage production of an herbaceous roadside *Solanum* species. A third and more important outbreak of meloid beetles was observed in the second week in June 1974 on *Enterolobium cyclocarpum*. These beetles, of a third unidentified species, were observed completely defoliating seedling and sapling *Enterolobium* plants. Large mature trees in the habitat were attacked; additionally, however, damage was inflicted principally on the youngest foliage at the end of the branches and toward the tops of the trees. A search of surrounding vegetation indicated that their feeding was completely restricted to *Enterolobium*. Some isolated saplings were apparently spared the almost complete defoliation common on plants growing in higher densities.

Other conspicuous defoliators noted in the study area included a curculionid beetle, *Phelypera distigma,* whose larvae feed on the early leaf production of *Guazuma ulmifolia* L. (Sterculiaceae) in the last 2 weeks of May and early June. Leaf damage seldom exceeded 50 percent removal of surface area, although a much higher percentage of all leaves received at least some damage. The larvae pupate in groups on the undersides of leaves, emerge as adults in mid-June, and continue to feed for a brief period of time in the same area before dispersing.

Heavy defoliations of the first leaf crop of *Bombacopsis quinata* (Jacq.) Dugand (Bombacaceae) by leaf-cutting ants were noted in May and June of both 1973 and 1974. The trees most severely defoliated, greater than 80 percent leaf removal, were clumped in distribution and located near a very large colony of *Atta* in regenerating deciduous forest. Larval tortoise beetles (Chrysomelidae, Cassidinae) were important herbivores removing 50 to 90 percent of the first leaf production of saplings of *Cordia alliodora* (R. & P.) Cham. (Boraginaceae) in late May and early June of 1973 and 1974. A roadside annual, *Sida* (*rhombifolia*?) (Malvaceae), lost its entire leaf crop to the brood of an unidentified arctiid moth in June 1973 and 1974. All of the above examples of outbreak defoliation on other plants in the study area were more serious than that noticed on the censused legumes, with the one exception of the complete defoliation of the final leaf crop of *Sesbania*.

Host-Specificity and Seasonality of Insect Herbivores

The breadth of individual herbivore species' host preferences and their population fluctuations throughout most of 1 year are examined in Figure 1. Actual host preferences, of course, may be considerably broader than that indicated, since only 12 potential food plant species were censused. My casual observations of other plant species in the study area failed to add additional plants to the host lists of the important host-specific herbivores. The number of host plants for the Orthoptera and some of the polyphagous Coleoptera, however, has almost certainly been underestimated.

The feeding preferences of *Calynda* and *Ancistrocercus* were remarkably similar—each species preferred *Cassia* and *Lonchocarpus* above the other 10 legume species. Both of these Orthoptera were conspicuously rare on *A. farnesiana,* a plant which otherwise had one of the largest overall herbivore loads (Figure 2). *Insara bolivari* was the important orthopteran grazer of *A. farnesiana*.

Six of the more important Hemiptera species, all in the family Coreidae, are included in Figure 1. All 6 species displayed preferences for a single legume species. Two of the species fed on *Enterolobium*, while the other 4 species fed on different legume species. Seven of the 12 censused legumes lacked any important sap-feeding insects. Four of the 6 coreids had comparatively high populations at the beginning of the study in mid to late wet season. The populations of these 4 species declined until they were practically absent from the censuses at the start of the dry season. Unfortunately, little can be stated concerning the recovery of the Hemiptera populations in the following wet season since 2 species occured on *Enterolobium* and 1 species on *Sesbania*, neither of which were censused beyond the end of the first wet season. The sharp increase in the numbers of *Burtinus* on *Sesbania* in November was in perfect synchrony with the other herbivore populations peaking at this time on this legume. *Capaneus* was recorded in fairly even numbers with a slight increase noticeable at the beginning of the second wet season in May on the evergreen ant-acacia, *A. collinsii*. A similar increase in the population of *Mozena* is noticeable on the evergreen *A. farnesiana* in May.

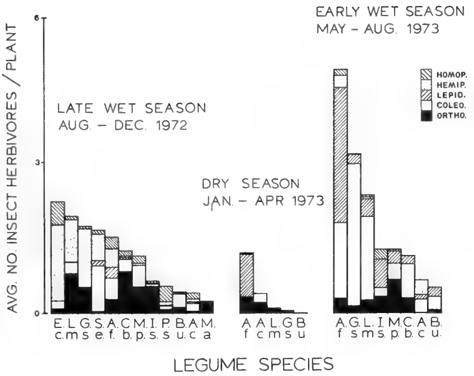


Figure 2. Seasonal variation in leaf predation. Three sets of bar graphs are drawn for the three major seasons of herbivore sampling. Each bar within a season corresponds to the total herbivore load associated with a particular legume species. Each bar is broken into sections indicating the relative importance of the major insect herbivore groups. Each bar can be identified by noting the initials of the legume species placed immediately below the horizontal axis.

Larvae of 5 Lepidoptera species, each occuring on a single host plant, appeared at the time of the first rains and first foliage flush in 1973. The larvae of *Semiothisa* were partial exceptions in that they were present on the foliage of *A. farnesiana* several weeks prior to the first rains. The other 4 species fed entirely on the first foliage appearing after the 3 to 4 months of deciduousness. *Ephyrodes* was an important defoliator of *Sesbania* during the month of November. Most of the Lepidoptera populations were present on their host plants for a relatively brief period, and the damage which they inflicted was quickly obscured by the continued production of new foliage.

Five species of Coleoptera are examined in Figure 1. Two of the species displayed the same extreme host-specificity noted for the important Lepidoptera. One of these, *Myochrous,* appeared suddenly on the foliage of *Sesbania* in late November. It was not observed feeding on any other plants in the study area at the time. The leaf-eating curculionid beetle, *Promecops,* fed exclusively on the foliage of *Gliricidia* in large numbers on practically all the wet season censuses. It was not recorded from sucker-sprout foliage of *Gliricidia* during the dry season. It reappeared on foliage approximately 1 month after the first rains in mid-May. The chrysomelid beetle, *Talurus,* was observed feeding on at least 4 of the legumes in the study. It first appeared in large numbers at the beginning of June, feeding heavily on the young foliage of *Lonchocarpus* and *Gliricidia*. One month later its population was virtually absent from censuses. The scarab, *Phyllophaga,* likewise peaked briefly on the June foliage of at least 4 of the legumes. *Leucothyreus,* a ruteline scarab, was one of the most important defoliators in the study area.

Discussion

This study has documented substantial differences in the feeding schedules of sap- and foliage-feeding herbivores. Foliage-feeding insects were principally active at night while sap-feeding insects fed both day and night. One hypothesis is that day-active vertebrate predators are important selective agents of these behavioral differences. Sap-feeding differs from leaf-feeding as a mode of harvesting resources by not requiring movement to renew consumed resources. Movement is certainly an important cue to vertebrate predators in prey detection (Marler and Hamilton, 1966). Sap-feeders, thus, are probably less susceptible to detection by diurnal predators than leaf-feeders. In addition to being able to feed without moving, the Homoptera are often exceedingly cryptic and have an explosive escape response. The Hemiptera are also sessile diurnal feeders, with a sluggish escape response and noxious smelling secretions released during disturbance. Alcock (1973) has described how red-winged blackbirds avidly capture but then release stinkbugs (*Euschistus*) unharmed. Most of the important coreid bugs in this study were easily captured during the day but were extremely noxious smelling. One species, *Pachylis*, has highly aposematic nymphs which feed in large and conspicuous aggregations on the terminal shoots of *Enterolobium*.

Nocturnal feeding witnessed among the Cicadellidae, Coleoptera, and Orthoptera may have evolved principally because of lowered rates of predation. Most Coleoptera species spent the entire day on the host plant hidden under leaves. Most Orthoptera species left their host plants during the day for roosts elsewhere. One of the more important herbivores in the study, *Ancistrocercus,* roosts during the day near the carton nests of aggressive social wasps (Wilson and Downhower, 1973). It should also be noted that nocturnal feeding habits do not entirely remove the risk of predation. Wilson (1971) has examined the feeding remains of the bat *Micronycteris* on Barro Colorado Island, finding tettigoniid grasshoppers and Scarabeid beetles as important dietary items. Meloid beetles also prove an interesting exception to the feeding schedules mentioned above. The 3 species of

Meloidae noticed defoliating plants in the study area were all active daytime feeders. Meloids are well known to reflexively bleed extremely irritating body fluids upon disturbance (Eisner, 1970). Chemical defenses among these insects may be an important factor allowing daytime activity in a manner analogous to that suggested for some Hemiptera.

Sap is a less concentrated resource than leaves and may require almost continual harvest for normal rates of growth and reproduction. Feeding on leaves, in contrast, may supply adequate nutrients in a short enough time period such that daytime feeding can be abandoned entirely. Physical factors, such as heat and humidity may also affect feeding schedules. Rockwood (1975) mentions that ground and air temperatures and humidity are correlated with switches to nocturnal foraging during the dry season among leaf-cutting ants. Other factors may additionally be involved in the preference of leaf-feeding insects for nocturnal activity.

Both leaf- and sap-feeding insects preferentially fed on young foliage toward the ends of growing shoots. The very youngest expanding foliage was seldom the site of herbivory. The slightly older, and usually nearly fully expanded though often texturally soft, foliage seemed to be the focus of most insects. The greatest abundance of this type of foliage naturally occurs in the first 2 months of the wet season as all the species that are deciduous during the dry season put out a fresh new crop of wet-season leaves. It was also my unquantified observation that the leaves produced in the first 2 months of the wet season were also the largest of the year, thus contributing to the temporary abundance of new foliage. The preferences of these insects for young foliage and stems and the occurence of the major defoliators in the first months of the wet season resembles the pattern of herbivory described by Feeny (1970) on oaks in England. The period of heaviest feeding corresponded to the time when foliage was tenderest and had the greatest quantities of free nutrients.

Summary

The observations presented in this paper lend support to the contention that plant foliage is a resource whose quality and quantity for insect herbivores vary considerably depending on time of year. Most of the evidence presented above indicates that the foliage of legumes in a lowland tropical deciduous forest is maximally available to folivores in the first 3 months of the wet season. It is during this time that practically all herbivore outbreaks were noticed in the study area as well as the time of the peaking of most populations of leaf-consuming Coleoptera and Lepidoptera species. Young foliage continued to be produced on all of the legumes censused after the first 3 months but the rate of production of new foliage was lower. Most holometabolous insects seemed to time their population emergences to the time when young foliage was being produced at the greatest rate and generally was most abundant in the habitat. Through the last 5 months of the wet season, population irruptions of leaf-feeding herbivores were rare on the woody perennial legumes while the dominant croppers of the smaller amounts of new foliage being produced were the tettigoniid and phasmid Orthoptera. It is hoped that these observations will provide a useful base for other experimental studies of plant-herbivore interactions in tropical habitats.

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Reptilian Arboreal Folivores

There are few arboreal reptiles that specialize in eating leaves, but several different reptilian stocks have evolved this way of life and seem presently quite successful at it, although none of them have radiated in this adaptive zone. It is easier to explain either why reptiles should be good folivores or why they should not than it is to explain both simultaneously.

The problem of the evolution of plant-eating in modern reptiles has attracted attention recently, and I have drawn heavily on the papers of Keeling (1974), Pough (1973), Ostrom (1963), Sokol (1967, 1971), and Szarski (1962), and discussions with E. E. Williams, R. Huey, G. Burghardt, H. Greene, C. Toft, and my colleagues at STRI. I have tried to reference points of fact and to credit ideas, but I have not tried to be complete; where several references were available, I have usually cited only one.

In the class Reptilia, herbivory is common in turtles and in several extinct orders; it is not known in modern crocodiles, the tuatara, or in snakes. In the rest of this paper I will deal with lizards, which include a variety of herbivores and the only arboreal reptilian folivores known today.

Lizard herbivores are varied in diet, diverse taxonomically, and widespread geographically.

Lizards eat a variety of plants and plant parts. Flowers, buds, and fruit (particularly red and orange berries; Halliman, 1920; Harris, 1964; Mayhew, 1963) seem to be preferred, especially by the partial herbivores. Some of the more exotic observations mentioned in the literature are: Geckos on a small island off New Zealand were seen lapping nectar from flowers, as many as 50 geckos feeding on 1 tree and 5 in a single flower (Whitaker, 1968). Australian skinks are recorded as destroying a strawberry crop by eating the ripening berries (Goin and Goin, 1963).

Individual *Angolosaurus* in South West Africa were found living in bare sand dunes and existing by eating the grass seeds that were blown across to them (Hamilton and Coetzee, 1969). *Uromastix,* an agamid and one of the most specialized herbivores in its dentition, is reported as eating straw and seeds as well as green leaves and as sometimes feeding on gazelle droppings (Dubuis et al., 1971). Perhaps the most improbable lizard herbivore is the marine iguana on the Galapagos Islands that dives to depths of 10 meters to graze on submerged algae (Darwin, 1957 edition).

Mature leaves are eaten regularly only by specialist herbivores. Plant material, particularly that rich in cellulose or protective secondary compounds, is probably digested less efficiently, more slowly, and is a less well-balanced diet than is animal food. But plants are more generally available and more easily caught than are animals.

Most lizards that regularly eat plant material also eat substantial numbers of animals. For most lizards, plants seem to be, at best, a supplementary food that is taken when the more desirable animal food is not available (Pearson, 1954). Even predominantly herbivorous lizards usually take animals when they can get them.

It has been suggested that lizards lack the machinery to cope with vegetation. Mature leaves are tough and Sokol (1967) suggests that only big lizards have the strength to deal with them. Herbivorous lizards do not have grinding or crushing teeth. Ostrom (1963) suggests that because of the kinetic skull of squamates, and particularly the mobile articulation of the quadrate to the skull, a lizard cannot exert sufficient pressure with its teeth to chew effectively. As far as I know, herbivorous lizards do not chew, except perfunctorily, but some lizards (e.g., *Dracaena*) have molariform teeth used to crush snail shells (but do not chew them). However, Hooton (1955) and Montanucci (1968) have described the dentition of herbivorous lizards, such as iguanas, as quite specialized, but for cutting leaves rather than crushing them. They do not shear the leaves, Bakker (personal communication) assures me, but rather perforate and tear them, like sheets of toilet paper.

Lizards do not have a gizzard and mechanical grinding probably is not important in the gut, although Sokol (1971) suggests that the occasional stone one finds in a stomach may have been eaten intentionally to serve this function. Intestinal floras functioning to break down plant material have not yet been identified in lizards, although both *Uromastix* and *Cyclura* may have masses of nematodes in the large intestine which have been suggested to have a mechanical-mixing effect prompting digestion. In contrast to carnivorous lizards, herbivorous lizards such as *Iguana* and *Uromastix* do have ceca, and valves have been described in the lower intestine which could function to slow the passage of food and increase efficiency of digestion.

Direct evidence of effectiveness of digestion is scant. Throckmorton (1973) reports 85-percent digestive efficiency on sweet potato root, roughly equivalent to that of insectivorous lizards fed on mealworms. Nagy (1973) reports lower efficiency on more fibrous material and Auffenberg (personal communication) reports very little digestion at all of leaves in a West Indian *Cyclura*. My gross examination of *Iguana iguana* guts suggests that they break down leaves quite effectively. We badly need hard data here, but it seems likely that plant material, particularly cellulose-rich materials such as leaves, is processed with less efficiency than is animal food and probably more slowly as well. Parker (1972) noted that the herbivorous *Dipsosaurus* grows more slowly than sympatric insectivorous lizards.

On the other hand, large quantities of leaves are easily available and an herbivore can usually keep its digestive apparatus full and working at maximum. Desert species in drought years are exceptions, as are females with a full clutch of eggs. *Iguana* and *Dipsosaurus* both have been reported to stop feeding while the clutch is reaching full development (Rand, 1967; Norris, 1953). There is literally not room for both food and eggs in the body cavity.

It may be that nutrient requirements other than that for energy are also involved in adapting to a diet of plants. The salt glands in iguanids may function to conserve water, but also to maintain the animals' balance between potassium and sodium in a potassium-rich plant diet (Sokol, 1967). Plants are frequently poor in calcium, which is important to any growing vertebrate. Protein may also be a problem (Marshall and Hook, 1960), although leaves are quite rich in protein. Many plants contain protective secondary compounds that are more or less toxic to herbivores. The detoxification of these may be risky or expensive metabolically. The problem that any one plant may not provide a balanced diet may be solved by eating a variety of plants or by specializing on a single plant and adapting the physiology to the available materials. This is common insect strategy, but rare in vertebrates.

Lizards are ectothermic; body temperatures drop at night, particularly in small individuals (Regal, 1966), and presumably digestion slows as peristalsis does. Herbivorous lizards bask and there is some suggestion that they select high temperatures. The energetic cost of endothermy probably would not offset the gain from continuous high digestion. But the possibility of putrefaction or fermentation proceeding faster than digestion at low temperatures is a real risk and zoo keepers report that this is a cause of death in tropical herbivorous reptiles kept in temperate areas.

In contrast to some mammalian herbivores (e.g., horses), herbivorous lizards spend little time feeding, and a great deal of time completely motionless. One has the impression that rate of digestion limits the energy intake and that they are very careful in their energy expenditures. In this they are like the sit-and-wait predators rather than the searchers. The sit-and-wait strategy is common in fish, amphibians, and birds, as well as in reptiles, but is relatively rare in mammals.

It has been noted that an herbivore such as *Uromastix* has a small home range (4-5 hectares) when compared with a comparably sized carnivore such as *Varanus* (200-500 hectares) (Saint Girons and Saint Girons, 1959). However, *Varanus* is a predator that actively searches for prey and Turner et al. (1969) report that the difference disappears if one compares the herbivorous *Dipsosaurus* with sit-and-wait insectivores. These have about the same home-range-size relative to their body size.

Among the morphological correlations with herbivory, one of the most striking is with size. Pough (1973), who has reviewed the situation extensively, shows that within lizard families it is the large species that are herbivorous, the moderate-sized ones that eat both plants and animals, and the small ones which tend to be strictly animal-eaters. Certainly there are large carnivorous lizards, but no small folivores. Within species, if there is an ontogenetic change, it is the large individuals that eat plants, the small ones that eat animals.

Several arguments have been advanced to explain the correlation. The first is that leaves are tough and to deal with them a lizard must be large and strong (Sokol, 1967). This can hardly hold for geckos drinking nectar, but may generally be true. Second, as the size of animal increases, its prey size must increase also, unless it specializes in something very abundant such as ants or plankton. Generally, large prey is less common than small prey, perhaps harder to catch and certainly more irregular in appearance. Anything which lives on infrequent prey might well need to supplement it with a secondary food such as plants.

Larger animals are energetically more efficient than are small ones and thus can exploit an energy-poor food supply. For reasons that are unclear, the per-gram energy requirement of all animals decreases as the size of the animal increases. The total energy requirement of a large animal is more than that of a small animal, but the increase is proportionately less than the increase in food-processing capability.

Though folivory is rare, herbivory is taxonomically widely distributed in lizards. It occurs in at least occasional members of the Iguanaidae (Cowles, 1946), Agamidae (Theobald, 1868a, 1868b), Teiidae (Holmberg, 1957), Gekkonidae (Mertens, 1962), Scincidae (Bustard, 1970), Gerrhosauridae (Fitzsimons, 1943), Lacertidae (Nikolški, 1963), Xantusiidae (Brattstrom, 1952), and Cordylidae (Broadley, 1954). Families without herbivorous representatives are generally small, poorly known, or highly specialized trophically (for example, the Pygapodidae, Helodermidae, Varanidae, Amphisbaenidae, and Chamaleonidae).

In lizards, herbivory is widespread geographically, occurring in all of the major zoogeographic regions. It is not equally common everywhere, but shows certain environmental correlations—it is most frequent in deserts, on mountains, and on islands; it is least prevalent in moist forests.

There are more or less specialized reptile herbivores in all of the major hot desert and semidesert areas of the world, with the possible exception of the Chaco in Argentina. In North America, Keeling (1974) found a clear inverse correlation between the percentage of lizards that were herbivorous and the annual rainfall. In at least 2 areas, in the southern Andes and in Pakistan (Minton, 1962), there are more herbivorous species of lizards at higher than at lower altitudes.

Both arid regions and high mountains are areas of low productivity. A broadening of diet and taking of more food from lower in the food chain in areas of low production is not surprising (Emlen, 1966; Huey, 1969; Pianka, 1970). Nor is it surprising that in these areas of low production ectothermic lizards and tortoises are more important as vertebrate herbivores than elsewhere. First, these are areas where heliothermy is easy and, second, ectotherms can maintain a much higher population on a given food base than can endotherms (Golley, 1968; Bakker, 1975). Thus, where food is scarce, a lizard might maintain a breeding population, where a mammal might not.

A disproportionate number of lizard herbivores occur on islands: New Zealand (Whitaker, 1968), Fiji (Cahill, 1970), the Philippines (Taylor, 1922), the Solomons (Parker, 1967), the Azores (Sokol, 1967), the Mascarenes (Vinson and Vinson, 1969), the Antilles (Grant, 1942), and the Galapagos (Van Denburgh and Slevin, 1913) all have lizard herbivores. Some of these islands are very arid, but others are not. Low productivity can not completely explain the relationship between herbivory and islands. Islands, because of their typically impoverished faunas, are areas of reduced competition between species and reduced predation. Where interspecific competition is low, relative to intraspecific competition, social selection for increased size may be particularly effective. In lizards, size and herbivory are closely related. Larger lizards are both better able to process plants and to have fewer appropriately sized animal prey available to them than are smaller lizards. If lizards on islands become larger because of social selection, they could, because of this size increase, become more herbivorous.

It also has been argued by Szarski (1962) that many herbivorous lizards, because of their energy-poor diet, have less energy available for reproduction than do carnivorous lizards. The argument continues that herbivory is thus favored in areas of low predation where mortality is low and can be balanced by a low recruitment. This may be true on islands and also in deserts and high mountains. Janzen (1973) suggested that on islands, in the absence of predators, lizards could bask more and thus be better able to digest plant material.

The inverse of the abundance of herbivores on deserts, mountains, and islands, is their relative rarity in the core areas of the mainland wet tropical forests and savannas. In the African wet forests there are no herbivores (Cansdale, 1955). In the mainland Indo-Malayan region there are no leaf specialists, although some of the larger agamids (*Physignathus*) eat some plant material. In the Indo-Malayan archipelagos, the Philippines and Indonesia, the agamid *Hydrosaurus* is an herbivore living among streams and climbing trees to eat leaves (Taylor, 1922). In the Australian region, there are no arboreal herbivores in the forests of Australia itself (Bustard, 1970); on New Guinea, the agamids of the genus *Goneocephalus* are arboreal herbivores and in the Solomon Islands there is also the skink *Corucia* which is more of a folivore than is *Goneocephalus* (Parker, manuscript). In the Neotropics, the pattern repeats itself—there are a number of herbivores in the arid areas (Cowles, 1946; Duellman and Duellman, 1959; Evans, 1951) and on tropical islands (Carpenter, 1970), but only a single widespread species, *Iguana iguana,* in the wet forests.

The correlations between herbivory and environment suggest that the constraints on reptilian herbivory are not primarily due to anatomical or physiological inadequacies of lizards, but must at least in part be due to ecological factors. One of these factors is predation. Janzen (1976) suggests that the absence of reptilian herbivores in Africa is part of a general depression of reptile biomass in that continent. He explains this as a result of heavy predation pressure on reptiles which occurs because of the large African ungulate fauna that supports large predator populations that can feed on reptiles, but are not dependent on them entirely. We will return to his argument later, in relation to the evolution of *Iguana.*

Iguana iguana is probably the most widely distributed and most successful arboreal reptilian folivore and the one about which most is known; although, as the following paragraphs make clear, we know very little about it as an herbivore.

Iguana iguana occurs in semiarid and arid habitats, on the north coast of South America, in the Cattinga of northeast Brazil (Vanzolini, 1972), in the *llanos* of Venezuela, along the gallery forests in Pacific Central America (Rand, 1957), and in a variety of wetter forests from Mexico (Alvarez del Toro, 1960) to Brazil (Rand and Humphrey, 1968), particularly, but not exclusively, along river margins (Hoogmoed, 1973). Nowhere does the species extend very far up the mountains nor much outside of the tropics.

Primarily arboreal, iguanas can come to the ground to move from tree to tree, to lay their eggs, and in some situations to feed. In some places, as in Islas Los Roques off Venezuela, they are terrestrial, living among rocks (Roze, 1956). In areas where they are not hunted by man, iguanas can reach high densities. They are common enough in certain parts of the *llanos* to be an important danger to the cotton crop. Iguanas are quite variable geographically, as one might expect in a reasonably sedentary animal inhabiting a variety of habitats.

Iguanas primarily eat leaves. They also eat fruit and flowers regularly and probably whenever possible. It would be surprising if they did not take buds and flush leaves in preference to old leaves. Still they do take a wide variety of mature leaves, biting and tearing off pieces with their specialized flattened and serrated teeth. They do not crush or grind the leaves, either in the mouth or in a gizzard. Judging from the condition in which the leaves appear in the lower intestine, they are able to digest them quite thoroughly. The lower intestine has a well-developed cecum and a series of valves that may help hold the gut contents until they are fully processed (Lönnberg, 1902). A specialized gut flora is to be suspected, but is as yet undemonstrated. Salt-secreting glands in the nostrils may help to maintain the ion balance in an animal on a potassium-rich plant diet. We badly need information on diet selection and digestive efficiency.

Iguanas are among the largest lizards, exceeded only by the monitors, and, as discussed above, there is a good correlation between size and herbivory in lizards. Many lizards that are herbivorous as adults are insectivorous as juveniles (Fleet and Fitch, 1974). A similar ontogenetic change in diet has been reported in certain turtles where a relation to the juveniles' greater need for calcium during rapid shell growth was important (Clark and Gibbons, 1966). Iguanas are exceptional in that even the very young juveniles are primarily herbivorous (Hirth, 1963; Henderson, 1974).

Iguanas have been reported to eat feces and carrion (Loftin 1965), but do so only occasionally and do not eat their own feces. Both adults and juveniles will take animal food when offered and young animals may need some animal protein for normal growth. To evaluate the possibility of food limitation in environments where mature leaves are superabundant, we need information about the physiological importance of the infrequently eaten foods and we have almost none.

One rarely sees iguanas eat anything and they spend most of their time motionless (Moberly, 1968, estimated 90 percent of the time). One has the impression that they minimize energy expenditure in daily existence and in this they are like smaller insectivorous members of the family that are sit-and-wait predators. Unlike the insectivores, the iguanas' energy intake appears to be limited by the rate at which they can process leaves internally. This may be deceptive and the occasional opportunity to gorge on fruit and flowers may be of greatest importance in their overall energy budgeting, particularly with respect to that available for reproductive investment. It is evident from the wide geographic and ecological distribution of iguanas that they are not extreme specialists in the species of plants that they can eat. Their limited mobility precludes them from exploiting widely dispersed food sources. We know almost nothing about their ability to detoxify secondary compounds, so it is very difficult to estimate what food is available to them in a given habitat.

We, as yet, understand little about the home-range utilization of iguanas. We do know that an iguana is frequently seen in the same tree, perhaps even the same branch, for several successive days and then disappears and may not be seen there again for days, weeks, or even months. Limited radio-tracking suggests either large home ranges or a wandering pattern (Montgomery et al, 1973). They are sometimes seen in trees with no food (e.g., coconut palms) and juveniles sometimes leave bushes in which they have been feeding and move to apparently identical ones, even though the first still has plenty of food. I suspect that these irregular movements may be related to predator avoidance. Iguanas, particularly young ones and females during nesting, are highly vulnerable to predation.

Iguanas lay large clutches of eggs once a year (Rand, 1967; Rand and Humphrey, 1968). A 2-kilogram female may lay 60 eggs with a total weight of 800 grams. There is a close correlation between female size and clutch size.

In Panama, iguanas probably mature in 2 or 3 seasons and live and continue to grow for a number of years thereafter. In Colombia, Mueller (1968, 1972) says that few live more than 10 years. He also compared populations in 2 areas; one with a strong dry season, during which there was little food for iguanas, and a nearby area with more uniform moisture and year-round food availability. The iguanas from the seasonal habitat were smaller and proportionately lighter than similarly aged iguanas in the less variable habitat. This argues strongly that in least certain habitats and at certain times of the year iguanas may be short of food.

Iguana iguana in the Neotropics has somehow achieved an ecological breakthrough into the arboreal folivore niche in the humid tropical forest that no other reptile can match. Although we have discussed several of the factors involved, we cannot identify the key adaptation. Certainly the strongest candidate and the first place to look is in the iguanas' apparently unusual ability to digest mature leaves.

Perhaps as difficult to explain as the success of iguana as a folivore is that fact that, having made what looks like an evolutionary breakthrough into a new adaptive zone, it has not radiated.

Barring some bizarre explanation, such as the lack of genetic plasticity, I can see only 2 explanations. First, that iguana has not had long to evolve in the mainland Neotropics. The family is known from the Cretaceous (Estes and Price, 1973), but the genus not before the Quaternary. Admittedly, the fossil record for lizards is poor and negative evidence of this sort is always suspect, but we have no evidence of a long history.

If, as Janzen (1976) suggests, iguanas could not survive in present-day Africa because of the predators, the Neotropics may also have been a much less suitable iguana habitat during the Tertiary when the mammal fauna of the New World was much more like that of Africa today. Indeed, if the Pleistocene mammal extinctions occurred 10,000-20,000 years ago (Martin and Wright, 1967), then the mainland Neotropics have become much more suitable for iguanas only very recently and, if their wide distribution is so recent, it is no surprise that they have not radiated.

If iguanas have appeared recently, then they have either evolved very rapidly [and one should remember that despite their archaic appearance, large lizards can evolve rapidly (the Galapagos Islands are at most a few million years old)], or they have invaded the mainland forests from some other habitat, possibly the adjacent arid habitats or perhaps, even more likely, the Antilles.

The second possibility is that the iguana niche is ecologically indivisible. By this, I mean that there is no way in which 2 iguana species could coexist without competing; that there is no way in which the critical resource can be partitioned, and I can envisage no critical resource but food.

Let us review the possibilities of resource partitioning. One of the most common in herbivores is specialization on specific food species. For herbivorous lizards, because of their large size, this is impossible in the tropical wet forest. No tree is big enough to support a breeding colony of iguanas and the diversity of tree species and dispersion of conspecific individuals, combined with the limited mobility of iguanas, makes their exploiting a number of individuals of the same tree species impossible.

Other methods of food resource partitioning used by lizards (e.g., differences in size, foraging techniques and foraging times) will not subdivide the arboreal folivore niche in the tropical wet forest. Habitat separation is a possibility and it should be noted that in Central America there is a close relative of *Iguana, Ctenosaura*, which lives in more arid habitats while *Iguana iguana* is more closely tied to wet areas. In South America, where *Ctenosaura* is absent, *Iguana* occurs in very dry situations as well as wet ones.

We end, as we began, with the unresolved paradox that very few lizards are successful herbivores, but at least one has been extremely successful over a wide area, but has not radiated.

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Avian Arboreal Folivores: Why Not?

Introduction

Selection basically favors attributes that increase or maintain the highest efficiency in energy extraction from the environment because this is correlated with reproductive success. The question basic to this paper, "Avian Arboreal Folivores: Why Not?" must therefore be introduced by a discussion of avian adaptative strategies. How do birds differ from other forms and how do these differences allow us to understand why folivory is rare in the Class? Obtaining and extracting energy from food provides a major source of selection on a species' morphology and physiology. However, neither the energy source, morphology, or physiology of species can be realistically separated from each other when we try to interpret the evolution of a group of organisms. We certainly cannot say, for example, that leaf-eating caused a change in morphology or physiology, for the changes were synergistic.

Advantages and Disadvantages of Obligate Leaf-eating in Birds

I restrict this dicussion to obligate leaf-eating, referring to birds that obtain most of their energy from leaves because, as will be shown, leaves may be an important nutritional component for many species that would not be called folivores. This discussion, therefore, is in part hypothetical because so few bird species are obligate leaf-eaters. Here I hope to show why this is the case.

Surely the main advantages of leaves as a potential food source are that they are abundant and easy to obtain. A major disadvantage relates to the extraction of energy from them for this requires a relatively long retention time such that leaves must be eaten in large quantity and they require a large storage space in the alimentary canal (Morse, 1975). Since birds are structurally adapted for flight, a particularly energy demanding form of locomotion (Hart and Berger, 1972; Tucker, 1971), extracting energy at a high rate is important.

The storage of leafy material to enable time for symbiotic bacterial digestion of cellulose is a major disadvantage for flying organisms (Morse, 1975). The weight of this undigested material increases the energy demanded by flight. Increasing body size to accommodate more leafy bulk is strictly counterproductive because a bird weighing twice as much as another requires 2.24 times as much power to fly (Pennycuick, 1969). Large birds, such as the Kori Bustard (*Ardeotis kori*), weighing about 11.9 kg are barely able to fly even without any additional load, such as food. These birds eat continually and are able to subsist on a continuous but small ingested supply of vegetable matter but without building up fat stores (Pennycuick, 1969).

Although there is a major disadvantage to leaf-eating in reducing flying efficiency, there is no reason to suspect that birds lack the capability to extract energy from leaves as efficiently as mammals. Cellulolytic bacteria are apparently rare in the avian ceca (McBee, 1971), but this probably only reflects the rarity with which birds use cellulose for energy, not an impossibility to do so. The honeyguides (Indicatoridae) have symbiotic bacteria that enable them to exist for at least 32 days on a pure beeswax diet (Friedmann and Kern, 1956). Microbial decomposition of cellulose has been found in cultures from the caeca of several species of grouse (Suomalainen and Arhimo, 1945; McBee and West, 1969). There are as yet few data on the extent to which the products of cellulose digestion provide nutrition to birds, but the ceca are important in maximizing the availability of absorbable compounds from ingested food (Thompson and Boag, 1975).

Coprophagy, which provides an excellent source of protein for some herbivorous mammals (Griffiths and Davies, 1963), may not be possible for birds. Luckey, et al. (1955) showed that B vitamins are synthesized in chicken ceca but that absorption was minimal because coprophagy is lacking. Coprophagy may not be possible for birds because they excrete uric acid and this is mixed with fecal matter in the cloaca. The embryonic necessity of uric acid production in birds (and reptiles) probably precludes the production of watery urine in adults (Benoit, 1950).

The Adaptive Radiation of Birds

The disadvantage of eating leaves by a flying animal discussed thus far include added weight, longer retention time, and slower energy release. But birds do not have to fly, and indeed many species do not. The evolutionary pathway to arboreal folivory may thus have been open to birds, but few species have chosen it. The adaptive radiation of birds may be canalized away from arboreal folivory by competition with other forms (Morse, 1975).

One of the evolutionary benefits afforded volant organisms is the exploitation of food that is distributed patchily and in such places that nonvolant forms cannot use it efficiently. Morse (1975) has discussed this in detail. When one watches birds inspecting leaves on small branches high in tree crowns, one is impressed with the combination of factors operating. First, the bird is able to move from branch to branch easily by flight. But this is also possible for leaping and climbing mammals. What is unique to the bird is the use of flight to chase "dislodged" insects that drop or fly from the leaves. For the nonvolant mammal these items are surely lost. Birds as insect predators may provide selection pressures favoring various forms of crypsis in insects (Robinson, 1969) rather than active escape. Thus, birds may be important in maintaining insects in a stationary position where nonvolant mammals can capture them.

Predator pressure on birds has tended to favor retention of flight as an escape mechanism for fully grown birds and has favored rapid development of young to the point where they can fly. Flight also allows birds to nest in sites that are inaccessible to certain predators. That flight permits escape from many predators may sound like a truism, but flight can be lost whenever predators are absent or other forms of escape (such as swimming) are more successful. Many island species have become flightless during a fairly short time span (Olson, 1973). As will be discussed below, folivory and flightlessness are evolutionarily related, and predator pressure may be an important contributory factor to explain why folivory is rare in birds.

Birds have 2 major ways of developing from hatching to an individual with adult capabilities of locomotion. In the precocial mode, young may be able to obtain most of their own food. In the altricial mode, all food must be provided to the young by the parent(s) while the young are incapable of locomotion. In both types of development, the young are vulnerable to a host of predators. This source of selection has favored the highest possible growth and development rates in birds (Rickleffs, 1968; 1969). This has also, given the option, favored food for young that permits rapid growth. Even fruit, which averages at least twice as much energy content as leaves (Jenkins, 1969), is rarely eaten as the sole diet by birds. As a diet for altricial young, fruit is nearly as rare as leaves (Morton, 1973).

That all birds lay eggs and most of them must bring food to their young in raw form is in significant contrast to mammals where milk provides nutrition for growing young. Much more time and energy must be expended per young by an adult bird than for a mammal in raising young because of the energy needed to make a round trip from the young to the food source for each food item. That most birds search for and bring single items of raw food to their young increases the energy needed by the adult for reproduction. This has resulted in many differences between birds and mammals, one of which is the need for high-energy food, which again precludes leaves. Selection has favored bringing large amounts of gathered food to young at one time whenever possible (such as regurgitation of crop contents). For many bird species this is not possible because the food is too large to be stored, or the capture of one food item reduces the bird's chances of capturing a second as long as it carries the first, or both.

This, in combination with the 2 factors presented above, provides a selective argument explaining the rare use of low energy food (leaves) by birds. Number 1 argues that birds are successful in the volant realm and less successful in herbivory than mammals because flight does not confer decided advantage in obtaining leaves. Because most birds are volant, they do best utilizing foods distributed patchily in time and space or in areas that nonvolant forms can exploit with difficulty. Number 2 states that, because most birds use flight to escape predators, the period before young animals are able to fly is reduced to the minimum. The need for rapid growth largely precludes the use of low-energy foods, such as leaves.

In combination, the factors discussed above provide reason enough to explain why folivory has not been selectively advantageous for birds. Additionally, they provide a means of predicting what a folivorous bird should be like and in what situation(s) it is likely to evolve.

We would expect the evolution of a large storage space relative to the size of the bird to allow large amounts of leaves to be digested at one time. This is particularly important to allow sufficient energy for survival during the night (or day) when the bird is not active or foraging. If young are fed on the same material, this storage space might serve a dual function in providing partially digested food for the young and in permitting the adult to carry sufficient food for itself while it is feeding young its reserve.

The leaf-eating bird would tend to avoid flying or perhaps lose the power of flight to bring its energy balance in tune with the rate of energy extraction possible from leaves. The loss of flight would in turn seem to make arboreal leaf-eating less likely because good climbing ability would require extensive alteration of the avian forelimb. In contrast, the terrestrial leaf-eating mode might be expected to evolve more frequently since the energy cost of walking is probably more in line with energy income from plant material than is flying.

We might further expect leaf-eating to evolve where predators are not common or that rather bizarre predator avoidance mechanisms might co-evolve with leaf-eating habits. This is especialy so for birds because, in general, adults tend to have few antipredator behaviors or capabilities except escape. The bottleneck probably occurs in reproduction. The need for an incubation stage and relatively active movement to and from the nest to furnish food to growing young makes young birds more vulnerable to predators than young mammals.

Leaf-eating Birds

In this section, I first describe the adaptation for leaf-eating occurring in two extant species, the Hoatzin (*Opisthocomus hoatzin*) and the Owl Parrot (*Strigops habroptilus*). Both species are highly convergent in ways directly attributable to their leaf-eating habits. We are justified in calling them convergent because they are quite unrelated, the Hoatzin being a cuckoo (order Cuculiformes) and the Owl Parrot, a parrot (Psittaciformes). The Hoatzin was, until recently, considered a galliform (chicken order) species. It is now considered to be related to the cuckoos based on data from electrophoretic comparisons of egg white proteins (Sibley and Ahlquist, 1973). Convergence in morphology is often a result of similar adaptations to similar habitats. In this case, however, the habitats are not at all alike and the convergence is most likely due to their feeding almost entirely on foliage.

The Owl Parrot, now extremely rare, occurs in New Zealand. Introduced mammals such as pigs, cats, dogs, stoats, ferrets, and rats are decimating it rapidly (Oliver, 1955). It is nocturnal, hiding in holes among rocks or beneath tree roots during the day. It nests in burrows which it digs. It is flightless but climbs trees to obtain fruit, nectar, and leaves, and is capable of gliding to the ground. The bird keeps runways open through the meadows by clipping off growing shoots of grass. The principal food items are leaves and young shoots of Snow Grass (*Danthonia flavensceus*), leafless twigs of *Carmichaelia*, and bracken fern rhizomes which may be stored for future use (Oliver, 1955). Cellulose is apparently not important to its nutrition for the bird has behavior adapted to reduce the cellulose content of its diet. It eats only the soft basal portion of Snow Grass shoots and it masticates twigs and other woody material to extract juices. They also strip Snow Grass leaf blades from their central veins and then retire to their sleeping places to chew them until the juice is extracted (Oliver, 1955). They then regurgitate the fiber in "dry balls."

The Hoatzin is restricted to riparian vegetation along the streams of the Orinoco River and Amazon River drainages in northern South America. Its habitat consists largely of the mangroves, *Lagunularia, Rhizophora,* and *Avicennia nitida,* interspersed with the prickly bush *Drepanocarpus* and the arum *Montrichardia arborescens.* The Hoatzin does not usually fly at all, but flops from branch to branch. It feeds on *Avicennia, Drepanocarpus,* and *Montrichardia* leaves, and fruit when present. The Hoatzin seems to spend most of midday resting, filling the crop in the early morning and evening (Grimmer, 1962). The birds are sedentary, sluggish, and poor fliers. I quote from Beebe (1909:57),

> "the first bird makes many false starts, crouching and then losing heart, but the next on the branch getting impatient, nudges him a bit, and at last he launches out into the air. With rather slow wing beats, but working apparently with all his power, he spans the wide expanse of clear bush, then the ten feet of water, then fifteen yards more of stumps, and with a final effort he clutches a branch. After several minutes of breathlessness, he makes his way out of sight into the depths of the brush. A second Hoatzin . . . fails ignominiously and falls midway. . . . Here a rest is taken, and for five or ten minutes the bird may feed quietly. Sometimes when the birds alight and clutch a twig, they are so exhausted that they topple over and hang upside down for a moment."

Young are fed on regurgitated arum leaf mush (Grimmer, 1962).

The Owl Parrot and Hoatzin share a peculiar morphological adaptation for leaf-eating and reduction or loss of flying ability. The morphological peculiarities are adaptations for increasing room for food storage and digestion. In the Hoatzin, the crop has assumed the function of the gizzard (Beebe, 1909). The crop, the principal enlargement of the esophagus, is abundantly supplied with glands, and with a powerful musculature. The true stomach is weakly developed, about one-fiftieth the weight of the esophageal region (Pernkopf, 1937, in Zisweiler and Farner, 1972). The Owl Parrot has the same modification of the crop. Both species also show a reduction of the front part of the keel of the sternum, permitting a greater area for food storage in the crop. When the Hoatzin's crop is filled, the weight makes balancing on perches difficult. Consequently the bird rests the sternal area on a branch to support the heavy crop.

The relationship between predation and folivory is well illustrated by the two folivores just described. The Owl Parrot, residing only in New Zealand, evolved in a relatively predator-free area and is now rapidly approaching extinction owing to predation from animals introduced by humans. The Hoatzin, however, has had to evolve specialized predator-avoidance mechanisms to overcome the difficulties posed by its sluggish movements and by the long time its slowly growing young require before achieving adult locomotory ability. Predation pressure seems the most likely factor that has restricted the Hoatzin to life along rivers. Nests are built in vegetation over water, 1 nest being attended by groups of 2 to 6 birds, and are often associated with wasp nests (Grimmer, 1962). The young hatch with well-developed forelimbs that include claws on what corresponds to the thumb and first finger. Within hours after hatching, the young use these claws and their feet in climbing about in the vegetation. When disturbed they are able to fall into the water, swim, and hide (Grimmer, 1962). The nesting adults defend the nest and young as a group by biting, and shield the nest from predators by covering it with spread wings. The Hoatzin illustrates the extreme modifications in morphology necessary for the bird to utilize leaves as food and the extreme morphological and behavioral adaptations needed for successful reproduction with increased vulnerability to predators.

Another flightless but terrestrial New Zealand bird, the Takahe (*Notornis mantelli*), a large gallinule derivative, also feeds largely upon grass. It seems to have little morphological modification for this diet but apparently compensates for the lack of storage space by eating prodigious quantities of grasses throughout the day. On a grass diet a Takahe voids about 8 meters (654 cm^3, 216 g dry weight) of feces daily (Reid, 1974). The length of the alimentary canal is only 18 percent of the length of feces voided daily.

There are 14 avian families whose species eat leaves, buds, or both to a considerable extent (Table 1), or 8 percent of the 168 existing families (from Morse, 1975) and 3 percent of existing avian species. These percentages are only rough estimates. Most of the species in the families listed are far from being "obligate" folivores; they more properly should be termed generalists that eat leaves along with fruit, seeds, and insects. Few of them are arboreal. The families are listed in approximate order of their evolution, the Ostrich, Rhea, and Emu being the most primitive extant leaf-eaters. Most of the species are terrestrial or aquatic forms that do not rely on flight to obtain their vegetable food.

The Ostrich, Rheas, and Emus are large flightless birds occurring in Africa, South America, and Australia, respectively. Plant material is only part of a generalized diet of insects, small vertebrates, and fruit.

The aquatic or marsh species (Anhimidae, Anatidae, and Rallidae) feed primarily on aquatic vegetation and, thus, may be obtaining a large amount of animal protein from micro-organisms growing on the leaves that they eat. At the same time, plants growing in water may have less cellulose content since they derive structural support from the dense water medium. The Takahe, discussed above, is the most specialized herbivore among the Rallidae.

The three gallinaceous families, the Cracidae, Tetraonidae, and Meleagrididae, contain some species that are specialized for arboreal folivory (Table 1). The cracids are neotropical species that eat largely fruit and insects, but eat some leafy matter. Some cracids eat quantities of flowers (e.g., *Ortalis garrula* eats *Combretum* flowers; personal observation), but this may be primarily for nectar.

The true specialists on leaves are some of the grouse species (Tetraonidae). Ptarmigan (*Lagopus* sp.), Spruce Grouse (*Canachites canadensis*), and Capercaile (*Tetrao urogallus*) feed on buds and leaves of conifers and heather. One of the best studied of these is the Red Grouse (*Lagopus lagopus*) which specializes on heather (*Calluna vulgaris*) for much of the year (Moss, 1969). Moss found that the grouse choose the most nutritious heather for feeding and that the grouse population density can be correlated with the nutritional content of heather. Another ptarmigan, the Icelandic Ptarmigan (*Lagopus mutus*), eats a wider variety of plant matter, but also selects the most nutritious ones (Gardarsson and Moss, 1970).

These grouse share certain adaptations for folivory. They are large in size and the largest are the most folivorous. They are able to store food in a large crop and remain inactive for long periods. Most of the feeding is done while walking or perched, with flight used rarely. The most specialized adaptation may involve changes in gut length that corresponds to variations in the fiber content in their food, both interspecifically (Leopold, 1953) and intraspecifically (Moss, 1972). Moss (1972) found that Red Grouse fed in captivity on a highly nutritious artificial diet gradually developed shorter ceca and small intestines. Their normal food, heather, contains 7 percent crude protein while the artificial feed contained 18-20 percent (percentage of dry weight). The ceca and small intestines of the captives were reduced to 54 percent and 72 percent respectively of their length in wild grouse after 4 years in captivity. Moss (1972) suggests that

> "guts are maintained at some optimum length by natural pressures that place birds with sub- and superoptimal lengths of gut at a disadvantage when they are competing with other individuals of the same and different species."

Cecal elongation occurs (Fenna and Boag, 1974) during periods of dependence on high-fiber content diets in the Spruce Grouse and Japanese Quail (*Coturnix coturnix*). Cecal elongation also occurs in captivity during periods of acclimation to cold environments independent of a change in diet. Apparently, a high-fiber diet and winter temperatures are correlated such that either condition will trigger cecal elongation.

The Seedsnipes (Thinocoridae) are found in southern South America and feed on seeds, buds, and green shoots. They are chiefly seed-eaters and the extent of leaf-eating or its importance is unknown.

The 6 species of Colies, all in Africa, are true omnivores. They are known to eat buds and "tender" leaves, as well as insects, fruit, and nestling birds. The relative quantities that they take of these foods is unknown, but they do not seem to show folivorous adaptations.

The 3 species of Plantcutters (Phytotomidae) are temperate South American in distribution. Together with 1 of the 3 species of New Zealand Callaeids, the plantcutters represent the only significant folivore group of the passeriformes. The bill is finely serrated and used for plucking buds, tender leaves, shoots, and fruit. The bill serrations may permit the efficient cutting of pieces from leaves but they also sever small plants at the base. Little else is known about their morphological adaptations for leaf-eating, if any. They are reported to be rather sluggish, weak fliers, which may be related to leaf-eating but, until more is known about the extent to which they consume leaves as opposed to higher energy food such as fruit, little can be said.

The New Zealand Kokapo or Wattled Crow (*Callaeus cinerea*) is restricted to little-modified and extensive remains of the original forest. It is being reduced by introduced mammalian predators (Thompson, 1964). It feeds mainly on young leaves and fruit, flies weakly and usually hops through

Table 1.—Avian families containing species which regularly eat green plants, buds, or both (from Morse, 1975).

Family	*species*	*Number of leafeating species*	*Number of species in family*	*Terrestrial or arboreal*
Struthionidae	Ostrich	1	1	T
Rheidae	Rheas	2	2	T
Dromiceidae	Emus	2	2	T
Anhimidae	Screamers	3	3	T
Anatidae	Geese, swans	21	145	T
Cracidae	Currassous, guans	38	38	A
Tetraonidae	Grouse	18	18	T and A
Meleagrididae	Turkey	2	2	T
Rallidae	Coots, gallinules, and rails	132	132	T
Thinocoridae	Seed snipe	4	4	T
Opisthocomidae	Hoatzin	1	1	A
Coliidae	Mouse-birds	6	6	A
Phytotomidae	Plantcutters	3	3	A
Callaeidae	Kokapo	1	3	A

branches, using the wings for balance.

The avian families listed in Table 1 contain most of the species that include green leaves in their diet. But there are isolated species in other families not listed that also eat leaves (*Strigops*, the Owl Parrot, is an outstanding example) that are discussed individually.

A species of bowerbird (Ptilonorhynchidae), the Tooth-billed Bowerbird (*Scenopoeetes dentirostris*), has a serrated bill similar to that of the plantcutter. This serrated bill was thought to function as a leaf-cutting tool but not for leaf-eating. This species, like other bowerbirds, makes a mating arena on the ground that it decorates with cut leaves (Marshall, 1951). The serrated bill is used to cut and eat pieces of leaf and this species may exist solely on the leaves of canopy trees for part of the year when fruit is not common (Lavery and Grimes, 1974). It may be very significant that this species is so rarely seen when resorting to folivory that it was once hypothesized to be migratory (Green, 1910). The folivorous period is probably a time of very little flying activity. The leaves are eaten during the winter when individuals are secretive and live mostly in the canopy of non-fruiting forest trees. During the breeding season, the birds eat fruit and are much more active. Thus, we may have an example of the use of leaves as food to survive one period and fruit to supply energy at a higher rate which permits breeding.

The "strategy" of the Tooth-billed Bowerbird, becoming folivorous during periods of low-energy need, seems likely to be more common in tropical birds than is presently known. Very little is known about the year-long diets of tropical birds, although one might not suspect this from a perusal of papers on tropical bird ecology where dietary categories are used for an ecological assessment of avian communities. Most tropical bird species are rather catholic in diet. We are taught what a "flycatching bill" looks like and we, therefore, feel justified in assuming that a bird with a "flycatching bill" eats flying insects. But the only real correlation between bill morphology and diet is that the bill is adapted for feeding on the food that is limiting, even though that may be for only a portion of the year. Thus the Eastern Kingbird (*Tyrannus tyrannus*) with the flycatching-bill-type eats insects in North America for 4 months and fruit in South America for 8 months (Morton, 1971).

It is only partly this bias toward artificial dietary categorization that has resulted in a great lack of information on what role folivory may play in supplying certain nutrients to birds, especially tropical species. Many fruit- and insect-eating tropical birds, when thoroughly studied, are found to take small amounts of foliar material. Jenkins (1969), studying 3 species of saltators (Fringillidae) in Costa Rica, found that they commonly eat the leaves, shoots, and flower corollas of certain plants. The saltators eat mainly a mixed diet of fruit and insects and have ecological and morphological counterparts in all tropical areas. Jenkins found that all 3 saltator species' diets contained a few percent of foliar material. He suggests that

> "leaves and flower corollas are most likely eaten as
> an easily obtainable dietary supplement for such

nutrients as calcium and phosphorus which are found in large quantities in many of them. The leaves of Ipomaea and Cucurbitoceae which are eaten by saltators are reputedly very nutritious . . . and are locally used for feeding rabbits and other livestock. . . . Saltators do not eat just any leaves or flower corollas, but only those of selected species."

Birds with a high fruit content in their diets might be expected to eat foliar material to obtain certain nutrients that are lacking or rare in fruit. Jensen's hypothesis is intriguing for it is operational and may provide insight into a little appreciated but extremely important evolutionary relationship among tropical bird diets, behavior, and competitive relationships. In tropical latitudes where there is year-round plant growth, many bird species are adapted to obtaining energy from several, nutritionally complimentary sources. Selection favors certain behavioral attributes (how much does cultural inheritance play?) that allow a bird to pick and choose from among plants, fruit, and foliage to obtain adequate energy and nutrition for survival.

This strategy is in contrast to insect- or flesh-eating, mainly because the animal foods are nutritionally richer than plant foods. The ecological niche relationships of birds which feed on animal matter are determined more by where their food is found (on a micro scale) and how it escapes while the fruit-eater niche relationships are determined by who finds the right combination of nutritionally compatible foods. It should be evident that the latter is probably restricted to the tropics.

While obligate leaf-eating is restricted to relatively few species, the contribution of nutritional elements from leaves to the diets of many tropical birds may be significant and important in their evolution and competitive relationships.

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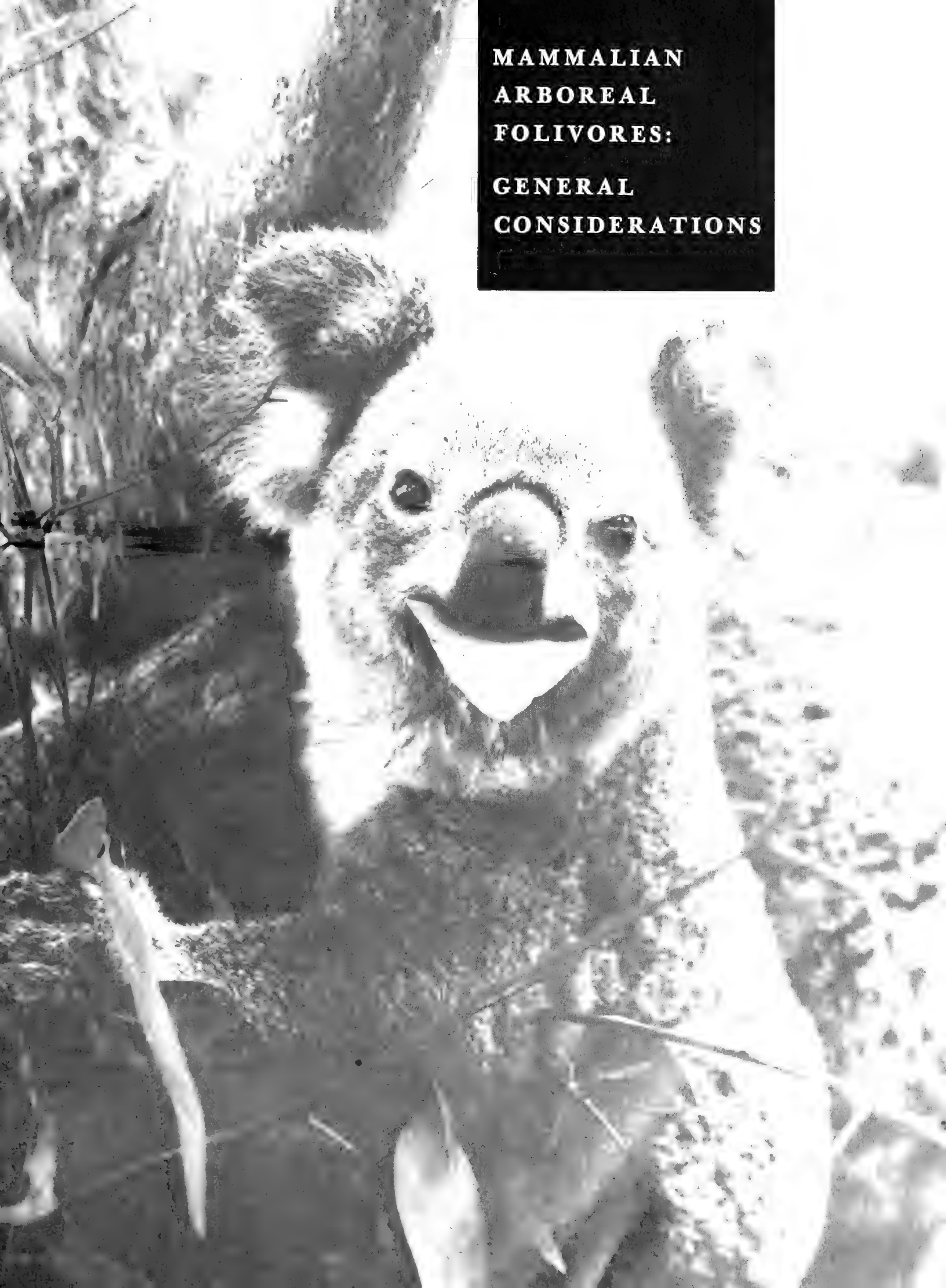
Phascolarctos cinereus, the koala, one of the most specialized mammalian folivores. (Photo courtesy Embassy of Australia)

MAMMALIAN ARBOREAL FOLIVORES: GENERAL CONSIDERATIONS



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The Evolution of Arboreal Herbivores in the Class Mammalia

Introduction

If we accept that certain features of tooth and skull structure are indicative of adaptations for the mastication of plant parts, then the fossil record indicates that the use of plant material by mammals has had a long evolutionary history. It seems safe to conclude that during the Jurrassic the non-Therian Multituberculata had evolved numerous adaptations for the mastication of plant parts (Clemens, 1971). Although many parts of a plant may be eaten by mammals, the term herbivore refers specifically to "a plant-eating animal . . . feeding especially on . . . herbaceous vegetation, green plants . . . especially those used for pasture,"[1] from the Latin *herba*, "a seed plant which does not develop woody persistent tissue." If we stick to the root meaning of *herba*, then we are really talking about grasses and forbs. The modern French meaning for *herbage* is more inclusive, "the succulent parts of herbaceous plants especially the foliage and young stems." Turning to the adjective herbaceous, we find a definition: " . . . having little or no woody tissue . . . having the texture, appearance or color of a leaf." Thus, contrary to less critical authors, when we speak of herbivores, we are not talking about fruits, seeds, sap, blossoms, nectar, cambium, and roots as foodstuffs, although all of these may well be eaten in addition to herbage.

The term arboreal presents fewer problems. Literally it means " . . . inhabiting or frequenting trees." Thus, an arboreal herbivore is a species which is adapted for foraging in trees and includes predom-

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[1] All quoted definitions from *Webster's Third New International Dictionary*, 1964.

inantly herbage in its diet. I take it then that soft stems and foliage would be the most important items of its diet and that we could properly speak of arboreal folivores (Latin, *folium* . . . a leaf; Latin, *vorare* . . . to eat.)

Long before terrestrial vertebrates appeared on the scene, arthropods, mollusks, and nematodes were utilizing leaves and stems of living plants as food sources. Judging from the fossil record, a number of reptiles took advantage of green plant parts as sources of energy for 160 million years during the Secondary (Olson, 1961). The mammals in turn occupied similar trophic levels during the decline of the dinosaurs. The full impact of this statement can only be appreciated if we consider that the plants and their vertebrate and invertebrate "predators" have co-evolved to the present time, and each succeeding wave of evolution has had to adapt to plants with protective devices already "honed" by the preceding lineages (Freeland and Janzen, 1974; Smith, 1970).

The Utilization of Plant Parts

The reproductive bodies of plants, e.g., blossoms, seeds, fruits and nuts, have always presented convenient packages of fats, carbohydrates, and protein to their respective predators (Orians and Janzen, 1974). In many cases, vertebrate predators aid in the dispersal of seeds, and the plant tolerates a certain predation level to "gain" a dispersing mechanism (Smith, 1970; Hladik and Hladik, 1969; Smythe, 1971). Leaves and shoots, however, are another problem since the leaf provides the plant with its energy-trapping mechanism. Predation on leaves has resulted in diverse chemical defenses by the plants (Freeland and Janzen, 1974). Silica, a common constituent of grass cell walls, is probably as much an adaption to reduce predation levels as it is a structural component (Metcalfe, 1960).

Leaves and stems contain plant starch and protein in their parenchyma cells and, if they can be triturated without any great energy expenditure, then net energy is available to the herbivore. It is well known, however, that much of the carbohydrate in leaves and stems is also incorporated in the cell walls and "vessel cells" of the leaf and stem in the form of cellulose and lignin. The structural carbohydrate cellulose is potentially a high energy source but it must be physically macerated to very fine particles (chewed) and then broken into simple sugars with the enzyme cellulase, an enzyme not produced by the cells of any vertebrate tissue (Hill, 1970). The retrieval of energy from cellulose thus depends ultimately on symbionts in the mammalian digestive tract and these are generally bacteria and/or protozoa. Hence, the utilization of leaves and stems, as a relatively complete source of energy, requires considerable morphological change in dentition, jaw musculature, and gut morphology (Moir, 1968; Greaves, 1974). Ultimately as plant and herbivore co-evolved, the herbivore adapted to those structural and chemical defense mechanisms which are evolved in response to the predation pressure (see Janzen, 1978).

The Problems of Acquisition

Arboreality

Clearly in order to be able to feed on leaves, the mammal must have some means of reaching the leaves of trees. In the case of a large mammal, it may be possible to stand on the ground while feeding on leaves, as exemplified by the ground sloths (*Megatherium*) or modern giraffes (*Giraffa*) and elephants (*Loxodonta* and *Elephas*). In this symposium, however, we are concerned with animals that actually climb in trees in order to reach edible portions. In order to restrict our definition to trees and treelike plants, we must exclude certain species which might be considered arboreal in their morphological adaptations but in fact do not forage in trees. These would include such rodent forms as *Micromys* or *Reithrodontomys,* the harvest mice, which are adapted for foraging in the tops of tall grasses. Clearly, these genera exhibit arboreal adaptations but cannot be considered arboreal in the sense that we are using the term here.

We come to an interesting point of potential controversy, since many plant species under certain growth conditions exhibit the form of a shrub, that is, a woody plant somewhat less than 2 meters in height. The vertebrate forms that forage in these shrubs could be considered arboreal and I will so consider them, even though by a strict definition *arbe* refers to a tree and not to a shrub.

The many forms of arboreality and the trophic levels exploited therein, as well as the types of locomotion evolved for each of the various physical substrates offered by plants, have been ably reviewed by Cartmill (1972), although his use of the term herbivore is too broad. For the purpose of this discussion, we are concerned with arboreal mammals that spend most of their foraging time in the tree or shrub branches; thus, we will eliminate many scansorial forms which forage mainly on the ground but also in the vegetation itself and instead will attempt to develop a rating scale in order to define degrees of arboreality. I propose a 5-point rating scale and consider those mammalian species arboreal which are rated equal to or greater than 3 on the scale.

Table 1.—Systematic and geographical breakdown for mammalian arboreal herbivores.

Taxon	Number of genera	Geographical distribution	Number of genera essentially terrestrial	Number of genera semi-arboreal Class 1–2	Number of genera arboreal Class 3–5	Degrees of herbivory expressed			Genera showing both arboreal and herbivorous rating
						< 0.1	1.0–2.0	≥ 3.0	> 3.0
Marsupialia	65	N.G. + Aus.	42	7	16	21	20	24	7
	15	C.A. + S.A.	2	4	9	10	5	0	0
	80		44	11	25	31	25	24	7
Insectivora	69	N.A., S.A., Eu. As., Af.	56	3	0	58	11	0	0
Dermoptera	1	S.E. As.	—	—	1	—	—	1	1
Chiroptera	178	Worldwide		volant		94	84	0	0
"Tupaiformes"[1]	5	S.E.As.	0	2	3	3	2	0	0
Primates	10	Mad.	0	0	10	1	4	5	5
	16	S.A.	0	0	16	1	14	1	1
	17	Af.	1	2	14	2	13	2	1
	11	As.	0	1	10	3	3	5	5
	54		1	3	50	7	35	12	12
Edentata	14	N.A., C.A., S.A.	9	1	4	10	2	2	2
Pholidota[2]	2	Af., As.	1	0	1	2	0	0	0
Lagomorpha	10	Worldwide[3]	10	0	0	—	—	10	0
Cetacea	38	Oceanic		aquatic		38	0	0	0
Carnivora	102	N.A., S.A., Eu., As., Af.	73	10	19	56	44	2	1
Pinnepedia	17	Oceanic		aquatic		17	0	0	0
Tubilidentata	1	Af.	1	0	0	1	0	0	0
Proboscidea	2	Af., As.	2	0	0	0	0	2	0
Hyracoidea	3	Af.	3	2	1	0	0	3	1
Sirenia	2	S.A., Af., As., Aus.		aquatic		0	0	2	0
Perissodactyla	6	Af., As., S.A.	6	0	0	0	0	6	0
Artiodactyla	80	Worldwide[3]	80	0	0	0	7	73	0
Rodentia	351	Worldwide	95	164	92	9	246	96	18 (29)[4]
Ordinal totals	1015		391 39%	196 19%	196 19%	326 33%	456 45%	233 23%	42 4% (5%)[4]

N.A. = North America; C.A. = Central America; S.A. = South America; Eu. = Europe; As. = Asia; Af. = Africa; Aus. = Australia; N.G. = New Guinea; Mad. = Madagascar.

[1] Tupaidae is considered an ordinal taxon.

[2] Pholidota is considered as composed of two genera: *Smutsia* and *Manis*.

[3] Except Australia and Antarctica (introductions not considered).

[4] Possible level of arboreal herbivory if arboreal category is not as restrictive and if some "marginal" species are included—see text.

Degrees of arboreality

Class 1. Species climbs in vegetation very little.

Class 2. Species is known to climb in order to obtain food; little structural specialization for arboreal locomotion.

Class 3. Species could be considered scansorial; structural modifications for arboreality are present. More than 50 percent of its time is usually spent foraging in trees.

Class 4. Species is strongly modified for an arboreal life, descent to the ground is rare, and little terrestrial foraging for food is noted.

Class 5. Extreme adaptation for arboreal life. The species does not locomote on the ground except to move from one isolated tree to another.

To qualify as arboreal, then, the species in question must spend over half of its foraging time in trees or shrubs and generally establishes its nest in a tree (see Table 1).

It goes without saying that effective use of trees as a food source and employing climbing as a means of reaching leaves sets some limit on size since the ability of the tree to bear weight and, in fact, efficiency of movement in the trees are seriously impaired when an animal becomes too large. The limits of size in existing arboreal mammals are illustrated in Figure 1 and that set of arboreal mammals which are also folivores is included in the same figure. As can be seen, arboreality does indeed set certain constraints on the size in terms of the upper limit that an animal can reach. Additionally, arboreal folivores seem to have a lower limit on size. As is discussed by McNab (1978), this limit on size in folivores may in some way be bound up with the efficiency of energy extraction from leaves, problems of detoxification, and the problems of heat loss in mammals which are below a certain critical size limit (see also Parra, 1978).

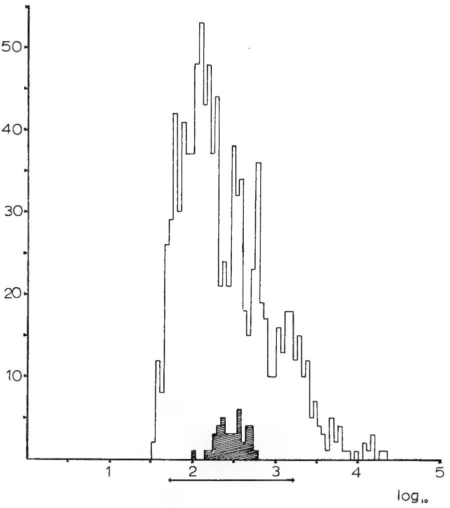

Figure 1. Frequency distribution of size classes for Mammalian Genera. An average size was calculated for each polytypic genus by determining the mean head and body length based on the average value for the two extreme values within the genus. This figure then is based on a mean value which may not characterize the true mean for a genus but will give an idea of the size class distribution. The distribution for arboreal herbivore genera is crosshatched. The range at the bottom of the figure illustrates the range for arboreal mammals. Ordinate = frequency; abscissa = $\log_{10}$ of average head and body lengths in millimeters.

Ingestion and mastication

The ingestion of leaves and stems may involve the use of the tongue, lips, teeth, and forepaws. For many arboreal herbivores, such as the sloth, the forepaws may be used to bring a branch of leaves within reach of the mouth where the leaf is bitten off using the teeth; the lips are little involved in the initial manipulation of the leaf itself. This is in contradistinction to many terrestrial browsing herbivores which feed upon leaves, such as *Rhinoceros, Tapirus, Elephas,* and *Giraffa*, where the lips, proboscis, or tongue are commonly employed in stripping leaves from stems.

The teeth are all important in the mastication of the leaf structure. One of the greatest advances in the evolution of the Mammalia was the differentiation of the teeth within the jaws into functional groups, incisors, canines, premolars, and molars (Peyer, 1968). One indication of adaptation to the mastication of leaves and green plant parts has been the tendency for the grinding surface of the molars and premolars to enlarge in those forms which are herbivorous (see Kay and Hylander, 1978). Enlarged tooth surface area permits a greater efficiency in subdivision of the plant material into small parts, thus increasing ease of either direct digestion of starch or indirect digestion of cellulose through microbial symbionts.

One prominent trend of known arboreal folivores is that the cusps have often been retained, thus permitting more of a pulping and shearing effect rather than grinding (Kay and Hylander, 1978). In fact, an extreme increase in the surface area of teeth and the evolution of complicated grinding surfaces seems to accompany adaptation to feeding on grasses rather than leaves (see Gregory, 1951). Indeed, feeding on grasses is usually accompanied by a second evolutionary trend, namely an increase in the height of the crown of the molars to create greater potential for molar use with wear or ultimately the conversion of the molars into rootless ever-growing structures (Peyer, 1968). In almost all arboreal folivores which have been examined to date, this trend toward hypsodonty is less than that seen in terrestrial grazers (see Figure 3). In the Bradypodidae, however, there is a trend towards hypsodonty, not expressed in such an extreme fashion by any of the other arboreal, herbivorous primates and marsupials. Of course, the molars of *Bradypus* and *Choloepus* lack enamel (Goffart, 1971) which may account for this difference in crown height.

Finally, the act of mastication itself requires that the lateral movements of the lower jaw relative to the upper be increased to create a grinding effect and, to this end, the pterygoid muscles have increased in size and extent of their attachment. The whole problem is ably reviewed by Crompton and Hiiemäe (1969) and Hiiemäe (1968).

Examination of fossil skulls is often instructive in the elucidation of trends toward herbivory, especially when sites for muscle attachment are examined in conjunction with tooth structure. In this way, the Multituberculata, Docodonta, and Taeniodonta can be designated as early herbivores, all of which are now extinct (Clemens, 1971). In many cases the lack of a complete appendicular skeleton prevents us from inferring whether these forms were arboreal or not, although sometimes the absolute size of the skull is a good indicator.

The Problem of Digestion and the Evolution of Herbivory

Some microbial symbionts exist in the digestive tracts of all mammals, hence, when we speak of the role of microbial symbionts as an adaptation to an herbivorous diet, we are talking more of degrees of adaptation rather than absolutes. Microbial symbionts may be involved in many processes other than that of the breakdown of cellulose to fatty acids (Howard, 1959). In fact, symbionts may be useful in the synthesis of the B-vitamin complex (Maynard and Loosli, 1969; Dougherty, 1965), and their by-products may be either absorbed from various parts of the gut or ingested by means of refecation, a process whereby feces, generally originating from the cecum, are reingested and passed through the gut a second time (Harder, 1949).

Strictly speaking, if an herbivore evolves to make greater use of the metabolic byproducts of microbial symbionts, it has a number of adaptive options: (1) It can increase the capacity of its stomach and create a specialized nonsecretory portion of it as a fermentation chamber. (2) Alternatively, it can lengthen its intestine increasing the surface area for absorption and the duration of passage of foodstuffs thus enhancing the time for microbial activity. (3) Finally, it can increase the number, extent, and size of various diverticula, especially a diverticulum at the junction of the large and small intestines, generally referred to as the cecum (Amerasinghe et al., 1971; Hladik, 1967; Vorontsov, 1962).

The alternate pathways are not mutually exclusive, and furthermore, the work of Vorontsov (1962) and Carleton (1973) shows that adaptations of the gut for increased microbial activity do not necessarily proceed in step with the evolution of dental modifications for the mastication of plant material. In fact, Vorontsov speaks of a mosaic of evolutionary changes where different parts of the alimentary tract may evolve somewhat out of phase. In some species the cecum ultimately becomes most important; in other closely related lines, the length of the small intestine becomes more important than does an increase in cecal diameter and size. Only very general trends can be discerned (Figure 2).

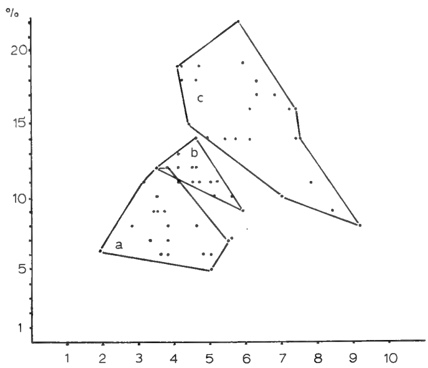

Figure 2. Relation between intestinal length and cecal length for a series of muroid rodents. Data from Vorontsov, 1962. Set (a): omnivores—feeding specialization class 2. Set (b): intermediate class with some plant parts ingested Class 2–3.0. Set (c): herbivores > 3.0 on rating scale. Ordinate = % of total intestine length occupied by the cecum. Abscissa = number of times the intestinal length exceeds the head and body length.

In the evolution of herbivory, often refecation or the reingestion of fecal material (Southern, 1942) serves as a useful method to increase the efficiency of absorption of the by-products of microbial activity (e.g., the Leporidae, *Lepilemur,* and *Aplodontia*) (Hladik and Charles-Dominique et al., 1971; Ingles, 1961). One of the most efficient processes for the digestion of plant material was evolved by the terrestrial order Artiodactyla, where the stomach has been modified to create a large fermentation chamber and the rapidly ingested plant material may be regurgitated and remasticated to increase the trituration of the plant substrate. Remastication of plant material temporarily stored in the stomach appears to be an adaptation involving only 2 mammalian orders, the the Artiodactyla and the Marsupialia (Family Macropodidae) (Tyndale-Biscoe, 1973). The evidence for remastication of plant material in arboreal folivores is weak, although it has been suggested but not confirmed for the three-toed sloth (Beebe, 1926).

Since the morphology of the gut cannot be easily deduced from fossilized hard parts and since gut modifications do not necessarily evolve in step with dental modifications, the reconstruction of the evolutionary history of arboreal herbivory is fraught with difficulties. It was probably an infrequent adaptation and, if the living Bradypodidae are any example, it has probably tended to persist, once evolved, especially in areas subject to little faunal disturbance or where the adaptation is so complete that evolution of a competitor is severely retarded.

Definition of an Arboreal Herbivore

Given a 5-point scale for the classification of arboreality, I will now proceed to develop a 5-point scale for the classification of herbivory. In order to accomplish this, I will draw upon the published field studies of arboreal herbivores from the Hladiks (1969, 1971, 1972), Charles-Dominique, et al., (1971), Sunquist and Montgomery (1973) and Montgomery and Sunquist (1975, 1978). The standards then will be the primate genera *Lepilemur, Presbytis, Alouatta,* and, from Montgomery's data, the edentate genera, *Bradypus* and *Choloepus*.

Most semiterrestrial (e.g., *Papio* and *Theropithecus*) and terrestrial (Cervidae, Bovidae, Equidae) herbivores present problems of classification since many species exhibit grass feeding (grazing) as well as folivory (browsing). Fortunately, the strictly arboreal forms do not utilize grasses and forbs to any extent and the grazer-browser problem is avoided (see Figure 4). The scaling for degrees of herbivory in the Class Mammalia is presented in Table 1. The ratings for many mammalian genera are not necessarily based on quantitative field studies, but rather on what is known of species food habits in captivity, and what can be inferred from our knowledge of their anatomy.

Degrees of herbivory are scaled in the following manner:

Class 1. Digestive tract shows little modification; dentition little modified for grinding; essentially omnivorous, but much "fruit" is utilized when available; some feeding on buds or shoots may occasionally be shown.

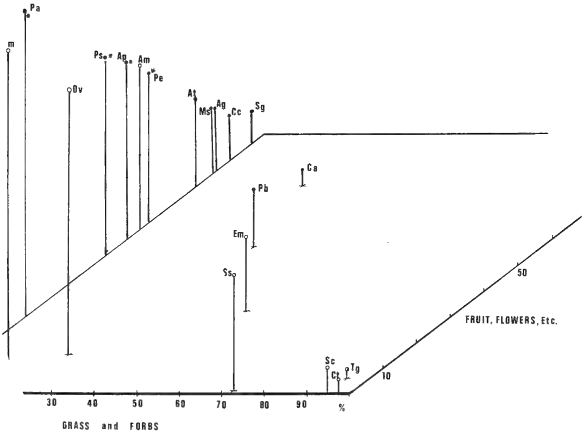

Figure 3. Feeding specializations for selected mammalian herbivores. Terrestrial grazers and browsers (folivores) can be separated into relatively distinct categories. The arboreal folivores as a set intergrade with arboreal species adapted for feeding on varying amounts of fruit and other plant parts. Seasonal variations in dietary intake are averaged. Percentages are based on either time spent feeding (Hladik and Hladik, 1969), actual stomach contents (Hofmann and Stewart, 1972), or actual weights of food consumed (NZP records). References consulted include Trippensee, 1948; Hladik and Hladik, 1969, 1972; Montgomery and Sunquist, 1975; Dunbar and Dunbar, 1974; Hofmann and Stewart, 1972; and unpublished records from the National Zoological Park. A. g. *Ateles geoffroyi*; A. m. *Ailuropoda*; A. p. *Alouatta palliata*; A. t. *Aotus;* B. i. *Bradypus*; C. a. *Cercopithecus aethiops*; C. c. *Cebus capucinus*; C. t. *Connochaetes taurinus*; E. m. *Elephas maximus*; G. *Giraffa*; M. m. *Madoqua*; M. s. *Macaca sinica*; O. v. *Odocoileus virginianus*; P. a. *Presbytis arygula*; P. b. *Papio anubis*; P. c. *Phascolarctos cinereus*; P. e. *P. entellus*; P. s. *P. senex*; S. c. *Syncerus caffer*; S. g. *Saguinus geoffroyi*; S. s. *Strepciceros*; T. g. *Theropithecus gelada*. Black circle = arboreal species; star = arboreal folivore.

Class 2. Digestive tract shows little modification for bacterial symbionts. Dentition may show slight modification for grinding or crushing. In addition to some animal food, often feeds on plant parts including seeds, fruit, buds, flowers, leaves, and sap.

Class 3. Digestive tract shows some modification, generally cecal enlargement and/or lengthening of the intestine. Dentition may show cusp modification to create crushing surfaces. Diet differs from Class 2 in that buds, blossoms, leaves, and young shoots begin to dominate in the diet (from 30 to 40 percent). If terrestrial the species may ingest occasional grasses—forbs, as well as leaves.

Class 4. Digestive tract further modified from Class 3. Stomach is often very enlarged and sacculated or cecum is greatly enlarged. Some bacterial digestion of cellulose in the stomach is implied. Leaves and grass comprise a significant percentage of the diet (greater than 40 percent) although blossoms, fruit, and other plant parts contribute to the diet. If terrestrial the species may be considered either a browser or grazer, depending on the proportion of leaves in its diet (see Figure 3).

Class 5. Differs from Class 4 in that the species, if arboreal, is close to being an "obligate" folivore. Gut is specialized for the breakdown of cellulose by bacterial and/or protozoan symbionts. Leaves, buds, and plant stems predominate in the diet. Specimens of arboreal forms taken as advanced juveniles or older for captive rearing are almost impossible to convert to an artificial diet. If terrestrial, the species is generally a specialized browser or grazer.

In Table 2 the arboreal herbivores or more properly the arboreal folivores are listed and their geographical distribution is included. Certain specialized mammals must be considered and discussed separately. For example, the flying squirrels of Southeast Asia may indeed exhibit considerable specialization toward an herbivorous diet. *Hylopetes* and *Pteromyscus* are partial folivores, while *Petaurista* is strongly folivorous. Degrees of folivory may vary from species to species in the same genus and generic trends in diet are probably difficult to determine accurately (see Muul, 1978). Charles-Dominique (personal communication) has informed me that several species of the West African flying squirrel family, Anomaluridae, are also strongly folivorous in their dietary habits, and I have included the genus *Anomalurus* as an arboreal folivore in Table 2.

Certain species of shrub-dwelling mice in the arid southwest of Africa (e.g., *Parotomys littledalei*) as well as *Dipodomys microps* in the southwestern United States utilize leafy material from desert shrubs (Coetzee, personal communication; Kenagy, 1972). In the latter case, *D. microps* is clearly not arboreally adapted, yet a major portion of its food intake does indeed come from leaf material (Kenagy, 1973). Because of its reduced arboreal ability, I have not included this latter species in my tabulation.

The gundis, Ctenodactylidae, may occasionally forage in low shrubs for leaves (George, 1974), as do hyraxes of the genera *Heterohyrax* and *Procavia* (personal observation). Because they do not appear to be "arboreal" in the strict sense, I have not tabulated these forms as arboreal herbivores either, although a more strict investigation of their behavior in the field might warrant their inclusion.

Given the arboreal herbivore genera as defined in Table 2, the relative rarity of the arboreal folivore as an adaptive syndrome can be gauged from Table 3. It will be noted that arboreal folivores include, at the least, 19 percent of all herbivore genera.

The Evolution of Arboreal Herbivores

The fossil record is (in its present state of development) of little assistance in determining the evolutionary history of arboreal herbivory, except to say that the trend was well established in the Eocene Plesiadapoids (Cartmill, 1974). The present distribution of arboreal herbivores includes all of the major continental land masses. The order Marsupialia accounts for 7 genera of arboreal herbivores distributed on both New Guinea and continental Australia (Collins, 1973). None of the living South American marsupials qualify as arboreal herbivores. The order Dermoptera includes 1 species in 1 genus distributed in Southeast Asia, a nocturnal glider, it obtains the bulk of its dietary intake from leaves (Wharton, 1950). The order Primates includes 12 genera which are arboreal herbivores, 5 from Madagascar, 1 from South America, 2 from Africa, and the remainder from Asia. Thus the arboreal herbivore niche is filled primarily by primates in Africa and Asia (See Petter, 1962; Martin, 1972; and Hladik, 1967). The order Edentata has 2 genera which qualify as arboreal herbivores which are found only in Central and South America (Montgomery and Sunquist, 1975). The carnivores perhaps include 1 genus of arboreal herbivore, the lesser panda (*Ailurus fulgens*) of the Himalayan foothills (Roberts, 1975). The African order Hyracoidea includes 1 genus which is typically arboreal and herbivorous, *Dendrohyrax* (Rahm, 1964).

The order Rodentia is imperfectly understood with respect to the extent of its arboreal herbivore

Table 2.—Systematic listing of mammalian genera showing advanced specializations for arboreal herbivory.

Taxon	*Number of species*	*Distribution*	*Arboreal rating*					*Herbivory rating*					*Sources*
			3.0	*3.5*	*4.0*	*4.5*	*5.0*	*3.0*	*3.5*	*4.0*	*4.5*	*5.0*	
MARSUPIALIA													
Phalangeridae													
* *Phalanger*[1]	7	Aus, NG, Cel		+						+			Collins, 1973
* *Trichosurus*	2	Aus		+				+					Tyndale-Biscoe, 1973
Wyulda	1	Aus	+					+					Fry, 1971
Phascolarctidae													
Phascolarctos	1	Aus				+						+	Sutton, 1934
Petauridae													
Pseudocheirus[2]	12	Aus, NG		+						+			Thomson & Owen, 1964
Schoinobates[3]	1	Aus				+					+		Fleay, 1947
Macropodidae													
* *Dendrolagus*	5	Aus, NG	+						+				Collins, 1973
PRIMATES													
Lemuridae													
Lemurinae													Petter, 1962
Hapalemur	2	Mad		+				+					Petter & Peyrieras, 1970
Lepilemur	2	Mad		+				+					Charles-Dominique, et al., 1971
Indriidae													
Avahi	1	Mad		+					+				Petter, 1962; Martin, 1973
Indri	1	Mad			+						+		Petter, 1962; Martin, 1973
Propithecus	2	Mad	+					+					Petter, 1962; Martin, 1973
Cebidae													
* *Alouatta*	6	S.A.				+		+					Hladik & Hladik, 1969
Cercopithecidae													
Colobinae													
* *Presbytis*[4]	13	As		← + →						← + →			Hladik & Hladik, 1972
Pygathrix	1	As											
Rhinopithecus	4	As		+					+				
Simias	1	As			+					+ ?			Medway, 1970
Nasalis	1	As				+					+		Medway, 1970
* *Colobus*	4	Af		+						+			Kingdon, 1971
DERMOPTERA													
Cynocephalidae													
Cynocephalus	1	As					+				+		Wharton, 1950
RODENTIA													
Sciuridae													
Petauristinae[5]						+		+ ?					
Petinomys	8	As											Phillips, 1935
Petaurista	4	As				+ ?			+ ?				Medway, 1969; Phillips, 1935
Anomaluridae													
Anomalurus	5	Af				+			+ ?				Rahm, 1969; Kingdon, 1974; Rosevear, 1969
Cricetidae													
Nesomyinae													
Brachytarsomys	1	Mad	+					+ ?					Petter, F., 1972
Lophiomyinae													
* *Lophiomys*	1	Af	+						+				Kingdon, 1974; Maliniak, pers. comm.
Microtinae													
Aborimus (Phenacomys) longicaudus	1	N.A.				+				+			Hamilton, 1962

Table 2. (Continued)

Taxon	Number of species	Distribution	*Arboreal rating*					*Herbivory rating*					Sources
			3.0	3.5	4.0	4.5	5.0	3.0	3.5	4.0	4.5	5.0	
Muridae													
Otomyinae													
Parotomys	2	Af	+						+				Walker, 1964; Coetzee, pers. comm.
Phloeomyinae													
* *Phloeomys*	2	Phil		+					+				Walker, 1964; Maliniak, pers. comm.
* *Crateromys*	1	Phil			+				+				Crandall, 1964
Murinae													
Thallomys	1	Af		+					+				Kingdon, 1974
Hapalomys	1	As		+						+			Medway, 1969
Erethizontidae													
* *Erethizon*	1	N.A.		+						+			Shapiro, 1949; Taylor, 1935
* *Coendou*	20	S.A.			+				+				Enders, 1935
Echinoprocta	1	S.A.	?						?				Walker, 1964
Chaetomys	1	S.A.	+?					+					Walker, 1964
Echimyidae													
Diplomys	4	S.A.			+					+			Tesh, 1970
Echimys	20			+						?			Walker, 1964
Capromyidae[6]													
* *Capromys*	2	W.I.	+						+				Mohr, 1939
C. (Mysateles)	2	W.I.			+					+			
Some possible candidates as arboreal herbivores in the Rodentia:													
Capromyidae—* *Plagiodontia*, marginal with respect to arboreal ability.													
Echimyidae—*Isothrix, Dactylomys, Lachnomys, Kannabateomys, Thrinacodus*, no data on feeding, but clearly arboreal.													
Petromyidae—*Petromys* rates marginal in arboreal ability.													
Ctenodactylidae—*Ctenodactylus, Pectinator, Massoutiera, Felovia*; rate marginal in arboreal ability (see text).													
EDENTATA													
Bradypodidae													
* *Choloepus*	2	S.A.				+				+			Montgomery & Sunquist, 1974
Bradypus	3	S.A.					+					+	Goffart, 1971
HYRACOIDEA													
Hyracidae													
Dendrohyrax	1	Af		+							+		Kingdon, 1974; Rahm,
CARNIVORA													
Procyonidae													
Ailurinae													
* *Ailurus*	1	As		+					+				Roberts, 1975

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*Genera studied at NZP within the interval 1964-1974. Abbreviations as in Table 1 with addition of: Cel = Celebes; W.I. = West Indies; Phil = Philippines.

[1] Two species known to be highly folivorous.

[2] One species known to be highly folivorous.

[3] A glider; comparable to *Cynocephalus*.

[4] Degree of folivory is somewhat variable.

[5] Discussion of group deferred to Muul (this conference).

[6] In the Capromyidae, *Plagiodontia* and *Geocapromys* do not rate a 3.0 on the arboreal scale, but are good herbivores.

Table 3.—Percentage breakdown of mammalian locomotor and feeding adaptations.

Locomotor adaptations	*Number*	*Percent*
Extreme aquatic	57	5.6
Aquatic 80% of life in water	63	6.2
Completely volant	178	17.5
Terrestrial < 1.0	391	39.0
Semi-arboreal ≥ 1.0-2.0	196	19.0
Arboreal ≥ 3.0	196	19.0
FEEDING ADAPTATIONS		
Essentially no direct plant feeding	326	33.0
Partial use of plants	456	45.0
May be considered herbivores ≥ 3.0	233	23.0
Percentage of arboreal genera which are herbivores	19% (or 27%)*	
Percentage of herbivore genera which are arboreal	16% (or 22%)*	
Percentage of all mammals which are arboreal herbivores	4% (or 5%)*	

*If we include several marginal rodent genera.

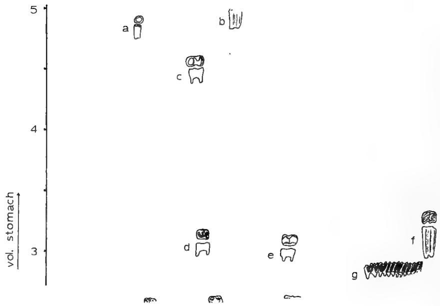

Figure 4. Molar development and specializations of the gastro-intestinal tract. Ordinate = Relative increase in the size of the stomach to accommodate gastric fermentation. Abscissa = Relative increase of cecum as a site for fermentation (scales are arbitrary). Arboreal folivores: a. *Bradypus*; d. *Anomalurus*; e. *Phascolarctos*; k. *Ailurus*; j. *Alouatta*; i. *Cynocephalus*. Terrestrial Grazers and Browsers: b. *Ovis*, c. *Macropus*, f. *Equus*; g. *Hydrochoerus*; h. *Microtus*. Carnivore: 1. Premolar of *Felis*. Drawings adapted from Gregory, 1951. Note the extreme hypsodonty for the long-lived grazers.

adaptations. It is proposed that the following genera be considered arboreal herbivores: *Capromys* from the family Capromyidae, 2 genera from the family Echimyidae, 2 genera from the subfamily Phloeomyinae, 1 genus from the family Anomaluridae, at least 2 genera from the subfamily Petauristinae, 1 genus from the subfamily Nesomyinae, and 1 genus from the subfamily Lophiomyinae (see Table 2). Of particular interest are the Capromyidae and Phloeomyinae, the former from the Greater and Lesser Antilles and the latter from the Philippine Archipelago, in particular the Island of Luzon.

Attributes of Arboreal Herbivores

Before turning to a discussion of the convergent evolution of arboreal herbivores, I should review some of the attributes of those species that have been identified. In size, arboreal herbivores are intermediate, ranging from 100 to 1,000 mm head-body length with the mode averaging slightly over 300 mm (see Figure 1). The dental patterns are highly variable (Figure 4). For the most part, some cusps are retained on the molars for pulping leaves. In the case of a species, such as *Cynocephalus*, one could hardly deduce that it was a folivore from inspection of the teeth alone (Gregory, 1951). Modifications of the stomach into partial fermentation chambers appears to have taken place in the macropod marsupials (Tyndale-Biscoe, 1973), colobine primates (Hladik, 1967; Kuhn, 1964), some rodents (e.g., *Capromys* (*Mysateles*) *melanurus* Dobson 1884), and New World sloths (Goffart, 1971). Other species of arboreal folivores appear to have modified their stomachs less, but rather increased the size of the cecum and/or length of the intestines. Whereas the colobine primates and, to an extent, *Bradypus* are diurnal, many of the folivores are nocturnal, including *Lepilemur* and most of the folivorous rodents. All arboreal folivores are confined to forested areas and the vast majority in tropical evergreen forests. The microtine rodent, *Arborimus* (*Phenacomys*), is an exception (Hamilton, 1962), since it has uniquely adapted to feed on conifer needles but only after it has removed the resin cone from each leaflet.

From research on *Lepilemur* (Hladik et al., 1971), it is evident that many of the arboreal folivores may live close to the limit of their energy budget. It would appear that the speed of locomotion is reduced, the home range is small, the litter size is small (usually one), and the pelage is often relatively dense (see Table 4). Heat conserving mechanisms predominate; the low reproduction potential may be an adaptation not only to arboreality but also in part an imposition placed by metabolic demands. As a result, the antipredator strategy often depends on crypticity. Direct predator avoidance, when it does involve escape mechanisms, often requires very little energy expenditure, such as gliding. In fact, the number of times gliding has been convergently evolved in mammalian arboreal folivores is strikingly high (see Table 5).

Exceptions to the preceding generalizations most often appear on islands where the normal predator component found on continental land masses is distorted. Very often, in conjunction with crypticity as an antipredator device and the slow mobility of the animal, arboreal folivores do not live in large cohesive social groupings, although they often have well-developed communication mechanisms for localizing their positions in space relative to one another (Montgomery and Sunquist, 1974).

Diversity and "Niche Width"

It has been remarked upon that arboreal folivores do not exhibit a high diversity when a restricted geographical area is studied (Tables 2, 3, and 5). In

Table 4.—Some vital statistics for arboreal herbivores[1]

Taxon	*Range of head-body length (mm)*	*Litter size*	*Longevity[2] (yrs)*
Marsupialia			
Phalanger	325–650	1–2	> 7
Trichosurus	320–580	2	> 9
Wyulda	~ 362	?	
Phascolarctos	600–850	1	
Pseudocheirus	180–450	1–3	
Schoinobates	300–480	1	
Dendrolagus	520–810	1	~ 14
Primates			
Hapalemur	330–370	1	> 12
Lepilemur	280–356	1	
Avahi	300–330	1	
Indri	~ 700	1	
Propithecus	458–530	1	
Alouatta	500–720	1	> 12
Presbytis	500–780	1	> 10
Pygathrix	600–820	1	
Rhinopithecus	600–800	1	
Simias	503–518	1	
Nasalis	550–720	1	
Colobus	450–490	1	> 12
Dermoptera			
Cynocephalus	380–420	1	
Rodentia			
Petinomys	127–406	~ 3	
Petaurista	305–585	1–2	
Anomalurus	216–432	2–3	
Brachytarsomys	210–250		
Lophiomys	275–360	1	> 5
Arborimus	104–106	2–3	
Parotomys	135–170	2–4	
Phloeomys	480–485	1	> 6
Crateromys	325–360	1–2	
Thallomys	120–158	1–4	
Hapalomys	120–135		
Erethizon	645–860	1	> 10
Coendou	~ 500	1	
Echinoprocta	< 400		
Chaetomys	430–457		
Diplomys	250–480	1–2	
Echimys	170–350	1	
Capromys	300–500	1–3	> 6
Bradypus	500–600	1	
Hyracoidea			
Dendrohyrax	400–600	1	
Carnivora			
Ailurus	510–635	2	> 10

[1] Data from Walker, 1964; *Phalanger, Pseudocheirus* and *Presbytis* are variable genera with respect to size.

[2] Captive records.

Table 5.—Some convergences in gliding and activity cycles for arboreal herbivores from different geographical areas.

Geographical Area	*Crepuscular*	*Diurnal*	*Nocturnal*	*Glider*
I. CONGO BASIN				
Rodentia				
Anomalurus			X	X
Primates				
Colobus guereza		X		
Colobus badius		X		
Hyracoidea				
Dendrohyrax			X	
II. MALAYA				
Rodentia				
Petaurista petaurista				X
Aeromys thomasi			X	X
Dermoptera				
Cynocephalus			X	X
Primates				
Presbytis obscura		X		
P. melanolophus		X		
III. MADAGASCAR (EASTERN FORESTS)				
Rodentia				
Brachytarsomys			X	
Primates				
Indri		X		
Propithecus		X		
Hapalemur	X	X		
Avahi			X	
Lepilemur			X	
IV. PANAMA				
Rodentia				
Coendou			X	
Edentata				
Choloepus			X	
Bradypus	X	X		
Primates				
Alouatta		X		
V. AUSTRALIA (EASTERN QUEENSLAND)				
Marsupialia				
Schoinobates			X	X
Pseudocheirus			X	
Trichosurus			X	
Phascolarctos	X			

short, we do not see a complicated "guild" of arboreal folivores as is observed in the carnivore and frugivore trophic specializations. This does not imply that the arboreal folivore niche is difficult to adapt to since, as will be demonstrated in the last section, given enough time, evolution of mammalian arboreal folivores on isolated land masses has frequently occurred. Rather, it means that occupancy of the niche does not allow for a greater variety of modes of exploitation.

It seems reasonable to assume that most arboreal folivores evolved from an arboreal, frugivorous form. We are often overwhelmed by the fact that terrestrial herbivores in the Palearctic and Nearctic derived from terrestrial ancestors. It should be pointed out that in the "insular" habitats of South America and Australia, during early mammalian evolution, the terrestrial herbivores derived not only from terrestrial ancestors but also from arboreal ancestors. The South American giant ground sloths (Megatheriidae) clearly derived from an arboreal ancestor, as did the rhinoceros-sized *Diprotodon* in Australia.

Occupancy of an arboreal niche places a certain upper and lower limit on size. An arboreal folivore cannot afford to become too small, since digesting leaves is relatively inefficient. To become very small would entail such a great heat loss that an herbivore might not be able to supply its food needs (see Parra, 1978). Of course, one solution is the development of a labile body temperature so that the animal can cool during inactive periods thus conserving energy. This secondarily acquired poikilothermy characterizes the Bradypodidae, *Lepilemur*, and, to some extent, the arboreal folivorous rodents (see McNab, 1978). Thus, the expression of feeding guilds, such as are often found in carnivores and frugivores, may be difficult, given the hypothesized constraints on the size of the animals themselves.

Arboreal Herbivores on Cuba and Luzon

An inspection of Table 6 will indicate a remarkable convergence in size, coloration, and habits for a series of independently derived arboreal rodent folivores in the Philippine Archipelago and in the Lesser Antilles.

A survey of the mammalian fauna for the Lesser Antilles indicates a great many recent extinctions (Allen, 1942; Hall and Kelson, 1959; Anthony, 1919, 1920, 1925–26), probably resulting from sustained predation by the original human colonizers. If we consider the recently extinct forms, then the faunal diversity for the larger Antillean islands (exclusive of Jamaica) can be portrayed to give some perspective on the low-diversity index for mammalian species in the Antilles when compared with the Republic of

Panama and the island of Trinidad (Figure 5). Cuba, with an area of 44,217 square miles, supported the largest number of mammalian species; 38 have been recorded of which 7 species are currently extinct. The smaller island of Hispaniola, with an area of 29,522 square miles, had 32 species of which 14 are now extinct. Puerto Rico, with the smallest area of slightly over 3,000 square miles, had at one time 19 mammalian species of which 8 are now extinct.

Most extinctions involved the larger forms including the giant ground sloths of the genera *Parocnus, Acratocnus, Megalocnus,* and *Microcnus.* In addition, the terrestrial caviomorph rodents belonging to the families Echimyidae, Capromyidae, and Heptaxodontidae were vulnerable to early extinction. Scansorial and arboreal forms survived better and, on Cuba, we still have 4 living species of capromyid rodents. Our knowledge of the natural history of Antillean rodents is confined to accounts written by Bucher (1937), Chapman (1892) and Mohr (1939). Captive information and aspects of their reproduction and behavior have been summarized by Eisenberg (1974) and Kleiman (1974).

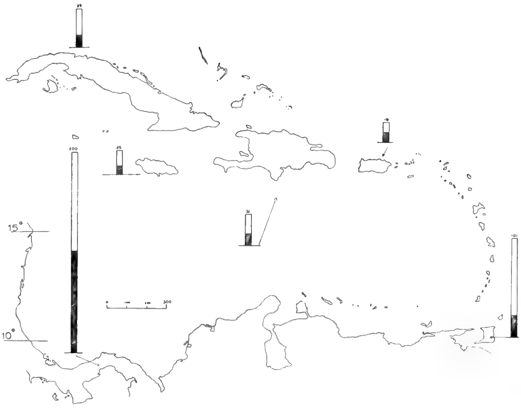

Figure 5. Map of West Indies and Northern South America. Note extremely low mammalian diversity in the Antilles. Scale in Km. Crosshatched area of bars = nonvolant mammals. Species lists from: Handley, 1966; Hall and Kelson, 1959; Goodwin and Greenhall, 1961; Anthony, 1920, 1925-26; and Beebe, 1952.

Table 6.—Convergences in the evolution of insular arboreal rodents.

	Cuba	*Luzon*
Scansorial omnivore	*Capromys nana*	. . .
Semiarboreal frugivore/folivore	*Capromys pilorides*	*Phloeomys cummingi* *Phloeomys pallidus*
Arboreal folivore/frugivore	**Capromys* (*Mysateles*) *melanurus*	*Crateromys schadenbergi*
	Capromys (*Mysateles*) *prehensilis*	. . .

*Chambered stomach figured in Dobson, 1884.

The picture that emerges from these accounts is a rapid radiation on the part of the capromyid rodents to fill terrestrial, semiarboreal and arboreal niches. To an extent, a similar radiation occurred on Hispaniola involving the genera *Plagiodontia, Isolobodon, Hexalobodon,* and *Aphraetreus* in the Capromyidae, and the extinct genera *Brotomys* and *Quemsia* in the families Echimyidae and Heptaxodontidae, respectively. On Puerto Rico the evolution of arboreality did not occur to any appreciable degree, although species from the same 3 rodent families found on Hispaniola were present. Thus, we are left with the conclusion that, on the largest of the Antillean islands with the greatest extent of tropical rain forest, unique arboreal rodents did evolve within the family Capromyidae with adaptions for the exploitation of leaves as a food source.

On Cuba, *Capromys nana* is a small rat-sized form, scansorial in habit, and by no means specialized for a strict folivore diet. *Capromys pilorides* is a slow-climbing animal with a marked preference for feeding on leaves and fruit, but not adapted for rapid arboreal movement as is the case with the 2 remaining species, *Capromys* (*Mysateles*) *prehensilis* and *C.* (*M.*) *melanurus.* These 2 species represent the ultimate in adaptation for an arboreal way of life with a partially prehensile tail by *C.* (*M.*) *melanurus* and the fully prehensile tail in *C.* (*M.*) *prehensilis.*

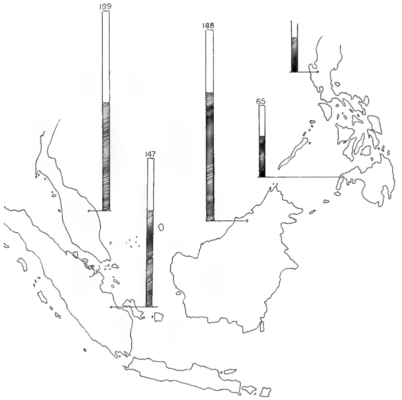

Figure 6. Map of Sunda Islands, Malaya and Philippines. Note reduced diversity on the Philippines. Legend as in Figure 5. Species lists from: Medway, 1963, 1969; Chasen, 1940; and Taylor, 1934.

The *melanurus* species group has one of the most complicated stomachs ever described for the Rodentia (Dobson, 1884). All of the foregoing background information serves to point up the fact that, given the absence of an endemic mammalian form exploiting leaves, the capromyid rodents in the presence of a tropical rain forest were able to radiate and occupy this niche.

Figure 6 indicates the diversity of mammalian species inhabiting the major islands of the Philippine Archipelago as compared with the species diversity of mammals in Malaya and Borneo. One of the more remarkable features of mammalian distribution in the Philippines involves recognition of the fact that the northern island of Luzon has been somewhat more isolated from the other islands of the Archipelago. Luzon shows a higher number of endemic insectivore and rodent species and does not share certain important faunal elements with Borneo as does the southern large island of Mindanao (Taylor, 1934). Luzon does not have the arboreal folivore, *Cynocephalus*, nor does it have an endemic species of langur monkey. Again, in the absence of an established endemic arboreal folivore, the rodents have adaptively radiated on Luzon to fill the folivore niche and this radiation is taxonomically distinct as the murid subfamily Phloeomyinae.

Our knowledge of the natural history of these endemic, muroid rodents is very sparse indeed. Wharton (1948) describes some features of the habitat. Taylor (1934) remarks on the noteworthy resemblance of *Phloeomys* to *Capromys* and notes that Cabrera, not knowing its geographic origin, originally identified the first specimen of *Phloeomys* as a species of *Capromys*. A perusal of the illustrations in Walker (1964) should convince anyone of the fundamental similarities between *Capromys pilorides* and *Phloeomys cummingi*. Both the species *Crateromys schadenbergi* and *Phloeomys cummingi* were maintained at the National Zoological Park. *P. cummingi* was still here when I took up my present position. Some data have been assembled concerning their captive maintenance which is summarized by Crandall (1964). Unfortunately, the necessary field studies are lacking to permit us to develop a picture of their ecology comparable to that which has been assembled for the Capromyidae. Suffice to say, however, that *Crateromys* and *Phloeomys* take a good deal of leafy material in their diet and, in many respects, appear to be ecological equivalents of capromyid genera as outlined in Table 6. I submit then, that once again, in the absence of established folivores, the murid rodents opportunistically radiated into this niche on the island of Luzon.

Concluding Remarks

It is highly suggestive from fragmentary accounts that arboreal herbivore adaptations may have been accomplished in part by certain of the large tree rats on some of the smaller islands in the East Indies. At the risk of becoming too speculative, I might mention that the murid genera *Pogonomys, Mallomys,* and *Tapagomys* would be worthwhile candidates for study in the Flores, New Britain, and New Guinea. Adaptations for the exploitation of leaves as a food source may indeed be present in these genera.

Although not available for study, the recently extinct cricetine genus, *Megalomys*, from Martinique, Santa Lucia, and Barbuda in the West Indies, may well have been excellent semiarboreal folivores (Walker, 1964). The degree of arboreality evolved by the species of this genus is somewhat debatable; nevertheless, some enterprising naturalist missed a fine opportunity before the last species was destroyed during the eruptions on Martinique in the early 1900s.

Thus, I do not believe it is difficult for a species to evolve the necessary adaptations to invade an arboreal, folivorous niche; however, it does appear that the niche is not "wide." Many forms of scansorial rodents are pre-adapted for becoming arboreal folivores and I need only think back on my acquaintance with *Neotoma fuscipes* in California to bring this fact home. As Linsdale and Tevis (1951) summarize in their monograph, its dietary versatility is extraordinary. The animal generally builds a terrestrial nest but often builds an arboreal one. It will forage in both oak and evergreen for foliage which it uses as a dietary supplement for the seeds, nuts, insects, and berries which apparently form the dietary staples. A species such as this is almost waiting for an opportunity to become an arboreal folivore, given either the continuous availability of foliaceous material or the lack of as yet poorly understood competitors. The surprising thing to me is that in the holarctic temperate zone more species of rodents have not evolved to arboreal, folivorous niches utilizing conifers in the manner that *Arborimus longicaudus* has in the northwest coast of North America.

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Energetics of Arboreal Folivores: Physiological Problems and Ecological Consequences of Feeding on an Ubiquitous Food Supply

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Introduction

The study of energetics has wide application because it theoretically permits all biologically important events to be incorporated into a unitary, quantitative statement. Energetics is especially important in species that have the high energy requirements associated with endothermy. Many factors, especially body size, climate, and food habits, influence the energetics of endotherms, and therefore the level and effectiveness of endothermy (McNab, 1974). It is the object of this paper to examine the consequences in energetics of feeding on a particular food: the leaves of trees.

The leaves of trees represent a large standing crop of potential food nearly worldwide in distribution, but in spite of its availability only insects use this resource to any appreciable extent. Few vertebrates use leaves as food, and most of those use leaves as a minor component of their diet. The few vertebrate folivore specialists include the two- and three-toed sloths of South America, the koala of Australia, the flying lemur of Southeast Asia, few reptiles, and fewer birds. Most mammalian folivores are arboreal. Their morphological distinctness (see Eisenberg, 1978) raises the question whether a distinctive physiological constitution is also a correlate of such food habits.

Methods

Body temperatures and rates of oxygen consumption (STP) were measured as a function of ambient temperature in the two-toed sloth, *Choloepus hoffmanni*; three-toed sloth, *Bradypus griseus*; prehensile-tailed porcupine, *Coendou prehensilis*; and Cuban hutia, *Capromys pilorides*. Oxygen consumption was measured in an open system employing a Beckman oxygen analyzer; body temperatures were recorded after a 2-hour (or more) exposure to a given ambient temperature.

The two-toed sloths were obtained by a commercial dealer from Colombia, or were borrowed from the Lincoln Park Zoo, Chicago. *Bradypus* was collected in the Panama Canal Zone, and studied on Barro Colorado Island. *Coendou* and *Capromys* were borrowed from the National Zoological Park, Washington, D.C.

Field measurements of the body temperatures of sloths were made on Barro Colorado Island by Gene Montgomery and M. E. Sunquist along with measurements of light intensity and ambient temperature. These data are converted in this paper into field energy budgets by calculating the cost of maintaining a given temperature differential and adding to it the energetic equivalent of activity. States of activity in the tree sloths were noted in the field (see Montgomery and Sunquist, 1978).

Results

The three-toed sloth, *Bradypus griseus,* maintains a low, variable body temperature; the mean T_b is equal to 33.5° at 30°C and to 31° at 7°C (Figure 1). Its basal rate of metabolism also is very low—only 42 percent of the value expected from body weight (Table 1); this value is similar to the 38 percent reported by Scholander et al. (1950) and Enger (1957). It is difficult to set the lower limit of thermoneutrality and, consequently, determine minimal thermal conductance. The best estimate probably is that the lower limit equals 18°C and that thermal conductance is 0.012 ccO_2/g hr°C, which is 75 percent of the value expected for a temperate mammal of 3.79 kg. The low conductance is due to a dense wool undercoat and a long, coarse overcoat.

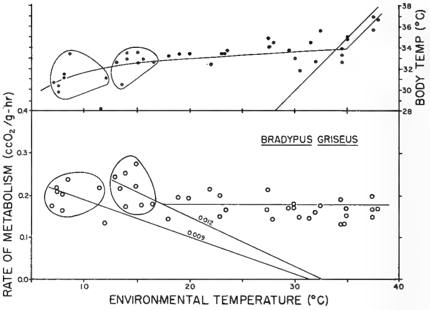


Figure 1. Body temperature and rate of oxygen consumption in 10 three-toed sloths, *Bradypus griseus*, as a function of ambient temperature.

Rates of metabolism equal to basal are found as low as 7°C in *Bradypus*; these values correspond to a lower limit of thermoneutrality equal to 11°C and a conductance of 0.009 ccO_2/g hr°C, which is only 56 percent of the value expected from body weight. This low conductance, however, may simply reflect a reduced peripheral circulation associated with a low body temperature. *Bradypus* almost appears to regulate its rate of metabolism by varying body temperature, whereas most endotherms regulate T_b by varying the rate of metabolism.

Choloepus hoffmanni, the two-toed sloth, regulates body temperature and the rate of metabolism in a manner similar to *Bradypus* (Figure 2). Its basal rate is equal to 45 percent of the value expected from weight (Table 1), which is similar to the 37 percent reported by Scholander et al (1950). Again, the lower limit of thermoneutrality is difficult to determine, as "basal" values can be found at ambient temperatures as low as 7 °C, although most of these values are associated with low body temperatures. If the lower limit of thermoneutrality is equal to 24 °C, thermal conductance is 0.018 ccO_2/g hr°C, which is 117 percent of the value expected from temperate mammals. However, if the lower limit is equal to 12°C, thermal conductance of 0.010 CCO_2/g hr°C, or 65 percent of the value expected. *Choloepus* appears to have a higher thermal conductance than *Bradypus*

Table 1.—Energetics of arboreal folivores.

Species	Weight (kg)	Basal rate ($ccO_2/g\cdot$hr)	Thermal conductance ($ccO_2/g\cdot hr°C$)	M_b/C		%			
				Observed	Expected†	Expected	T_b*	T_l	References
Trichosurus vulpecula	1.98	0.315	—	—	22.7	—	36.2	—	Dawson and Hulbert, 1970
Dendrohyrax dorsalis	2.21	0.340	—	—	23.6	—	—	—	Hildwein, 1972
Capromys pilorides	2.63	0.227	0.019	11.9	24.3	49	35.7	24	This study
Coendou prehensilis	3.28	0.282	0.019	14.8	25.7	58	36.7	26	This study
Bradypus griseus	3.79	0.181	0.012	15.1	26.7	57	33.0	18	This study
Choloepus hoffmanni	4.25	0.188	0.018	10.4	27.4	37	34.5	24	This study
Phalanger maculatus	4.25	0.256	0.021	12.4	27.4	45	34.7	21	Dawson and Degabriele, 1973

†Expected $M_b/C = 3.4w^{+0.25}$

* T_b at lower limit of thermoneutrality, T_l, in degrees centigrade.

mainly because *Choloepus* lacks the dense undercoat found in the three-toed sloth. Morrison (1945) has reported that pregnancy in the three-toed sloth improves temperature regulation, but that was not found to be the case in a two-toed sloth in this study (Figure 2).

Data on the energetics of thermoregulation in the prehensile-tailed porcupine, *Coendou prehensilis*, are presented in Figure 3. This species has a basal rate equal to about 63 percent of the value expected from body weight; it has a minimal thermal conductance equal to about 109 percent of that expected from temperate mammals, which is surprisingly low considering that its insulation is mainly derived from a coat of spines having no undercoat of fur over most of its body. The lower limit of thermoneutrality in this porcupine is not defined by the minimal conductance, but rather by a conductance 155 percent of that expected. The shift from one conductance to the

Figure 2. Body temperature and rate of oxygen consumption in 3 two-toed sloths, *Choloepus hoffmanni*, as a function of ambient temperature. Data on the body temperature of koala, *Phascolarctos cinereus*, taken from Morrison (1962).

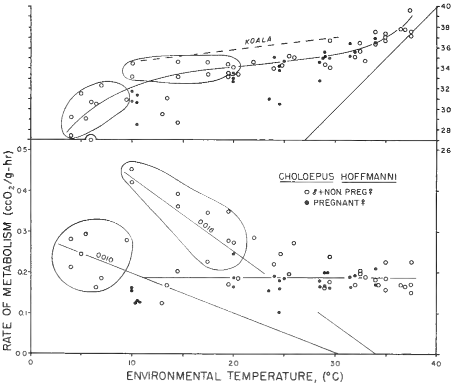
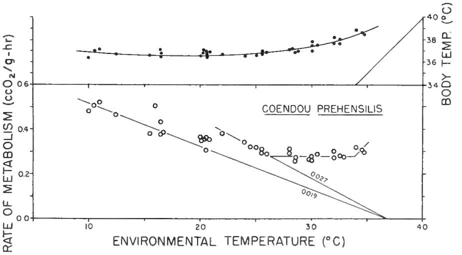


Figure 3. Body temperature and rate of oxygen consumption in one prehensile-tailed porcupine, *Coendou prehensilis*, as a function of ambient temperature.



other between 25° and 20°C may involve a change in posture and, thus, in functional surface area. *Coendou*, unlike *Bradypus* and *Choloepus*, regulates its body temperature precisely down, at least, to 10°C.

The hutia, *Capromys pilorides*, has a low basal rate of metabolism (48 percent), which, in conjunction with a somewhat smaller body size, produces a lower and more variable body temperature than is found in *Coendou* (Figure 4). *Capromys* has a thermal conductance 97 percent of that expected from temperate mammals of the same size.

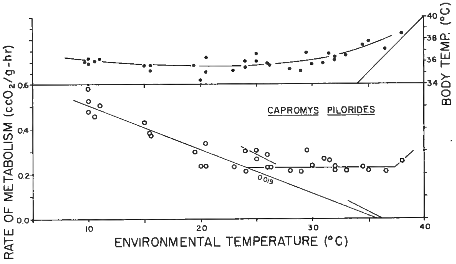


Figure 4. Body temperature and rate of oxygen consumption in one Cuban hutia, *Capromys pilorides*, as a function of ambient temperature.

Discussion

The energetic consequences of a folivorous diet

Mammals that feed to an appreciable extent on leaves apparently are characterized by low basal rates of metabolism (Figure 5). South American tree sloths are extreme examples, but a similar conclusion can be derived from other species. For example, the lowest basal rate in hyraxes occurs in the arboreal, foliovorous *Dendrohyrax* (Hildwein, 1972). The basal rates of goats are lower than those of ungulates that feed strictly on grass (Brody, 1945). In fact, the degree to which the basal rate is depressed is related to the (estimated) proportion of the diet that is made up of leaves (Figure 6). This correlation ($r = -0.874$) holds both within and among taxonomic groups.

It is unfortunate that some of the species most highly adapted to feeding on leaves, such as *Phascolarctos* and *Cynocephalus*, have not been studied. However, the koala regulates body temperature only a little better than the tree sloths (see Figure 2; Morrison, 1962), which suggests that it too has a low basal rate of metabolism.

Why is a low basal rate correlated with a folivorous diet? Three explanations come to mind.

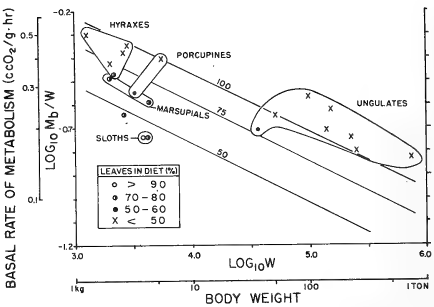


Figure 5. Basal rate of metabolism as a function of body weight in various folivores and their relatives. The curves labeled 100, 75, and 50, represent Kleiber's standard curve (1960), 75 percent and 50 percent of that value, respectively. Data taken from Bartholomew and Rainey (1971) on *Heterohyrax*, Brody (1945) on *Capra* and *Equus*, Dawson and Degabriele (1973) on *Phalanger*, Dawson and Hulbert (1970) on *Trichosurus*, Hildwein (1972) on *Dendrohyrax*, Irving, et al. (1955) on *Erethizon*, Short (1963) on *Odocoileus*, Taylor and Lyman (1967) on *Taurotragus*, Taylor, et al. (1969a, 1969b) on *Connochaetes* and *Kobus*, Taylor and Sale (1969) on *Procavia*, and this study on *Bradypus*, *Choloepus*, *Coendou*, and *Capromys*.

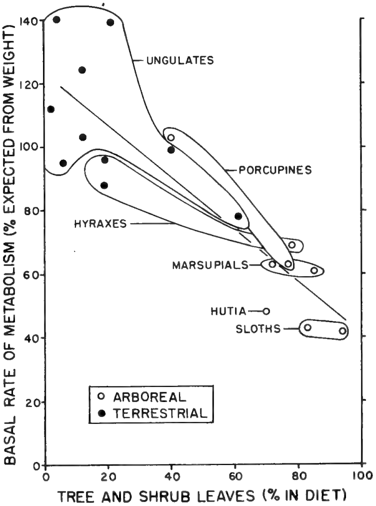


Figure 6. Basal rate of metabolism as a function of the proportion of the diet consisting of the leaves of trees and bushes. Data on metabolism as in Figure 5. Information on food habits estimated from Lamprey (1963) and by consultation with J. F. Eisenberg. From the lowest to the highest proportion of leaf intake, the genera are: *Connochaetes*, *Kobus*, *Bos*, *Equus*, *Procavia*, *Taurotragus*, *Erethizon* and *Odocoileus*, *Capra*, *Capromys*, *Trichosurus*, *Coendou*, *Dendrohyrax*, *Choloepus*, *Phalanger*, and *Bradypus*.

(1) Leaves may have a high fiber and cellulose content and, consequently, have a low *available* caloric density. According to this explanation, any species feeding on such a food will have a low rate of metabolism because of a limit placed on the maximal bulk that can be processed in a day. This limitation means that the available energy intake per day is fixed at a level below that expected from the standard curve relating basal rate to body size in mammals. However, Dougall et al. (1964) indicate that there is no clear distinction to be made between the fiber content of browse and grasses, and, in fact, grasses may have a lower protein content than browse. Nevertheless, a noticeable difference may exist in digestibility between these foods.

(2) The major predators of tree leaves are insects; this predation is reduced by plants through the production of a series of organic molecules, including various alkaloids, terpines, phenols, and toxic amino acids. These compounds in general are toxic to mammals as well as to insects (Freeland and Janzen, 1974). For example, Schmidt-Nielsen (1964) has discussed some of the physiological difficulties encountered by desert mammals in handling oxalic acid. The low basal rates of folivorous mammals may reduce (a) the intake of toxic substances and (b) the cost of their detoxification, which is sometimes accomplished by the addition of a glucose molecule, thereby reducing the net energy intake. Insects, the principle predators on leaves, also apparently have an adaptive response to feeding on leaves: the few, scattered data available on insect larvae having these habits show (a) lower rates of metabolism (Figure 7) and (b) slower growth rates (S. Progoff, personal communication) than insects with other food habits.

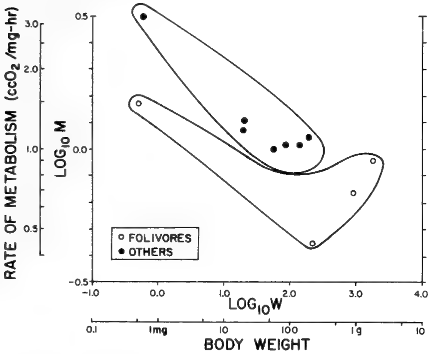


Figure 7. Standard rate of metabolism in larval insects as a function of body weight in folivorous species and in species with other food habits. Data taken from Keister and Buck (1974); corrected to $T_a = 25° C$ by using $Q_{10} = 2$.

(3) Arboreal mammals have a muscle mass as low as 23 percent of the total body mass, while terrestrial species have up to 53 percent of their total weight as muscle (Grand, 1978, and personal communication). The reduction in muscle mass is apparently most marked in larger arboreal species, which are rather sedentary. Small arboreal species, such as the tree shrew (*Tupaia glis*) and tree squirrels, are very active; consequently they have a larger proportion of their mass as muscle (Grand, personal communication). Low basal rates of metabolism are correlated with muscle masses less than 33 percent of the total mass (Figure 8). Furthermore, the scope of metabolism is greatly diminished in species with a small muscle mass: normally the maximal steady-state rate of metabolism is about six times the basal rate (Brody, 1945; Hemmingsen, 1960; Jansky, 1962), but it is only 2.0 to 2.4 in some prosimians and 1.5 to 2.3 in sloths. The reduction in the basal rate and in the scope of metabolism means that there is a great reduction in the maximal sustainable rate of metabolism during a cold exposure, a condition that leads to poor temperature regulation. This explanation suggests why some arboreal mammals having food habits other than folivory—most notably the prosimians *Nycticebus* (C. Palacio, personal communication) and *Perodicticus* (Hildwein and Goffart, 1975)—are such poor thermoregulators.

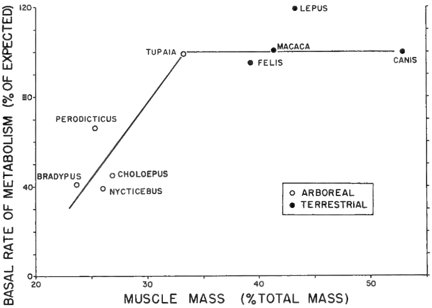


Figure 8. Basal rate of metabolism (relative to values expected from weight) as a function of the proportion of the body mass that is muscle. Data on rates of metabolism taken from Brody (1945), Schmidt-Nielsen, et al. (1965), Yousef, et al. (1971), C. Palacio (personal communication), and this study.

It is not clear how these factors interact to determine the low basal rates of arboreal folivores. The fact that terrestrial folivores, such as goats, have low basal rates suggests a direct effect of food habits, and thus may well reflect the influence of toxic substances in the leaves of trees (and shrubs). However, it also appears that the reduction in the relative size of the muscle mass markedly effects the basal rate and the scope of metabolism. Thus, most arboreal folivores must be rather large (usually 1 to 5 kg) to handle large quantities of a food having a low caloric and nutritional density, which in an arboreal setting leads to a sedentary existence and its consequences in energetics. At the present time, therefore, the peculiarities in the energetics of arboreal folivores appear to result from some combination of food habits and arboreality (Table 1).

The excellent insulation of the tropical *Bradypus* undoubtedly is compensatory for a low basal rate of metabolism (Scholander et al., 1950; McNab, 1974) and permits the maintenance of a larger temperature differential with the environment than would otherwise be attained. Similarly, a low thermal conductance is compensatory for a low rate in small anteaters, armadillos, and marsupials (McNab, 1974). *Choloepus* has a somewhat higher basal rate (due to a more diversified diet?) and a higher thermal conductance than *Bradypus*. Dawson and Degabriele (1973) have described the cuscus (*Phalanger maculatus*) as a marsupial sloth; its size, physiological characteristics, and diversity in food habits make it similar to *Choloepus*. One might expect the koala to be similar to *Bradypus*, given the restricted nature of its diet.

Field energy budgets of tree sloths

The basal rate of metabolism is a convenient index to the energetics of endotherms, but of greater importance is knowledge of the long-term daily expenditure in the field. The daily expenditure is a sum of the expenditures for homeostasis and for activity.

Homeostatic power outputs for endotherms are reasonably easy to calculate, if the energy expenditure is known as a function of environmental temperature and if the appropriate environmental temperatures are known. An even more accurate means of evaluating this expenditure, especially for species showing poor temperature regulation, is to express energy expenditure as a function of the temperature differential between an animal and its environment (Figure 9). These data were used in conjunction with the telemetered field measurements of T_b and T_a obtained from sloths on Barro Colorado Island, (Figure 10, Table 2). In *Bradypus* the homeostatic expenditure is essentially constant (3.8 watts = 3.3 kcal/hr) in both the wet and dry season because ΔT never exceeded the maximal value compatible with thermoneutrality (ΔT_l = 15°C, Figure 9, Table 2). In the one 2-day period in which *Choloepus* was monitored ΔT exceeded ΔT_l (11°C, Figure 9, Table 2). Its homeostatic expenditures varied between 4.5 (3.8) and 5.3 watts (4.5 kcal/hr). The expenditures for *Choloepus* are greater than those for *Bradypus* because it is larger, has a higher basal rate, and has a poorer fur coat (in lacking the wool undercoat) than *Bradypus*.

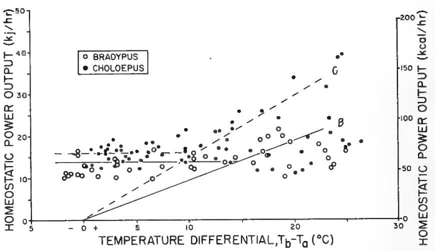


Figure 9. Homeostatic power output in *Bradypus* and *Choloepus* as a function of the temperature differential between the body and environment. Based on the data in Figures 1 and 2, assuming that the mean body weight for *Bradypus* is 3.79 kg and for *Choloepus* is 4.25 kg.

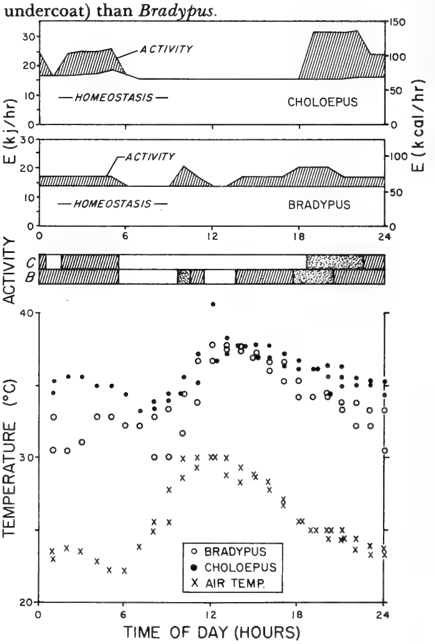


Figure 10. The relation of body temperature, activity, and energy expenditure to time of day in *Bradypus* and *Choloepus*. Data from Montgomery and Sunquist (personal communication). For means of calculating energy expenditure, see text.

Table 2.—Estimated field energy expenditures in Bradypus and Choloepus.*

	Bradypus					*Choloepus*				
	Homeostasis		*Activity*†		*Total*	*Homeostasis*		*Activity*†		*Total*
Hour	ΔT(°C)	*kJ*	*Amount*	*kJ*	*kJ*	ΔT(°C)	*kJ*	*Amount*	*kJ*	*kJ*
0100	8	13.78	+	3.45	17.23	11.5	16.70	o	0.0	16.70
0200	6.5	13.78	+	3.45	17.23	11.5	16.70	+	8.00	24.70
0300	7.5	13.78	+	3.45	17.23	12	17.50	+	8.00	25.50
0400	10	13.78	+	3.45	17.23	12	17.50	+	8.00	25.50
0500	10.5	13.78	+	3.45	17.23	13	18.90	+	8.00	26.90
0600	10	13.78	o	0.0	13.78	12	17.50	o	0.0	17.50
0700	8	13.78	o	0.0	13.78	9.5	16.00	o	0.0	16.00
0800	7.5	13.78	o	0.0	13.78	8.5	16.00	o	0.0	16.00
0900	6.5	13.78	o	0.0	13.78	7	16.00	o	0.0	16.00
1000	5	13.78	+ +	6.89	20.67	6	16.00	o	0.0	16.00
1100	6	13.78	+	3.45	17.23	6.5	16.00	o	0.0	16.00
1200	7	13.78	o	0.0	13.78	7.5	16.00	o	0.0	16.00
1300	8	13.78	o	0.0	13.78	9	16.00	o	0.0	16.00
1400	8.5	13.78	+	3.45	17.23	9	16.00	o	0.0	16.00
1500	8.5	13.78	+	3.45	17.23	9	16.00	o	0.0	16.00
1600	8.5	13.78	+	3.45	17.23	9.5	16.00	o	0.0	16.00
1700	9	13.78	+	3.45	17.23	10	16.00	o	0.0	16.00
1800	9	13.78	+ +	6.89	20.67	11	16.00	o	0.0	16.00
1900	9	13.78	+ +	6.89	20.67	11	16.00	+ +	16.00	32.00
2000	9.5	13.78	+ +	6.89	20.67	11	16.00	+ +	16.00	32.00
2100	9	13.78	+	3.45	17.23	11	16.00	+ +	16.00	32.00
2200	9	13.78	+	3.45	17.23	11.5	16.70	+ +	16.00	32.70
2300	9	13.78	+	3.45	17.23	11.5	16.70	+	8.00	24.70
2400	9	13.78	+	3.45	17.23	11.5	16.70	+	8.00	24.70
Total		330.8		75.9	406.6		394.9		112.0	506.9
(%)		(81)		(19)	(100)		(78)		(21)	(100)

*Based on field measurements of temperature and activity by Montgomery and Sunquist on 15 and 16 February. Energetic estimates assume that mean weight for *Bradypus* is 3.79 kg and for *Choloepus* is 4.25 kg.

†Amount of activity: o not active either of 2 days at given hour; + active one day; + + active both days. Assumed energy equivalents of activity: *Bradypus*, 0 = 0 kJ, + = 0.25 basal, + + = 0.50 basal; *Choloepus*, 0 = Oks, + = 0.50 basal, + + = 1.00 basal.

The energetic equivalent of activity is more difficult to determine, an estimate of which was made in the following manner. Montgomery and Sunquist (personal communication) recorded whether a sloth was active in the field for 2 days at the hourly periods in which body and environmental temperatures were measured (Figure 10, Table 2). Therefore, for each hour of the day a sloth could have been active on neither day, one day, or both days. If the sloth was not active at a particular hour on either day, the energy expenditure for that hour was taken to be equal to the cost of homeostasis. If the sloth was active on one day, the increment in metabolism for activity was taken to be 0.25 times basal for *Bradypus* and 0.50 times for *Choloepus*. If the sloth was active on both days at a given hour, the increment was assumed to be 0.50 M_b for *Bradypus* and 1:00 M_b for *Choloepus*. These maximal rates correspond to the metabolic scopes for the sloths, which are 1.5 in *Bradypus* and 2.3 in *Choloepus*.

The mean energy expenditure for *Bradypus* is estimated to be 95.5 kcal/day (Table 3). This estimate does not agree with the rates of leaf consumption calculated by Montgomery and Sunquist (1975) from estimated rates of feces production. They conclude that *Bradypus* produced approximately 7.4 g dry feces/sloth-day. By assuming that digestion was 50 percent efficient, the dry intake of leaves was 14.7 g/day. If

Table 3.—Estimated energy budgets of free-living sloths.*

Species	*Date*	*Sex*	*Energy Expenditure (kJ)* *Homeostasis*	*Activity*	*Total*	*Total* *kcal*	*watts*	*Activity (% total)*
Bradypus griseus	21-22 August	preg. ♀	330.8	48.3	379.1	90.6	4.39	13
B. griseus	23-24 August	preg. ♀	330.8	103.4	434.2	103.7	5.03	24
B. griseus	28 August	♂	330.8	58.6	389.4	93.0	4.51	15
B. griseus	29 August	♂	330.8	89.6	420.4	100.4	4.87	21
B. griseus	30 August	♂	330.8	37.9	368.7	88.1	4.27	10
B. griseus	15-16 February		330.8	75.9	406.6	97.1	4.71	19
Mean *Bradypus*			330.8	69.0	399.7	95.5	4.63	17
Choloepus hoffmanni	15-16 February		394.9	112.0	506.9	121.1	5.87	21

*Estimated from field measurements of temperature and activity by Montgomery and Sunquist, assuming a mean body weight equal to 3.79 kg for *Bradypus* and to 4.25 kg for *Choloepus*.

the caloric value of leaves is about 3700 cal/g (Golley, 1969), the total daily intake is about 54.4 kcal, which is only 57 percent of the expenditure estimated in this paper. That is, it is estimated here that *Bradypus* probably consumes about 26 dry g leaves/day. The conflict between the estimate of energy expenditure and the estimate of food consumption may reflect higher rates of decay in the feces than assumed by Montgomery and Sunquist.

There is an appreciable daily variation in energy expenditure for activity. For example, *Bradypus* may expend more than twice as much energy for activity on one day as the same individual did on another day (Table 3). The estimates of field energy expenditures suggest that activity may account for 10 to 25 percent of the total expenditures. For *Bradypus*, at least, the variability in daily expenditures is due mainly (if not exclusively) to variations in activity. And the variation in activity from one day to another in the same individual is equal to the variation among individuals. *Choloepus* had a larger absolute expenditure for activity, because of its larger body weight and higher metabolic scope, but this expenditure occupied no greater fraction of the total daily expenditure than in *Bradypus* (Table 3). Finally, it should be noted that the periodicity for activity, and therefore for energy expenditure, is markedly different between these two sloths: *Bradypus* is irregularly active throughout the day, except possibly between 0500 and 0800 hours, while *Choloepus* is rather strictly nocturnal (Figure 10, Table 2).

Conclusion

We know little about the physiological and ecological interactions between trees (and shrubs) and the animals that use their leaves as a food resource. It does seem reasonably certain, however, that feeding upon these leaves affects the consumers in a manner not found in other herbivores, such as grazers or frugivores. This difference may reflect (1) the ecological strategies of plants that protect their photosynthetic apparatus but encourage the dissemination of their seeds, and (2) the ecological strategies of mammals living on an energy-poor food in a geometrically precarious environment. We obviously need many more data on arboreal folivores, especially the koala, colugo, and certain primates. A study of the energetics of the small, temperate, arboreal red tree-mouse, *Phenacomys longicaudus*, would permit the examination of the effect of a small body size. Furthermore, a study of the energy expenditure of some terrestrial specialists on leaves, such as elephants and the giraffe, or the comparison of the (grazing) white and (browsing) black rhinos, might permit the separation of the influence of folivory from the influence of arboreality.

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Water Metabolism of the Koala (*Phascolarctos cinereus*)

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Introduction

In general terms, the physiological parameters which could limit an animal to a particular environment include the availability and quality of food, the thermal environment and the adaptations of the animal to that environment, and the availability of water together with the animal's water requirements. In order to maintain its normal water content, all the water that an animal loses must be offset by the water it takes up. The rate at which water is lost and taken up (i.e., water turnover rate) is a reflection of both the availability and the utilization of water.

The various avenues for water uptake are drinking water, preformed water (free water) in the food, and the water produced by the metabolism of the food (metabolic water). Drinking water is generally at a premium in the arboreal environment, being available

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either on the ground or as dew on the leaves during the night and early morning. The availability of preformed and metabolic water, the major inputs of water for an arboreal mammal, depends on the nutritional composition and palatability of the leaves being eaten.

Water is lost as urinary water, fecal water, metabolic water (water which would have been produced by metabolism of the feces), and evaporative losses. Water loss in the urine is regulated by the kidney via antidiuretic hormone which is released from the pituitary in response to an increased osmotic concentration in the blood. The free water content of the feces appears to be regulated by the colon, while the metabolic water content of feces is a reflection of the digestive efficiency of the animal. The amount of water required for evaporative cooling depends on the activity of the animal and its adaptation to a particular thermal environment.

Although a large number of studies of various aspects of water metabolism have been reported for a number of mammals, investigations into the complete (i.e., partitioned) water balance of mammals have been carried out largely on rodents, ungulates, and perameloid and macropodid marsupials, none of the species being arboreal.

This paper discusses the water metabolism of the koala (an animal which is alleged to never drink in the wild) in the context of its energy metabolism and thermoregulation. The koala, an extremely specialized arboreal folivore (Freeland and Janzen, 1974), is unusual among the arboreal marsupials in that, in common with the tree-kangaroos (Breeden and Breeden, 1970), it does not appear to use any form of shelter. This independence from shelter appears to be widespread, however, among arboreal eutherians. The koala has broad ecological requirements similar to those of the greater glider *(Schoinobates volans)* (Eberhard, 1972, Marples, 1973; Smith, 1969; Tyndale-Biscoe and Smith 1969a, 1969b). The alleged slothlike nature of the koala (Troughton, 1973) makes its ecological and physiological characteristics particularly interesting, since another arboreal marsupial, the spotted cuscus *(Phalanger maculatus)*, exhibits a pattern of thermal adaptation to the tropics similar to that of the sloths (Dawson and Degabriele, 1973). A detailed account of the methods used in this study is given by Degabriele (1977).

Studies of Wild Koalas

Geographic variation in water metabolism

Total body water, water turnover rate, and biological half-life ($T_{1/2}$) of water were calculated from dilution of tritium-labeled water (TOH) (Richmond, Langham, and Trujillo, 1962). The measurements were carried out during summer on 9 wild koalas representing the 3 geographical races (Figure 1). Three individuals from Magnetic Island *(P. c. adustus)*, 3 from Sydney *(P. c. cinereus)*, and 3 from Philip Island *(P. c. victor)* were studied. The mean body weights of koalas from the 3 races were 6.8 kg, 6.4 kg, and 8.3 kg, respectively. Environmental conditions are not markedly different in the 3 locations (Australian Bureau of Meteorology). There were no significant differences between the 3 samples with respect to total body water, water turnover rate, and biological half-life ($t < 0.4$, $p > 0.7$), and the results were pooled (Table 1).

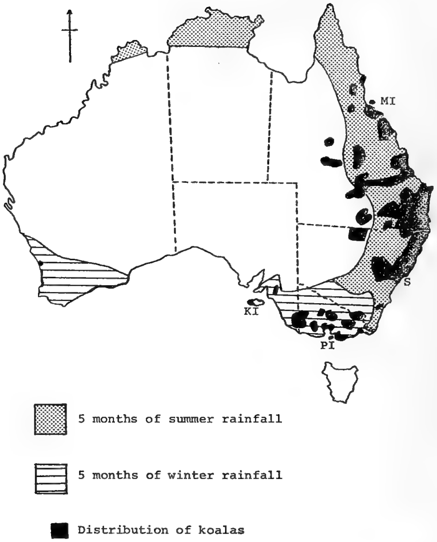

Figure 1. Distribution of the koala throughout Australia. MI = Magnetic Island; PI = Philip Island; KI = Kangaroo Island; S = Sydney.

The homogeneity of these results indicates that, irrespective of geographical location, the microhabitat of the koala remains rather constant, at least with respect to water requirements and supply. The preformed water content of *Eucalyptus punctata* leaves lies between 45 and 50 percent (Table 2), indicating that, when there is a plentiful food supply, there should also be a plentiful water supply provided by the leaves. It can be assumed that the leaves of other species of *Eucalyptus* contain at least as much water as those of *E. punctata* since a level of water content below about

Table 1.—Metabolism of tritiated water by 9 wild koalas of the 3 geographical races.

Measure	*Mean S.E.*	*Unit*
Body weight	6.91 ± 0.41	kg
Total body water	5.35 ± 0.32	litres
	77.4 ± 0.3	% body weight
Water turnover	122.0 ± 3.4	g/kg day
rate	179.0 ± 3.7	g/kg$^{0.8}$ day
Half-life ($T_{1/2}$)	4.4 ± 0.1	days

Table 2.—Preformed water content of Eucalyptus punctata **leaves and feces from koalas fed these leaves, given as percentage of wet weight.**

		Winter	
	Summer	*a*	*b*
Leaves	48.5	46.4	45.5
Feces	54.0	52.3	43.0

a: drinking water available
b: drinking water withdrawn

40 percent leads to desiccation and death of *Eucalyptus* leaves (J. H. Palmer, personal communication).

Total body water

Koalas have a relatively high level of total body water (77.4 percent), similar to the levels found in other ruminantlike marsupials (Denny, 1973; Kennedy and Heinsohn, 1974). If one assumes that the fat-free body weight of the koala contains 75 percent water (Hulbert and Gordon, 1972), then the high level of total body water lends support to the observations that the koala has a characteristic lean carcass (Degabriele, 1977); Eberhard, 1972) and that the very large cecum holds significant amounts of moist material (Eberhard, 1972).

Water turnover rate

The water turnover rate for koalas (179.0 g/kg$^{0.8}$day) is higher than the mean eutherian level of 123 ml/kg$^{0.8}$day (Richmond, et al., 1962), measured in the laboratory, and double the rate of the brush-tailed possum, *Trichosurus vulpecula,* (96.0 ml/kg$^{0.8}$day), and the rock-wallaby, *Petrogal inornata,* (98.9 ml/kg$^{0.8}$day) (Kennedy and Heinsohn, 1974), both measured in the wild. It is also nearly three times the previously reported turnover rate for koalas (63.9 ml/kg$^{0.8}$day) (Eberhard, 1972). Eberhard's figures need to be viewed with considerable caution, however, because his animals were recently captured koalas which were losing weight throughout the period of the measurements. Water turnover rate (Table 1) expressed relative to the four-fifths power of body weight negates the effect of varying body size and allows comparison within and between species (Richmond, et al., 1962). An interesting comparison can be made between the short-nosed bandicoot *(Isoodon macrourus)* and the koala. The water turnover rate of bandicoots living in a waterless island habitat (131.3 ml/kg$^{0.8}$day) is similar to that of the koala, but it is considerably higher (243.8 ml/kg$^{0.8}$day) for bandicoots on the water-rich mainland (Hulbert and Gordon, 1972). Thus the arboreal microhabitat of the koala may be likened to a waterless island where the food supply incorporates a water supply.

Kidney morphology and function

The right kidney was collected from 8 freshly dead koalas. The koalas died either at Taronga Zoo, Sydney, or at the Department of Agriculture District Veterinary Station, Armidale, Kidney size was estimated (Sperber, 1944) by $\sqrt[3]{\text{length} \times \text{breadth} \times \text{height}}$. Medullary and cortical thicknesses were measured and expressed as relative thicknesses (Sperber, 1944), by:

$$\text{Relative thickness} = \frac{\text{actual thickness} \times 10}{\text{kidney size}}$$

Cortical and juxtamedullary glomerular volumes were determined by measuring the long (L) and short (B) diameters of glomeruli projected onto a screen (Figure 2A) and calculating volume (Palkovits and Zolnai, 1963) by:

$$\text{Volume} = \frac{\pi}{6}(L \times B)^{2/3}$$

The ratio of glomerular to cortical tissue was measured by superimposing a 20 cm × 20 cm grid on the projected image of a microscope slide and counting the number of glomeruli falling on an intersection of the grid lines (400 points). The relative medullary tubular density within the cortex (Figure 2B) was calculated in a similar manner.

The main features of the morphology of the koala kidney (Table 3) support the view that the koala has a simple kidney with a single papilla (Sperber, 1944). The relative medullary thickness, which is greater in

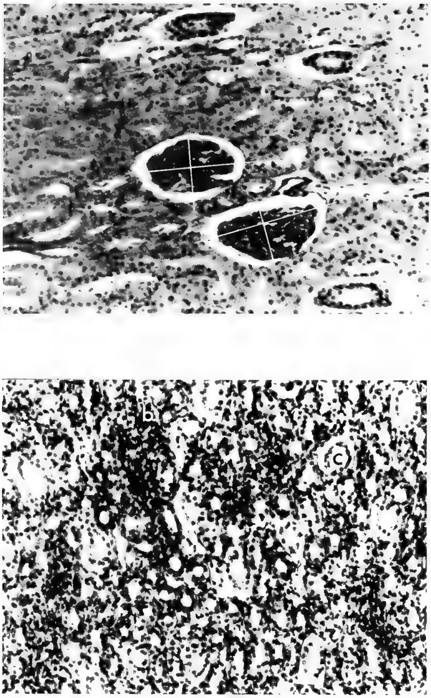

Figure 2. A. Glomeruli from a koala kidney showing the two measurements taken. B. Renal medullary tissue of a koala showing tubules (t), blood vessels (b), and collecting ducts (c).

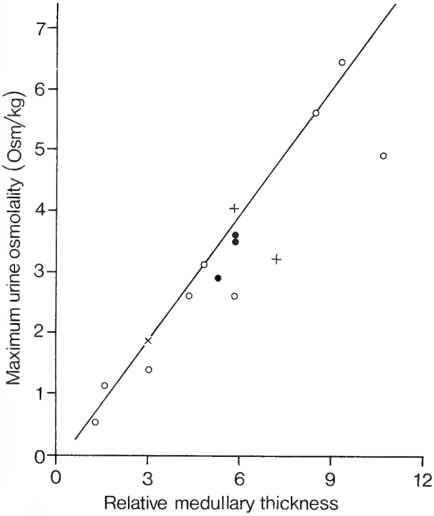

Figure 3. Relationship between maximum urine osmolality and relative medullary thickness for a number of animals. Eutherian data (open circles) from Schmidt-Nielsen and O'Dell (1961); peramelid marsupial data (solid circles) from Hulbert and Dawson (1974b); macropodid marsupial data (open triangles) from Denny (1973); koala figure denoted by solid triangle.

animals with greater urine-concentrating capability (Schmidt-Nielsen and O'Dell, 1961), was 3.0 for the koala. Relative medullary thickness in the koala (Figure 3) indicates that maximum urine concentration is comparatively low, suggesting that the koala is adapted to a habitat where water is not limiting. Other aspects of kidney morphology support this suggestion. The length of the renal papilla (Figure 3), which increases with dry habitat and diet (Schmidt-Nielsen, 1958), lies between that of the platypus *(Ornithorhynchus anatinus)*, a water-living monotreme, and that of the dry habitat dasyurid marsupial *Antechinomys laniger* (Sperber, 1944). The difference in volume between the cortical and juxtamedullary glomeruli is greater in species from dry habitats than in those from a water-rich habitat (Munkacsi and Palkovits, 1965). The difference in glomerular volume for the koala (Figure 4) is 60 percent, considerably less than that for the jerboa *(Jaculus jaculus)*, a desert rodent (101 percent), or the bush baby *(Galago senegalensis)*, a semidesert-inhabiting subprimate (161 percent) (Munkacsi and Palkovits, 1965). The relative proportions of the cortex and medulla given over to filtration also suggest that the koala kidney is adapted to a habitat with plentiful water. The proportion of cortical tissue occupied by glomeruli is only 8 percent and the relative medullary tubular density is about 30 percent (Table 3).

Studies of Captive Koalas

The tritiated water measurements from wild koalas, and the observations on kidney morphology, show the koala to be an animal whose microhabitat is not normally limiting with respect to water. To obtain a more detailed account of the water balance, 5 koalas were housed individually in cages and water inputs and outputs were partitioned. The mean body weight of these koalas was 6.1 kg (S.E. 0.8 kg). Water inputs were from drinking water, preformed water in the

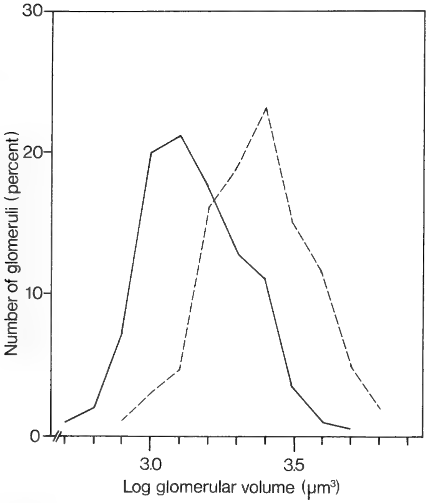

Figure 4. Frequency distribution curves of cortical (solid line) and juxtamedullary (broken line) glomeruli in the koala kidney.

Table 3.—Morphological features of the kidney of the koala. The kidney is of the papillary type according to Sperber's (1944) classification.

Feature	*Mean size S.E.*	*Units*	*N*
Size	29.6 ± 0.9	mm	8
Relative medullary thickness	3.0 ± 0.3	mm	8
Cortical glomerular volume	1538.77 ± 46.86	μm^3	200
Juxtamedullary glomerular volume	2584.21 ± 76.13	μm^3	200
Average glomerular volume	2061.49 ± 51.74	μm^3	400
Glomeruli to cortex tissue ratio	8.45 ± 0.19	%	10
Relative medullary tubular density	32.91 ± 0.45	%	100

leaves of *Eucalyptus punctata* fed to the koalas, and metabolic water. Water outputs were urinary water, fecal water, metabolic water, and water lost through evaporation.

Drinking water was measured as daily weight change of the water container, corrected for evaporation. Preformed water content of the food was calculated from the weight lost by freshly collected leaves which had been dried to constant weight at 105°C, corrected for losses due to steam-volatile oils (Southwell, 1973). Metabolic water was calculated (Schmidt-Nielsen, 1964), after the nutritional composition of the leaves was determined (Table 4). Urinary water was determined from the weight lost by samples which had been dried to constant weight at 105°C. Fecal water loss was determined by measuring the water content of freshly voided pellets and extrapolating to the total dry weight of feces produced each day. The metabolic water content of the feces was determined in a manner identical to that for the leaves (Table 4). Koalas were not deprived of drinking water in summer because some risk to them might have been involved. During the summer measurements minimum air temperature ranged between 17° C and 21° C while the maximum ranged between 23° C and 35° C. The corresponding temperature ranges in winter were 4° C to 12° C, and 14° C to 19° C.

Table 4.—Nutritional composition of Eucalyptus punctata **leaves and koala feces, in g/100 g dry weight.**

	Ash	*Fiber*	*Protein*	*Fat*	*Carbo-hydrate*
Leaves	3.29	13.55	5.56	31.00	46.60
Feces	3.13	13.40	9.86	30.06	43.55

Water turnover rate

The water turnover rate of captive koalas under a variety of conditions (Table 5) was about a half or less than that for wild koalas (Table 1), the most likely cause being restrictions on activity imposed by small cages. Just as the water turnover rates of koalas in the wild were similar to those of island populations of the short-nosed bandicoot, so also were the turnover rates under laboratory conditions similar (Hulbert and Dawson, 1974b). In common with other marsupials (Dawson and Hulbert, 1969, 1970; MacMillen and Nelson, 1969), the koala has a reduced level of energy metabolism (Degabriele, 1977) compared to eutherians. Likewise, in common with other marsupials (Denny and Dawson, 1972, 1975; Hulbert and Dawson,

Table 5.—Partitioned water intake and loss in koalas under various conditions in g/kg day, except where noted. Percentages of total intake or loss are shown for each partition. The total number of animal days (n) is shown.

	Summer	*Winter*	*Winter*
	n = 31	*n = 39*	*n = 14*
	Mean S.E.	*Mean S.E.*	*Mean S.E.*
INTAKE:			
Water drunk	14.7 ± 2.5 (26%)	18.2 ± 3.3 (26%)	0
Preformed water in leaves	25.1 ± 1.4 (45%)	30.3 ± 1.8 (44%)	26.6 ± 2.0 (58%)
Metabolic water	15.9 ± 0.9 (29%)	20.9 ± 1.3 (30%)	19.0 ± 1.4 (42%)
LOSS:			
Urinary water	11.0 ± 1.4 (20%)	10.6 ± 1.4 (15%)	8.7 ± 1.7 (19%)
Preformed water in feces	11.5 ± 0.6 (21%)	17.2 ± 0.8 (25%)	5.2 ± 0.2 (11%)
Metabolic water	5.7 ± 0.3 (10%)	9.2 ± 0.4 (13%)	4.1 ± 0.1 (9%)
Evaporative water loss	27.5 ± 2.7 (49%)	32.4 ± 4.6 (47%)	27.6 ± 4.0 (61%)
Total	55.7 ± 3.5 80.0 $g/kg^{0.8}$ day	69.4 ± 5.4 92.3 $g/kg^{0.8}$ day	45.6 ± 3.4 63.3 $g/kg^{0.8}$ day

1974b; Kennedy and Heinsohn, 1974; Kennedy and MacFarlane, 1971; MacFarlane, et al., 1971), the captive koala (with drinking water ad lib.) has a water turnover rate (Table 5) only 65 to 75 percent of the eutherian level under similar conditions (Richmond, et al., 1962). Since water turnover rate appears to be correlated with metabolic rate (Hulbert and Dawson, 1974a, 1974b; MacFarlane and Howard, 1972; MacFarlane, et al., 1971), especially when water turnover rates are measured in the laboratory in the absence of stress, the reduction in water turnover rate in the marsupials (about 70 percent of the comparable eutherian level) should be regarded as a phylogenetic characteristic of the order Marsupialia.

Water input

The performed water in the leaves used as food was the major avenue of water intake at all times. The relative contribution of drinking water to water input was the same (26 percent) in summer and winter, although more water and food were consumed during winter (Table 5). The proportion of water obtained from the metabolism of food was 29 to 30 percent when drinking water was available. When water was withheld, the absolute amount of metabolic water remained unchanged whereas its relative importance increased substantially. Similarly, the absolute amount of preformed water changed little when water was withheld, but the relative amount increased. The water input directly associated with the food (preformed and metabolic water) remained reasonably constant at 40 to 50 g/kg day irrespective of season or the availability of drinking water. This indicates that either the demands on water were being adequately met at all times or that nutritional requirements or the ability to detoxify the essential oils in the leaves or the actual bulk of the leaves being eaten were the limiting factors.

Water loss

Evaporative water loss accounted for the major proportion of water lost. This was followed by water lost in feces, including both preformed and metabolic water. Urinary water loss was generally the least important component. Withdrawal of drinking water resulted in a considerable decrease in the amount of preformed and metabolic water lost with the feces.

Evaporative water loss

The increase in water turnover rate in winter compared with summer (Table 5) is reflected in an increase in evaporative water loss. It was a relatively cool summer so that active cooling by evaporation was probably at a low level. A decrease in the water turnover rate during winter, which occurred with withdrawal of drinking water, resulted in a decrease in evaporative water loss to the level recorded when water was freely available in summer. Presumably this is some sort of maintenance level of evaporative water loss both in summer and winter, excluding the requirements for active cooling under thermal stress.

Fecal Water Loss

The water content of the koala's feces (Table 2) is comparatively low (MacMillen, 1972), even when drinking water is available. When water is withdrawn, fecal water content drops from 52 percent to 43 percent which is the same as the fecal water content of the dehydrated camel (Schmidt-Nielsen, 1964).

Urinary water loss

When drinking water was withdrawn during winter, the koala remained in water balance by reducing water turnover rate to 67 percent of the former level, by reducing fecal water output to 35 percent of the previous rate (Table 5), and by increasing urine osmolality to 1.2 times the former level (Table 6). Withdrawal of drinking water probably stressed the kidney maximally with respect to the capacity to concentrate urine, as indicated by comparison between the urine osmolality under minimal water conditions and under Pitressin stress (Table 6). Pitressin (an antidiuretic hormone) was used to induce production of maximally concentrated urine because, like the beaver (Schmidt-Nielsen and O'Dell, 1961), the koala will not eat "dry" food so that dehydration without food deprivation is not possible. Pitressin-assayed antidiuretic activity has been demonstrated in the pituitary of the koala (Yesberg, et al., 1967).

Table 6.—Chemical composition of koala urine collected under various conditions.

	Summer	*Winter*		
	Water available	*Water available*	*No water available*	*Pitressin stress*
Na^+ (mEq/l)	218.0 ± 32.5*	191.0 ± 29.0	324.1 ± 28.0	503.4 ± 33.5
K^+ (mEq/l)	104.8 ± 19.7	46.4 ± 13.2	234.6 ± 47.2	444.7 ± 59.1
$(Na^+ + K^+)$ (mEq/l)	322.8 ± 42.6	237.4 ± 38.1	558.7 ± 44.2	948.1 + 81.2
Urea (mMol/l)	203.0 ± 32.0	258.7 ± 37.4	342.1 ± 27.0	213.8 ± 27.6
Osmolality (mOsm/kg)	1212.6 ± 79.5	1414.1 ± 89.4	1691.6 ± 133.6	1842.8 ± 79.3

*All urine values are mean ± SE.

Water conservation

Since the koalas were able to remain in water balance in winter in the absence of drinking water, it is instructive to consider the changes in urine osmolality (Table 6) and fecal water content (Table 2) to see if the resultant saving in water output accounts for the water drunk. A decrease in the preformed water content of the feces from 52.3 percent to 43 percent saves 3.0 g water/kg BW/day. An increase in the urine osmolality from 1414.1 to 1691.6 mOsm/kg conserves 1.6 g of water, while an increase to 1842.8 mOsm/kg (under Pitressin stress) conserves 2.5 g of water. A reduction in evaporative water loss from 32.4 to 27.6 g/kg/day saves a further 4.8 g of water. Thus, the total saving in water output (9.4 to 10.3 g) still leaves 8.8 to 7.9 g of drinking water unaccounted for. The deficit is made up, however, if the reduction in intake of food and preformed water is taken into account.

When the availability of water is not restricted, there is no apparent relationship between the concentrations of electrolytes and urea (Figure 5A). When the urine is being concentrated maximally there is a negative interdependence of urea and electrolyte concentrations (Figure 5B). This indicates that, as more electrolytes are excreted, less urea is excreted. The koala kidney is characterized by the absence of an inner medullary zone (Figure 3), in common with the pig, the beaver and the mountain beaver (*Aplodontia rufa*), all of which exhibit this urea-electrolyte interdependence (Pfeiffer, 1968), which has also been documented for several other mammals (Pfeiffer, 1968; Schmidt-Nielsen, et al., 1961; Schmidt-Nielsen and Pfeiffer, 1970). The interdependence of urea and electrolyte concentrations has been attributed to active tubular reabsorption of urea (Schmidt-Nielsen, 1958), resulting in considerable economy of water required for renal excretion.

Water balance and ambient temperature

The amount of water produced by metabolism for every gram of oxygen consumed can be calculated on the basis of the nutritional composition (Table 4) of the leaves and feces (Schmidt-Nielsen, 1964). With the rates of evaporative water loss and the corresponding oxygen consumption figures at various ambient temperatures (Degabriele, 1977), and the ratio of metabolic water production to oxygen consumption,

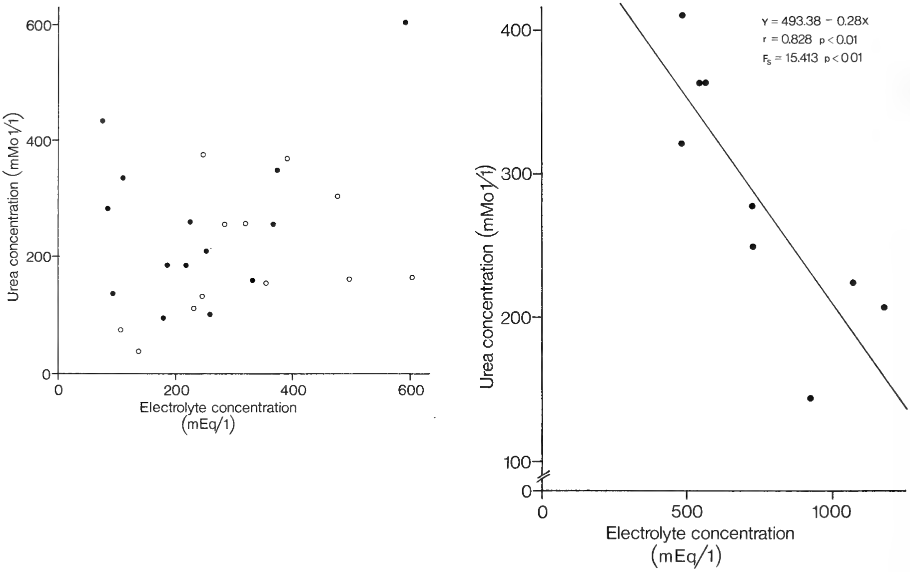

Figure 5. Urea concentrations plotted against total electrolyte concentrations in the same urine sample.
A. Urine samples collected under ad lib. water conditions during the summer (open circles) and winter (solid circles).
B. Urine samples collected under conditions in which the kidney was concentrating maximally. The regression line fitted to the data (Y = 493.38 − 0.28 X) is calculated by the method of least squares.

Millen, 1972). Evaporative water loss is adequately compensated for by metabolic water production up to an ambient temperature of at least 25 °C (Table 7). When evaporative water losses (Degabriele, 1977) are expressed in terms of percentage of body weight lost per day (Figure 6) evaporative water losses from the present study (Table 5) correspond to those for an ambient temperature of about 27 °C. When the percentage of water turnover in the wild given over to evaporative water loss is calculated from the corresponding proportions for caged koalas, the ambient temperature corresponding to this level of evaporative water loss (5.98 percent body weight per day) is 30 °C. Thus the requirements for evaporative cooling by the koala are adequately provided for up to an ambient temperature of about 30 °C. Ambient temperature in the microenvironment of the koala rarely exceeds 30 °C for long periods (Degabriele, 1977).

Conclusions

The koala occupies a microhabitat which provides an adequate water supply and which imposes demands on evaporative cooling which are adequately met by metabolic water production. When drinking water is not available, the koala takes in water in the leaves it

Table 7.—Relationship between metabolic water production and evaporative water loss in the koala at various ambient temperatures (T_a).

T_a	*MWP/EWL*
5	3.14
10	2.99
15	2.29
20	2.29
25	1.82
30	0.59
35	0.32
40	0.28

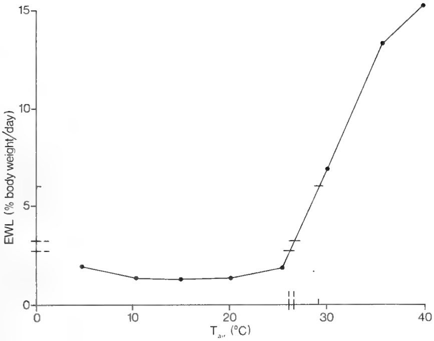

Figure 6. Relationship between ambient temperature (T_{air}) and evaporative water loss (EWL) for the koala (Degabriele, 1977). The ambient temperature range corresponding to the evaporative water losses found in the present study is indicated on the axis.

eats, and remains in water balance by producing a reduced volume of a more concentrated urine, by actively reabsorbing urea at the kidney and, most importantly, by achieving a considerable reduction in the performed water content of the feces. Water content of leaves in a *Eucalyptus punctata* tree ranges from 65.3 percent wet weight for new-growing leaves to 42.7 percent wet weight for older, more fibrous leaves. Thus the koala can control, to some extent, the water input by the choice of leaves used as food. The foregoing conclusions have not taken into account the evaporative cooling requirements of a thermal load during summer.

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The Dental Structure of Mammalian Folivores with Special Reference to Primates and Phalangeroidea (Marsupialia)

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Introduction

Without exception, continent-wide radiations of arboreal mammals have successfully adapted to feeding on leaves, bark, buds, and other coarse and difficult-to-chew foods. The physical and chemical properties of these foods place unique demands upon the digestive systems of these animals. The purpose of this paper is to examine the dental adaptations of several independent radiations of placental and marsupial arboreal folivores. We will emphasize both their similarities and differences with an eye toward understanding the basis of their adaptations.

Regional differentiation of the dentition in mammals reflects differences in function between the front teeth and the cheek teeth. The initial stage of feeding involves acquiring a bite of food. This is *ingestion* and it usually involves the use of incisors, canines, or premolars. Food is chewed before swallowing. This is called *mastication* and is accomplished primarily by the molar teeth. Since dental structure is influenced largely by selection for optimal designs for acquiring and breaking down food, differences in morphology most often can be related to the physical properties of the foods.

The simple formula of tooth structure being related to tooth function is rendered inexact by the unique ancestry of each animal. Thus, species which eat foods requiring large amounts of shearing during mastication need not necessarily emphasize the same molar shearing blades. The choice of the blade may be preconditioned by earlier reorganizations in molar structure. For example, the Xenarthra (North and South American edentates) had undergone extreme reduction in the molar teeth, including nearly complete loss of enamel, by Eocene times (about 50 million years ago). The subsequent radiation of sloths into arboreal folivorous niches has been accompanied by a reorganization of shearing blades quite unlike that of other mammalian folivores.

The fact that heritage influences dental shape allows us to refine our understanding of the essential mechanical features of the folivorous adaptation. For example, if it were demonstrated that one group of folivores had high crowned molars with long shearing blades while another group had low crowned molars with long shearing blades, one would conclude that molar crown height is not essential for a folivorous diet. This could mean that crown height is a special adaptive feature related to something found in the diet or behavior of one species and not in the other, or that the ancestors of the high crowned species passed through a stage where high tooth crowns were selected and genetically canalized. A choice between the alternatives of habitus or heritage depends upon detailed knowledge of the diets of living species in question.

A diet containing a high proportions of leaves, flowers, stems, and shoots is likely to be very high in structural carbohydrates (fiber). Based on their physical properties, it would appear that foods high in structural carbohydrates require considerably more mechanical processing to be converted into a suitable form for digestion. These requirements should show up in the dental anatomy of folivores. We will look separately at ingestive and masticatory designs in each group.

Vorontsov (1962) suggests that some rodent groups (gerbils for example) display considerable variation in some parts of the digestive tract while their molars are much less variable. He attributes this to a kind of mosaic evolutionary process where the dentitions are only marginally adapted to perform their jobs while the morphology of the gut is much more in tune with the animal's feeding behavior. Based on Vorontsov's interpretation, Eisenberg (1978) suggests that one should look with caution on dietary inferences based solely on the morphology of a single system (for example molar structure). He suggests that one should cross check these inferences against other systems, and, since this is not possible when fossil mammal species are studied, unequivocal interpretations of their feeding behavior may be impossible.

Vorontsov's conclusions should be viewed with caution at 3 levels. First, many statements cannot be checked because he presents no dietary information about the species he studied. Second, in the case of gerbils, his data show that increasing molar complexity (as expected for increased dietary fiber) is correlated with increases in the length of the cecum, suggesting that, contrary to his interpretation, these 2 systems *are* indeed in step with each other. Third, and more fundamental, it is important to remember that the dentition is a *mechanical* food-processing device while the digestive tube functions primarily in *chemical* food processing, assimilation, and waste elimination. The dentition is responding evolutionarily to the physical properties of foods (as well as grit and other exogenous substances in ingested material) while the gut tube is responding to the chemical properties of ingested food.

In the case of rapid environmental changes, an animal's behavior may change more rapidly than its morphology. Thus, any dietary interpretation based on morphology may be slightly out of phase with the present behavior. But if an animal's morphology were too far out of step with its environment, extinction would result. It is not surprising then that, as we shall demonstrate, minor dental variations correspond remarkably well with what is known of dietary preferences of species in the wild.

Diet and Body Size

Insectivorous and folivorous arboreal mammals differ consistently in body size (Figure 1) (with some exceptions among rodents, see Eisenberg 1978). The largest living primate insectivore *Galago senegalensis* attains a body weight of approximately 250 g. The smallest living folivorous primate, *Lepilemur mustelinus*[1], weighs about 700 g. The largest insectivorous phalangeroid, *Eudromicia caudatus*, is an order of magnitude smaller than the smallest arboreal phalangeroid folivore, *Pseudocheirus peregrinus*. Most arboreal insectivores probably do not attain body weights above 300 grams because they cannot locate enough insects to meet their daily requirements. Arboreal and terrestrial mammals that specialize in eating social insects (ants, termites) can attain larger

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[1] The monotypic genera listed below are all referred to by genus in the text: *Lepilemur mustelinus*, *Varecia variegatus*, *Avahi laniger*, *Indri indri*, *Symphalangus syndactylus*, *Gorilla gorilla*, *Pongo pygmaeus*, *Theropithecus gelada*, *Erythrocebus patas*, *Brachyteles arachnoides*, *Burramys parvus*, *Phascolarctos cinereus*, *Dactylonax palpator*, *Distoechurus pennatus*.

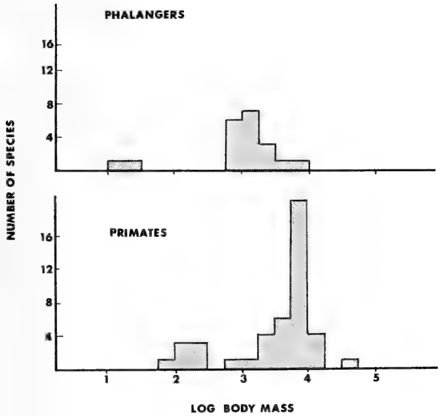


Figure 1. Histogram of primate and phalangeroid species abundance (vertical axis) at different log body sizes (horizontal axis). Stippled peaks at the left represent insectivorous species; cross-hatched peaks at the right are folivorous species.

body sizes because their prey are more abundant. At small body size, acquisition of sufficient amounts of energy is also a problem. Since oxygen consumption per unit body mass gets larger as animals get smaller (Kleiber, 1961), the energy requirements of a mammalian insectivore place theoretical minimum limits on attainable body size.Neither placental nor marsupial arborealists approach their respective energy-imposed size minima, since there are many smaller terrestrial mammalian insectivores.

That there are few arboreal folivores smaller than 700 grams may be explained by the nature of leaves as a food source. Most of the energy found in leaves is stored as structural carbohydrates (Boyd and Goodyear, 1971). Aided by microorganisms in their digestive tracts, it is possible for folivorous mammals to break down some of this material into usable form. However, it is necessary to process a large bulk of leaves to meet energy requirements. The smallest size attained by "bulk processing" leaf-eaters may represent a balance between increasing energy consumption per unit body mass on one hand and food-processing time on the other. Parra (1978) presents evidence to suggest that cellulose digestion is rate controlled; the longer cellulose remains in the digestive tract the more will be digested. Small mammals have shorter food passage times than large ones so that an increase in body size will increase passage time and digestive assimilation.

Malagasy Prosimians

Among Malagasy prosimians, at least some species of *Lemur* are moderately folivorous; *Lemur fulvus* eats a high proportion of leaves whereas *Lemur catta* takes more fruit in its diet but still consumes a large quantity of leaves (Sussman, 1974). Species of *Lepilemur* and *Hapalemur* are strongly folivorous. Charles-Dominique and Hladik (1971) report that *Lepilemur mustelinus* has more leaves and flowers in its diet than any other primate species so far studied. *Hapalemur griseus* eats bamboo as well as papyrus (Petter and Peyrieras, 1970). Malagasy indriids (*Propithecus* sp., *Avahi* sp. and *Indri* sp.) reportedly eat large amounts of bark, leaves, flowers, and buds (Jolly, 1967; Petter, 1962a, 1962b, 1965; C. M. Hladik, 1978). *Propithecus verreauxi* in some areas in the dry season eats up to 75 percent leaves and dormant buds (Richard, 1974 and 1978).

Among prosimians, the anterior dentition (i.e., canines and incisors) and the premolars are used in ingestion. All extant prosimians (excluding *Daubentonia*) have their lower anterior dentition arranged in a procumbent comblike configuration and use these teeth extensively in grooming (Buettner-Janusch and Andrew, 1962). Some species also use their anterior teeth during ingestion and this use is reflected in their morphology. In captive situations *Lemur fulvus* only rarely uses its incisors in feeding (Ibanez, personal communication), whereas *Propithecus verreauxi* may often be observed prying and digging into wood with its lower anterior teeth. This behavior has also been observed in the wild. Richard (1978) notes that in arid regions, *Propithecus verreauxi* uses its tooth comb to gouge into the trunks of succulent trees.

Compared to lemurids and cheirogaleids, the indriid tooth comb is quite stout. Although it is not unusually long or wide compared with other lemurs (Figure 2), it is composed of 2 fewer teeth. Thus the remaining teeth in the comb are larger in size. From histological observations, the tooth comb of *Propithecus verrauxi* is more powerfully anchored to the alveolar process than it is in either *Galago crassicaudatus* or *Lemur fulvus* (Hylander, in preparation). It would appear from both its gross and histological appearance, the tooth comb of *Propithecus*, when compared to other nonindriid prosimians, is better adapted to resist relatively large biting forces. The folivorous prosimians *Varecia variegatus*, *Lepilemur mustelinus*, and *Hapalemur griseus* have rather gracile tooth combs. Thus the stoutness of the indriid tooth comb is not related to leaf-eating per se.

There is also a considerable amount of variation in the maxillary incisors in prosimians. In *Lepilemur* sp. the maxillary incisors are absent; in *Hapalemur* sp.

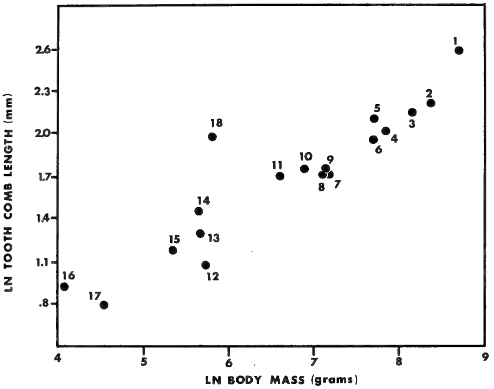


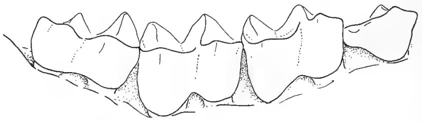
Figure 2. Relative tooth comb length in prosimians. Symbols: 1, *Indri indri;* 2, *Lemur variegatus;* 3, *Propithecus verreauxi;* 4, *Lemur mongoz;* 5, *Lemur macaco;* 6, *Lemur catta;* 7, *Hapalemur griseus;* 8, *Nycticebus coucang;* 9, *Galago crassicaudatus;* 10, *Avahi laniger;* 11, *Lepilemur mustelinus;* 12, *Cheirogaleus medius;* 13, *Galago senegalensis;* 14, *Galago elegantulus;* 15, *Loris tardigradus;* 16, *Galago demidovii;* 17, *Microcebus murinus;* 18, *Phaner furcifer.*

they are quite small. Within the highly folivorous indriids, there is a wide range of size in maxillary incisors indicating that there are distinct feeding differences that relate to food ingestion. Compared to *Propithecus* sp., the maxillary incisors of both *Avahi langur* and *Indri indri* are poorly developed. Whether this morphological difference reflects more bark or fruit eating among populations of *Propithecus* is uncertain. It is clear, however, that the wear potential of the maxillary incisors is greater in *Propithecus.*

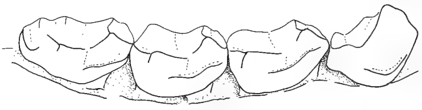
The premolars of prosimians are often used during ingestion. Observations on captive animals at Duke University demonstrates that prosimians commonly slice fruits and leafy materials into bite-sized pieces between the premolars. Among folivorous prosimians, there is a strong tendency to develop the shearing capabilities of the premolar dentition. Presumably this is an adaptation to deal with diets high in fiber content. An analogous situation, to be discussed in more detail below, is encountered in the molar dentition of folivorous marsupials.

In summary, the anterior dentition of prosimian folivores does not exhibit a uniform pattern. Highly folivores forms such as *Propithecus* sp. and *Lepilemur* sp. have maxillary dentition that ranges from being well developed to congenitally missing, respectively. In the mandibular dentition, the tooth comb in *Propithecus* sp. is made up of 4 stout teeth while in *Lepilemur* sp. it is a rather gracile structure that is made up of 6 slender teeth. In contrast with the variability of the incisors of leaf-eating lemurs, shearing is always emphasized in the premolar region in the folivorous forms.

The molars of folivorous Malagasay prosimians are larger for their body size than is typical for frugivorous prosimians, perhaps because folivorous foods require large amounts of preparation before swallowing. The postcanine dentitions of *Propithecus verreauxi,* a folivore, and *Cheirogaleus major,* a frugivore, are compared in Figure 3. The molars of *P. verrauxi* have long trenchant shear-blades and high cusps, a condition found among many folivorous primates. Primary shearing blades are situated on the medial and lateral edges of the crown. The intervening crown surface tends to be an irregular undulating plane. When the teeth first occlude, the outer and inner rows of shearing blades commence contact almost simultaneously, but sharp-edged blades on the lower molars do not shear simultaneously along the entire length of the corresponding upper molar shearing blades. Instead, the blades are brought together at an angle so that shearing is focused at a single point of contact moving along the blade. A similar design is seen in a pair of scissors. After food has been cut into pieces by the edges of the crown, it is crushed and bent between undulating crown surfaces. Following crushing, food in the molar basins is ground by movement of the crowns parallel to the planes of contact. The molars of *C. major* are typical of frugivorous pri-



Propithecus verreauxi



Cheirogaleus medius

Figure 3. Comparison of the postcanine dentitions of 2 Malagasy prosimians, a, *Propithecus verreauxi;* b, *Cheirogaleus major. Propithecus* has relatively high cusps with long shearing blades, a characteristic folivorous adaptation. *Cheirogaleus* has lower, more rounded cusps and less discrete shearing blades, typical of most gumivorous and frugivorous primates.

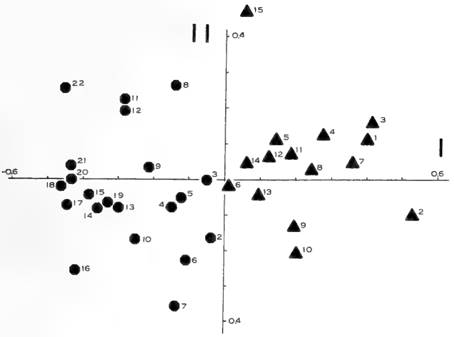


Figure 4. Principal coordinates analysis of molar shape for noncercopithecid primates. The horizontal axis is the first principal coordinate, the vertical axis is the second. Leaf-eating species cluster to the right, fruit- and gum-eaters to the left. Insectivorous prosimians were included in this analysis but are not displayed here. Redrawn after Kay (1975). Where not otherwise indicated, males and females have been lumped. Symbols: octagons are frugivorous or gumivorous primates (known or inferred from dental structure); triangles are folivorous primates (known or inferred from dental structure). Leaf-eaters (triangles): 1, *Alouatta villosa* males; 2, *Alouatta villosa* females; 3, *Pongo pygmaeus* females; 4, *Pongo pygmaeus* males; 5, *Gorilla gorilla* males; 6, *Gorilla gorilla* females; 7, *Hapalemur griseus*; 8, *Propithecus verreauxi*; 9, *Lemur fulvus*; 10, *Lemur rubriventer*; 11, *Indri indri*; 12, *Lemur variegatus*; 13, *Symphalangus syndactylus*; 14, *Lepilemur mustelinus*; 15, *Avahi laniger*. Frugivores (octagons): 1, *Galago alleni*; 2, *Lemur catta*; 3, *Pan troglodytes* males; 4, *Pan troglodytes* females; 5, *Pithecia pithecia*; 6, *Cheirogaleus major*; 7, *Galago crassicaudatus*; 8, *Galago elegantulus*; 9, *Pan paniscus*; 10, *Hylobates klossi*; 11, *Phaner furcifer*; 12, *Microcebus murinus*; 13, *Aotus trivirgatus*; 14, *Perodicticus potto*; 15, *Daubentonia madagascariensis*; 16, *Chiropotes satanas*; 17, *Cebus capucinus* females; 18, *Cebus capucinus* males; 19, *Callithrix jacchus*; 20, *Saguinus geoffroyi*; 21, *Saimiri sciureus*; 22, *Ateles geoffroyi*.

mates in having less trenchant, shorter, shearing blades on lower, more rounded, cusps.

Figure 4 shows the results of the principal coordinates analysis of the second molars of primates excluding Old World monkeys. The details of this analysis are presented in Kay (1973, 1975) but the method of data transformation in this and subsequent analyses deserves some attention here. Changes in shape and body size are related in a complex manner to the preservation of function at different sizes. Adjustments must be made for these changes before functional comparisons are possible. Each tooth dimension was corrected for body size by comparison with an empirical regression equation calculated for a large number of related species. For example, if the length of a shearing blade for an average 30-gram primate is 4 mm, and the 30-gram species we wish to look at has a blade 10-mm long, this difference can be expressed as a percentage; our hypothetical species would have a shearing blade which is 150 percent longer than is empirically expected for a species of that size. The dimensions used in this study were chosen to reflect specific functional adaptations in the molar teeth. Measures of the length of the shearing blades, the heights of the cusps, the sizes of the crushing basins, and the length of contact between the molars were included. The first principal coordinate of the analysis is a size axis. In this instance, species that have high cusps, long shearing blades, and large crushing surfaces cluster to the right on the axis, whereas those that have proportionally smaller tooth features cluster to the left.

In Figure 4, species of the following prosimian genera *Avahi, Indri, Propithecus, Lepilemur,* and *Hapalemur* fall to the right; they have some combination of high crowns, large crushing surfaces, and long shearing blades. This is in contrast with species of the frugivorous and gumivorous prosimian genera such as *Phaner, Microcebus,* and *Cheirogaleus.* For a more detailed survey of the molar adaptations of lemuroids, see Kay, Sussman and Tattersall (1978).

Hominoidea of Africa and Asia

The dominant arboreal folivores of Asia and Africa (excluding Madagascar) are the Cercopithecoidea and Hominoidea. None of the prosimian species are folivorous in these regions. Among Hominoidea, the siamang (*Symphalangus syndactylus*,) of Sumatra and the Malay Peninsula feeds on a moderately high percentage of leaves in contrast to *Hylobates* species which take much more fruit in their diets (Chivers, 1972). *Pongo pygmaeus* from Sumatra and Borneo also takes about 50 percent leaves, bark, buds, and flowers in its diet (McKinnon, 1971, 1974). In subsaharan Africa, *Pan troglodytes* has a predominantly frugivorous diet (Goodall, 1963, 1965; Suzuki, 1969). Horn (personal communication) has indicated that the diet of *Pan paniscus* is similar to *Pan troglodytes*. The semiterrestrial *Gorilla gorilla* eats a high proportion of shoots, pith, bark, leaves, and even rotten wood (Donisthorpe, 1958; Jones and Sabater-Pi, 1971; Schaller, 1963).

The relationship between incisor size and diet has been investigated in several Old World anthropoids by Jolly (1970a). He hypothesized that frugivorous species (*Pan* and *Papio*) tend to have larger incisors than folivorous or graminivorous forms (*Gorilla* and *Theropithecus*). Hylander (1975a, 1975b) has refined and extended Jolly's observations for most cerco-

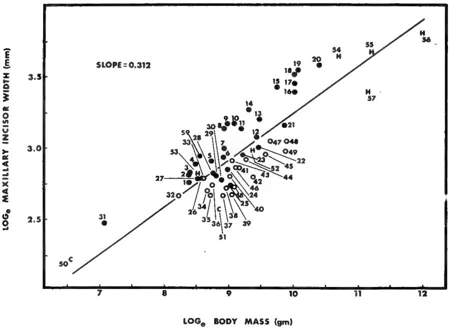


Figure 5. Relative incisor size among Anthropoidea. Symbols: Cercopithecines (closed circles): 1, *Cercopithecus pogonias*; 2, *Cercopithecus denti*; 3, *Cercopithecus cephus*; 4, *Macaca fascicularis*; 5, *Cercopithecus nictitans*; 6, *Macaca cyclopis*; 7, *Macaca mulatta*; 8, *Macaca nigra*; 9, *Cercocebus albigena*; 10, *Macaca maura hecki*; 11, *Cercocebus torquatus*; 12, *Macaca sylvana*; 13, *Macaca speciosa*; 14, *Macaca nemestrina*; 15, *Papio hamadryas*; 16, *Mandrillus sphinx*; 17, *Mandrillus leucophaeus*; 18, *Papio anubis*; 19, *Papio cynocephalus*; 20, *Papio ursinus*; 21, *Theropithecus gelada*; 22, *Macaca fuscata*; 23, *Erythrocebus patas*; 24, *Cercopithecus mitis*; 25, *Cercopithecus lhoesti*; 26, *Cercopithecus ascanius*; 27, *Cercopithecus aethiops*; 28, *Allenopithecus nigroviridis*; 29, *Cercopithecus neglectus*; 30, *Cercopithecus hamlyni*; 31, *Miopithecus talapoin*; 59, *Macaca sinica*. Colobines (open circles): 32, *Procolobus verus*; 33, *Presbytis frontatus*; 34, *Presbytis aygula*; 35, *Presbytis rubicundus*; 36, *Presbytis potenziani*; 37, *Presbytis cristatus*; 38, *Presbytis phayrei*; 39, *Presbytis senex*; 40, *Presbytis obscurus*; 41, *Colobus angolensis*; 42, *Presbytis johni*; 43, *Colobus badius*; 44, *Pygathrix nemaeus*; 45, *Presbytis entellus entellus*; 46, *Colobus guereza*; 47, *Rhinopithecus roxellanae*; 48, *Presbytis entellus schistaceus*; 49, *Nasalis larvatus*; 58, *Simias concolor*. Ceboids (C): 50, *Saimiri sciureus*; 51, *Alouatta villosa*. Hominoids (H): 52, *Symphalangus syndactylus*; 53, *Hylobates moloch*; 54, *Pan troglodytes*; 55, *Pongo pygmaeus*; 56, *Gorilla gorilla*; 57, *Homo sapiens*.

pithecoids, hominoids, and 2 ceboids. The results of these studies in Figure 5 illustrate the allometric relationship between the natural logarithms of maxillary incisor width and body weight for the taxa analyzed. For the sake of convenience, interpretation of hominoids, cercopithecoids, and ceboids will be made separately.

As seen in Figure 5, there is a near separation of colobines from cercopithecines. Most colobines fall below the regression line while most cercopithecines fall above it. This is true even when colobine body weights are reduced by up to 25 percent to account for gut contents. Thus, relative to body size, the leaf-eating colobines generally have smaller incisors than the more frugivorous cercopithecines. Among the lesser apes, *Symphalangus syndactylus* is more folivorous than various species of *Hylobates*. *S. syndactylus* has smaller incisors than expected for a typical anthropoid of its body size while *Hylobates* species have larger incisors.

Of the remaining hominoids, the chimpanzee is highly frugivorous, the orang is mixed frugivorous and folivorous, and the gorilla is highly folivorous. The diet of *Homo* varies considerably from one population to the next. As expected, *Pan troglodytes* falls well above the regression line (has large incisors), *Gorilla gorilla* falls below it with small incisors, and *Pongo pygmaeus*, has incisors intermediate in size between *Pan* and *Gorilla*. *Homo*, like *Gorilla*, falls below the line but unlike *Gorilla*, the diet of *Homo* is not highly folivorous. The relatively small incisors in *Homo* are probably related to food-preparation techniques that result in relatively less incisal preparation of foods.

In summary, relative to body size the more folivorous hominoids tend to have smaller incisors than the more frugivorous forms. The adaptive significance of this finding is thought to be related to differential tooth use. Extensive incisal preparation prior to mastication (i.e., cutting, tearing, or pulping of food objects before chewing them with the postcanine teeth) ordinarily is not necessary for leaves, stems, berries, grasses, seeds, buds, or flowers. It is necessary, however, when ingesting large, tough-skinned fruits. The increased frequency and duration of incisal preparation of fruits causes increased amounts of attrition and abrasion of the anterior dentition. Enlarged incisors represent an adaptive response to delay dental obsolescence under these conditions.

Hominoid molar morphology also reflects dietary preference. From Figure 4, the values on the first principal coordinate separate the folivores *G. gorilla*, *S. syndactylus*, and *P. pygmaeus* from frugivorous species of *Hylobates* and *Pan*. *G. gorilla*, and *S. syndactylus* have higher cusps, more acutely angled and longer shearing blades, and larger crushing basins than species of *Hylobates* and *Pan*. *Pongo pygmaeus* represents an interesting contrast with other pongid folivores in having crenulate enamel with bulbous cusps and nontrenchant shearing blades. However, the molars of the species are extremely large given its adult body size; this is associated with extremely enlarged crushing surfaces. Crenulations of the enamel on the postcanine occlusal surfaces may aid in the grinding of foods. The shearing edges along the margins of this tooth are relatively quite long.

African Cercopithecidae

African and Asian Cercopithecidae are divided into 2 subfamilies, the Colobinae and the Cercopithecinae.

The former is primarily folivorous, and the latter mainly frugivorous. At a more subtle level, considerable variation occurs in the proportions of leaves and fruit in the diets of African colobines (Clutton-Brock, 1974, 1975; Struhsaker, 1975). Some African cercopithecines are highly frugivorous; e.g., *Miopithecus talapoin, Cercocebus albigena* (Malbrant and Maclatchy, 1949; Jones, 1970; Jones and Sabater-Pi, 1968; Gautier-Hion, 1971). Others such as *Cercopithecus ascanius* eat very high proportions of leaves and green shoots as well as fruits (Haddow, 1952). *Cercopithecus aethiops* eats large amounts of leaves, flowers, and bark in addition to fruits (Dunbar and Dunbar, 1974; Struhsaker, 1967; Gartlan and Brain, 1968).

There is a strong tendency for the exploitation of terrestrial forest, savannah woodland, and savannah niches by African cercopithecines (Jolly, 1970b). Among the genera which have made this transition are *Mandrillus, Papio, Erythrocebus, Theropithecus,* and *Cercopithecus aethiops*. This has been accompanied by increases in the dietary proportions of grasses and/or other high-fiber foods in these species (Hall, 1965, 1966; Malbrant and Maclatchy, 1949; Washburn and Devore, 1961; Devore and Washburn, 1963; Aldridge-Blake, et al., 1971; Dunbar and Dunbar, 1974; Altmann and Altmann, 1970; Kummer, 1968; Kummer and Kurt, 1963). The process appears to have gone farthest in *Theropithecus* which is almost wholly terrestrial and feeds almost exclusively on grass leaves (Dunbar and Dunbar, 1974). For an extensive dietary review of cercopithecids, see Kay (1978).

Variations in the proportions of leaves and fruits in the diets of cercopithecids are correlated with morphological differences in their dentitions. Apart from differences in the relative thickness of the enamel among certain species, cercopithecid incisors vary mainly in size. Similar to hominoids, more folivorous cercopithecid species have smaller incisors than their frugivorous relatives (Figure 5).

Behavioral studies by Clutton-Brock (1974, 1975) state that *Colobus badius* includes a larger percentage of fruit in its diet than do sympatric populations of *Colobus guereza*. A more recent study of these species in the same area suggests that the reverse is the case (Struhsaker, 1975). Hylander (1975) found that *C. badius* has relatively larger incisors than *C. guereza*, which would tend to support Clutton-Brock's findings. The skulls that were measured are sampled from areas where the two species are allopatric, however, so this result should be viewed with caution.

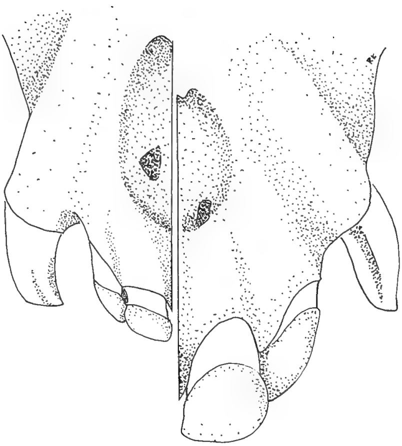


Figure 6. The incisor size of *Erythrocebus patas* (left) and *Cercocebus albigena* (right) standardized for the breadth of the piriform aperture. This illustrates the variability in incisor size in cercopithecines. *Erythrocebus* is largely graminivorous while *Cercocebus* eats very large quantities of fruit.

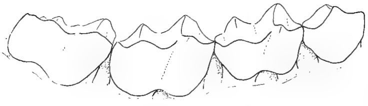
There is considerable variation in incisor size among African cercopithecines (Figure 6). This variability relates to differences in diet and ingestive behavior. *Miopithecus talapoin, Ceropithecus cephus, Cercocebus torquatus,* and *Cercocebus albigena* subsist to a considerable extent on fruit. As expected, these largely frugivorous primates have relatively very large incisors (they fall well above the regression line in Figure 5). The various species (or subspecies) of *Papio* also have relatively large incisors. Although a few populations of *Papio* sp. are said to be highly folivorous or graminivorous, when ecological conditions permit *Papio* includes a large amount of fruit in its diet.

In addition to food object size, another factor that probably affects the amount of incisor tooth wear is the inclusion of dietary grit. Presumably a terrestrial animal that selects food objects from the ground ingests more grit than an animal that selects the same food object directly from a tree or shrub. An increase in the amount of dietary grit would have the effect of increasing the amount of tooth wear. The inclusion of large amounts of grit (from both roots and fallen fruit) might in part explain why various *Papio* populations have such large incisors. For example, *Papio anubis* often pulls grass rhizomes from the ground with its incisors, unlike sympatric populations of *Theropithecus gelada* that pull these same rhizomes out with their hands (Dunbar and Dunbar, 1974).

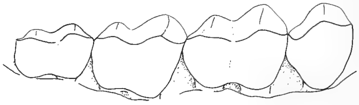
The gelada baboon (*Theropithecus*), a terrestrial primate that feeds primarily on grasses, has relatively very small incisors. As noted by Jolly (1970a), small incisor size in this species may be related to its habit of feeding on small objects, and to the rather infrequent use of its incisors for food preparation. The patas monkey (*Erythrocebus patas*), another predominately graminivorous terrestrial primate, also has relatively small incisors (Figure 6). Although this primate also eats small fruits and berries, it ignores a large tough fruit that is commonly eaten by sympatric populations of *Papio* sp. (Hall, 1965). Like *Theropithecus*, *Erythrocebus* often eats objects which require relatively little incisal preparation. Drills and mandrills (*Mandrillus* spp.) have relatively large incisors (Figure 5). This implies that they eat a large amount of fruit requiring extensive incisal preparation.

A number of African cercopithecines have relatively small incisors: *Allenopithecus nigroviridis, Cercopithecus mitis, C. neglectus, C. hamlyni,* and *C. lhoesti*. Their small incisors suggest a high fiber diet. *C. mitis,* in addition to eating fruits and bamboo shoots, includes a large amount of leaves in its diet. Stomach contents and observations on a small number of animals suggest that the diet of *C. neglectus* consists of both leaves and fruit. On the basis of their relatively small incisors, the diet of *C. hamlyni, C. lhoesti,* and *Allenopithecus* may include food objects that require relatively little incisal preparation. The fact that *Allenopithecus* has some sacculation of the stomach (Hill, 1966) takes on additional interest here, because this type of visceral specialization is usually present only in folivorous primates.

The molars of Cercopithecidae are high crowned. Two ridges cross each upper and lower molar, producing a "bilophodont" condition. Located along the medial and lateral edges of the crowns are sharp shearing edges. The 2 cross ridges (or lophs) on the lower teeth fit into corresponding embrasures on the uppers and vice versa. The ridges act as guides for the shearing action of the medial and lateral crown edges. Crushing surfaces on the crown form a continuous undulating surface along the whole molar tooth row. Their uneven conformation may produce bending in some rigid foods. Compared to most primate species, Old World monkeys have molars with higher cusps and crowns, longer shearing blades and slightly larger crushing surfaces relative to body mass (Kay, 1978). Other primate species which eat significant proportions of leaves (for example, species of *Propithecus* and *Alouatta*) approximate this condition. Therefore the general configuration and design of Old World monkey molars suggests a somewhat folivorous ancestry for the group. In addition, variations among living species of the group are strongly correlated with corresponding differences in diet (see Figure 7).



Alouatta villosa



Ateles belzebuth

Figure 7. Comparison of the lower P_4 - M_3 dentitions of a, *Alouatta villosa*; b, *Ateles belzebuth*. Comparison with Figure 3 illustrates that *Alouatta* is convergent in molar shape with *Propithecus* and *Ateles* with *Cheirogaleus*. The former pair have trenchant shearing blades, high crowns, large crushing surfaces, and acutely angled cusps; the latter have low rounded cusps and reduced shearing and crushing.

Based on a previous analysis (Kay, 1973), leaf-eating monkeys would be expected to have larger teeth than fruit-eaters. The reverse, however, often proves to be the case. No special dietary significance can be attributed to the species values of a principal coordinates analysis of tooth dimensions regression adjusted for body mass. However, an analysis of tooth-length (rather than body-size) allometrically adjusted dimensions yields first coordinate values which are

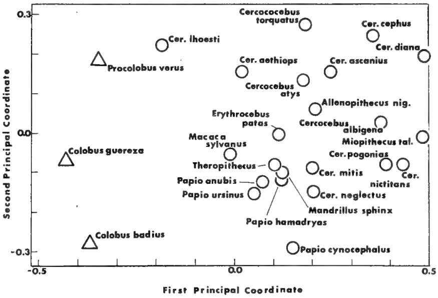
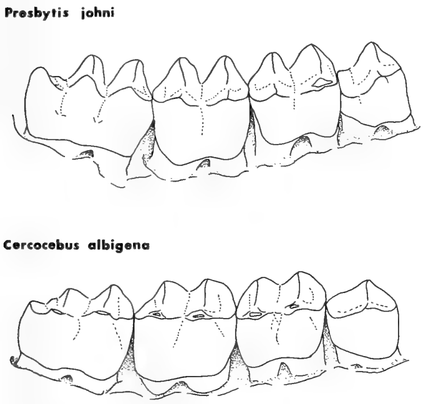


Figure 8. Principal coordinates analysis of molar shape among African cercopithecids. The first coordinate separates primarily leaf-eating species to the left from primarily fruit-eating species to the right. The triangles are colobines, the circles are cercopithecines. The group of Cercopithecines at the center eat large proportions of grass. Redrawn after Kay, (1978).

readily interpretable in terms of diet. The results of a principal coordinates analysis of 7 molar dimensions among Cercopithecidae regression adjusted for tooth length are illustrated in Figures 8 and 10 (Kay, 1978). For convenience African and Asian species are displayed separately although all were included in a single analysis. Due to negative factor loadings, species which fall to the left on the first coordinate have a combination of sharper and longer shearing blades, higher cusps, and larger crushing basins than do those which plot to the right. This finding corresponds well with the visual impression of molar design of leaf- versus fruit-eating species (Figure 9). As expected, species of *Colobus* have low values, while frugivorous cercopithecines like *Miopithecus talapoin* and *Cercocebus albigena* have very high values. Closer examination of the values on the first principal coordinate reveals additional dietary information. Studied in areas where they are sympatric, Clutton-Brock (1974, 1975) suggests that *Colobus guereza* eats more mature leaves and less fruit than does *Colobus badius*. The morphology of the second molars of the two species is fairly similar, but *Colobus badius* falls slightly to the right of *Colobus guereza* agreeing with Clutton-Brock's findings (the separation between these species is not large, however). One additional African colobine, *Procolobus verus*, falls immediately between *C. guereza* and *C. badius*, but slightly closer to *C. badius*. A high fiber diet with some fruit would be inferred (see Booth, 1957).



Presbytis johni

Cercocebus albigena

Figure 9. Comparison of the lower P_4 - M_3 dentitions of *Presbytis johni*, a folivorous colobine and *Cercocebus albigena*, a frugivorous cercopithecine. Cercopithecids in general tend to have high cusps regardless of diet but folivorous species have sharper cusps with more sharply defined shearing blades as well as larger crushing surfaces.

Cercopithecines, which are primarily found in semi-arid savannah and woodland savannah, eat high proportions of grasses, rhizomes, leaves, buds, and hard beans. High grit and high fiber content foods are common in their diets. Species in this group whose diets are fairly well known are *Cercopithecus aethiops*, *Papio ursinus*, *Papio anubis* and *Theropithecus gelada*. All of these species have much lower values than other African cercopithecines which eat more fruit. Qualitative information on other species of *Papio* and *Erythrocebus* indicate diets roughly similar to *P. anubis*. Not surprisingly, *P. hamadryas* and *Erythrocebus patas* cluster with these species.

Cerocebus albigena and *Miopithecus talapoin* appear to be the most frugivorous of the well-known African species; the 2 species also have extremely high first coordinate values. *Cercopithecus ascanius* eats high proportions of leaves and not surprisingly falls immediate between *Cercopithecus aethiops* and *Miopithecus talapoin*. The diets of the remaining African species are less well known. On the first axis, *Cercopithecus cephus, C. pogonias, C. nictitans*, and *C. diana* cluster with *M. talapoin* and *Cercocebus albigena* and so are probably primarily frugivorous. *Cercopithecus mitis* and *Cercopithecus neglectus* cluster with *C. ascanius*, indicating that they may be more folivorous than other forest-dwelling Cercopithecines. *Allenopithecus nigroviridis, Cercocebus torquatus* and *Cercocebus atys* all have distinctively lower values on the first axis than *Cercocebus albigena*. Possibly they eat more leaves.

Macaca sylvana, the sole representative of that genus in North Africa, has an extremely coarse diet which includes the buds and leaves of conifers (Deag and Crook, 1971). Not surprisingly this species falls to the left of all but one African cercopithecine. Perhaps the most interesting African cercopithecine studied is *Cercopithecus lhoesti*. Practically nothing is known of the diet of this species but its molar morphology suggests that it is one of the most folivorous of extant cercopithecines; with its long shearing blades it falls within the range of Asian colobines.

Asian Cercopithecidae

Cercopithecoids from Asia conform in a general way to their African counterparts: colobines are more folivorous than are cercopithecines. Of the colobines, the Ceylonese *Presbytis senex* and *P. entellus* are the best known. *P. senex* is highly folivorous; in Ceylon its diet is 60 percent by weight mature leaves and shoots, 12 percent flowers, and 28 percent fruits

(Hladik and Hladik, 1972). *Presbytis entellus* takes more fruit in its diet; quantitative analysis by Amersinghe, et al. (1971) and Hladik and Hladik (1972) point out the importance of leaves, shoots, and flowers (55 percent by weight) but emphasize also the significance of fruit in the diet (45 percent by weight). Similar findings on *P. senex* and *P. entellus* have been reported by Muckenhirn (1972). The diet of *P. entellus* in India includes a fairly large amount of fruit. Although quantitative data are lacking for the remaining mainland colobines, a number of observers have confirmed a strong preference for leaves in the diet.

The best known colobines in Southeast Asia are *Nasalis larvatus, Presbytis obscurus* and *P. melalopmos. Nasalis larvatus* was reported by Banks (1949) and Davis (1962) as feeding on young leaves, buds, and shoots of mangrove and pedata trees. Kern (1964) concludes that at least 95 percent of this species' diet consists of leaves, tender vines, and shoots. The diets of the sympatric species *Presbytis obscurus* and *P. melalophus* were compared in Malaya by Curtin (1976). She showed that the former was much more folivorous than the latter. The diets of the remaining species of Sundaland leaf-monkeys are poorly documented.

Cercopithecines from Asia are ordinarily grouped into a single diverse genus *Macaca*. Species of this genus conform to the general pattern seen among African cercopithecines; increasing terrestriality often correlates with increasing use of foods high in fiber and probably grit content. Detailed analysis of dietary preferences is available for *Macaca fuscata*. Almost one-half of its yearly diet consists of grass, leaves, twigs, and flowers. This is taken in large part from the ground (Izawa, 1971, 1972; Suzuki, 1965). The semiterrestrial *Macaca speciosa* reportedly feeds largely on leaves, roots, and fruit (McCann, 1933; Bertrand, 1969). On the basis of numerous field studies the diets of *Macaca mulatta* (at least in India), *Macaca fascicularis* and *M. nemestrina* probably contain more fruit than *M. speciosa* and *M. fuscata*. The diet of *Macaca sinica* is well known. During both wet and dry seasons it eats at least 75 percent fruit (Hladik and Hladik, 1972; Muckenhirn, 1972). Evidence for the feeding of the Formosan and Celebesian macaques is anecdotal at best.

As among African forms, there is a considerable amount of variation in relative incisor size among Asiatic cercopithecids. As seen in Figure 5, macaques tend to have larger incisors than colobines. *Macaca fuscata* is the only Asiatic cercopithecine to have smaller than average incisors for its body size. For many months of the year it subsists largely on bark, leaves, buds, twigs, roots, berries, and even lichen. Although this animal eats fruits, the bulk of its diet probably consists of food objects that probably require little incisal preparation. The North African *Macaca sylvana* also has relatively small incisors when compared to other members of this genus. Again it appears that the major portion of its diet consists of objects that require relatively little incisal preparation.

Macaca fascicularis, Macaca sinica, and *Macaca nemestrina* are highly frugivorous. Figure 5 demonstrates that these macaques, as well as *Macaca nigra* and *Macaca maura*, have relatively large incisors. On the basis of incisor size, one would predict that the diet of the Celebesian macaques consists to a large extent of large food objects (most likely large fruits). Although not shown in Figure 5 (no males sampled), *Macaca silenis* also has very large incisors. *Macaca silenis* is said to eat fruits, flowers, nuts, and buds, but its favorite food consists of the unripe nut of a chestnut-like fruit. Sugiyama (1968) states that it takes the Macaca, using both hands and teeth, about 10 minutes to crack open these unripe nuts.

Asian colobines have relatively small incisors. In Ceylon, *Presbytis entellus* and *Presbytis senex* are sympatric. In these areas, *Presbytis entellus* is more frugivorous than *Presbytis senex*, and these dietary differences are reflected in relative incisor size with *P. entellus* having relatively larger incisors than *P. senex*. Caution should be used in the interpretation of this result, since the *P. entellus* sample comes from India, not Ceylon.

On the basis of the relationship between incisor size and diet, certain dietary predictions have been made (Hylander, 1975a, 1975b). Of the sympatric colobines found on the Mentawi Islands, *Presbytis potenziani* is probably more frugivorous than *Simias concolor*. There are several colobine species on Borneo that are sympatric in portions of their range. Unfortunately, except for *Nasalis larvatus*, little is known of their diets. Judging from incisor dimensions, *Presbytis frontatus* is probably much more frugivorous than the highly folivorous *Nasalis larvatus. Presbytis rubicundus* and *Presbytis aygula* fall somewhere between these forms. Following a recent primate census, C. Wilson (personal communication) has noted that Bornean *Presbytis rubicundus* and *Presbytis aygula* seem to have similar diets and probably are more frugivorous than *Nasalis*. She has also indicated that *P. frontatus* is widely ranging, suggesting that it is more frugivorous than other Bornean colobines. On Sumatra, *Presbytis cristatus* is more folivorous than sympatric populations of *Presbytis melalophos* (C. Wilson, personal communication). In Figure 5 *Presbytis cristatus* is positioned like the other highly foliv-

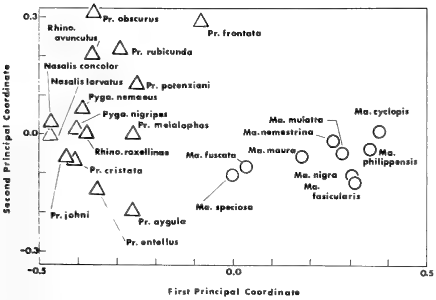


Figure 10. Principal coordinates analysis of molar shape among Asian cercopithecids. The first coordinate separates primarily leaf-eating species (to the left) from primarily fruit-eating species (to the right). Triangles are colobines, circles are cercopithecines. Redrawn after Kay (1978).

orous Asian colobines, i.e., *Presbytis johni*, *Nasalis larvatus*, and *Simias concolor*. The incisors of Sumatran *P. melalophos*, although not included in Figure 5, suggest that it is more frugivorous than *P. cristatus*.

The molars of Asian cercopithecoid species conform generally to the pattern which has emerged from African species; the folivorous colobines, have lower values than the cercopithecines on the first principal coordinate in Figure 10. Most of the Asian colobines belong to the widespread and diverse genus *Presbytis*. As noted above, *P. senex* is more folivorous than *P. entellus* in Ceylon. The second molars of *Presbytis johni*, an Indian form possibly conspecific with *P. senex*, have a structure which suggests a highly folivorous component in the diet whereas the molars of *P. entellus* have first coordinate values suggesting a more frugivorous diet. Of the remaining Asian colobines *Nasalis larvatus* is extremely folivorous. Not surprisingly, *Nasalis* has the smallest score of any species on the first coordinate in Figure 10.

Little or no quantitative dietary data are available for the remaining Asian colobines but molar structure may indicate something about their habits. In addition to *Nasalis larvatus*, specimens of 3 other Bornean species were studied. Molar structure indicates that *Presbytis frontatus* is the most frugivorous of all the colobines. *Presbytis rubicundus* and *Presbytis aygula* have higher values than *Presbytis entellus*. They presumably include a considerable amount of fruit in their diet.

Analysis of the molars of *Presbytis cristatus* and *P. melalophos* from Sumatra suggest that the former is more folivorous than the latter, and C. Wilson (personal communication) reports that this is probably the case. Curtin (1976) reports that Malaysian *P. obscurus* consistently eats more leaves than sympatric *P. melalophos*.

Two endemic colobines on the Mentawai Islands are distinct from one another in their molar morphology. The molars of *Simias concolor* are similar to those of *Nasalis larvatus*, indicating that the former is almost wholly a leaf-eater; *Presbytis potenziani* has a larger first coordinate value that is larger than *Presbytis entellus* and is comparable to that of *Presbytis aygula*. It probably eats more fruit than *Simias*.

Specimens of the remaining Asian colobines used in this study are largely or wholly geographically isolated from each other. *Rhinopithecus avunculus*, *Rhinopithecus roxellanae*, *Pygathrix nemaeus* and *Pygathrix nigripes*, and *Presbytis obscurus* all have about the same values for the first principal coordinate. All fall intermediate between *Presbytis johni* and *P. entellus* indicating moderate to high percentages of leaves in their diets.

Nine species of the genus *Macaca* were studied. *Macaca sylvana* was discussed with the African species. Of the remaining 8, (*Macaca speciosa*, *M. fuscata*, *M. cyclopis*, *M. mulatta*, *M. nemestrina*, *M. fascicularis*, *M. nigra*, and *M. maura*), only the diet of *Macaca fuscata* has been adequately reported. As noted above, fibrous materials amount to about one-half of its yearly diet. The molar structure is consistent with these findings; *M. fuscata* has a first coordinate value similar to African cercopithecines which are known to have high fiber diets (species of *Papio*, *Erythrocebus*, *Theropithecus*, and *Cercopithecus aethiops*). Behavioral information on the other macaques studied is inadequate to allow certain dietary assessment. Inferred from molar structure, the diet of *Macaca speciosa* must be similar to *Macaca fuscata*, probably containing significant proportions of leaves, bark, and buds. *M. speciosa* is widely sympatric with *M. mulatta*; the molar structure in the latter indicates a diet containing more fruit than *Macaca speciosa*. Analogous molar differences suggest that *M. speciosa* eats more leaves than *M. fascicularis* and *M. nemestrina* where they are all sympatric. The molar morphology of *M. nemestrina* and *M. fascicularis* suggests that these widely sympatric species eat mainly fruit. Molar structure suggests that the diet of the Formosan *Macaca cyclopis* is extremely frugivorous. Of the Celebes species *M. maura* falls intermediate between *M. fuscata nemestrina*. It may eat more leaves than *M. nigra* which clusters with *M. fascicularis*.

New World Primates

Folivorous arboreal niches in Central and South

America are occupied by anthropoids and xenarthrans. Of 16 generally recognized genera of neotropical anthropoids, only *Alouatta* is known to be a specialized folivore. At Barro Colorado Island *Alouatta palliata* yearly eats about 40 percent by weight new and mature leaves, buds, and flowers (Hladik and Hladik, 1969). *A. palliata* in dry season riparian forests of Costa Rica spends about 90 percent of its feeding time eating leaves and flowers (Glander, 1975). The percentage of fruits increases slightly in the wet season, reducing the folivorous proportion to about 85 percent. These values for *Alouatta* contrast markedly with those for other New World species whose diets are well known; *Ateles* sp. takes 20 percent by weight folivorous material, *Cebus* sp., 15 percent; *Aotus* sp., 30 percent; *Saguinus*, 10 percent (Hladik and Hladik, 1969).

The incisors of only 2 platyrrhine species have been analyzed relative to body weight (Hylander, 1975b). As seen in Figure 5, highly folivorous *Alouatta palliata* has relatively small incisors while the frugivorous *Saimiri sciureus* has large ones. This is essentially the same pattern that was exhibited by both the hominoids and cercopithecids; when corrected for body size, the leaf-eating anthropoids tend to have smaller incisors than the more frugivorous ones. It has recently been suggested by Zingeser (1973) that *Brachyteles arachnoides* is probably more folivorous than species of *Ateles* and *Lagothrix*. Based on the size of the anterior dentition relative to both the size of the skull and the posterior dentition, this suggestion seems reasonable. Like species of *Alouatta*, *B. arachnoides* is a fairly large primate with very small incisors (see photographs in Elliott, 1913; and James, 1960).

The convergence between the molars of *Alouatta villosa* (Figure 7) and *Propithecus verrauxi* (Figure 3) is remarkable. This species resembles *P. verrauxi* in having relatively high crowns, sharp cusps, long trenchant shearing blades, and expanded crushing surfaces. A comparsion of fruit-eating prosimians (Figure 3) and New World anthropoids such as *Ateles belzebuth* (Figure 7) is also instructive. Both have relatively low crowns, with short, rounded, and indistinct shearing blades. Dental proportions in these frugivores give the appearance that they have broad and enlarged crushing surfaces but, relative to body size, the whole tooth and its crushing surfaces are reduced. *Alouatta villosa* has a high value on the first principal coordinate confirming a better than average development of shearing blades and crushing surfaces as well as cusp height while other cebids and callitrichids have low values, indicating fruit or gum in their diets (Figure 4). The species used in this study belonged to the genera *Cebus, Saguinus, Saimiri, Ateles, Aotus, Chiropotes,* and *Callithrix*. The genus *Brachyteles* has similarities with *Alouatta* in molar structure suggesting that, like *Alouatta*, it eats a considerable amount of leaves (Zingeser, 1973).

New Guinean and Australian Phalangeroidea

The large diversity of arboreal diprotodont marsupials indicates a long and complicated evolutionary history for the group. Dietary information on the burramyids is inadequate since it is based mainly on preferences of captive animals but it is unlikely that any species are folivorous. Fecal analysis by Dimpel and Calaby (1972) indicates an insectivorous preference for *Burramys parvus*. Green (1973) suggests that the natural foods of *Eudromicia lepidus* may be predominantly insects.

Among the Petaurinae there are both folivorous and gumivorous species. A strongly gumivorous diet has been reported for species of *Petaurus* (Brazenor, 1934; Troughton, 1951; Wakefield, 1961, 1970; Fleay, 1933a, 1954; Ride, 1970). Species of *Pseudocheirus* and *Schoinobates* are both highly folivorous. Thomson and Owen (1964) analyzed 78 stomach contents of *P. peregrinus* and reported an extremely limited food preference: 98 percent of the material came from 2 plant species. They have reported that in some tree species mature leaves were preferred over young ones. Other authors confirm the preference in *P. peregrinus* for leaves but note that flowers, fruits, and berries were also important (Ride, 1970; Green, 1973).

Schoinobates volans is apparently almost completely folivorous (Samuel, 1937; Fleay, 1933b; Troughton, 1951). Recently Marples (1973) examined the contents of 133 stomachs and found leaves, buds, and bark of local *Eucalyptus* species. The diet of *Gymnobelideus leadbeateri* is known only from 1 stomach which contained beetles and crickets (Ryan, 1963). In addition to fruits, blossoms, and honey, *Dactylopsila* and *Dactylonax* sp. eat insect larvae which are extracted from under bark with the aid of elongate fingers and a pair of enlarged incisors (Troughton, 1930, 1951; Fleay, 1942; Ride, 1970).

Among the phalangerines, Wallace (1869) states that *Phalanger maculatus* has a diet of leaves, fruit, and animal prey. Species of *Trichosurus* are much better known. Their diet consists mainly of bark, buds, leaves (especially of *Eucalyptus*), and fruit as well as grasses (Troughton, 1951; Jones, 1921; Green, 1973; Dunnet, et al., 1973). This species has been extensively studied in New Zealand where it was introduced. Gilmore (1967) analyzed stomach contents of 814 specimens at all seasons and found that leaves occur in almost all stomachs while fruits, berries, flowers, and seeds occur in about 10 percent of the stomachs. Mason (1958) reports similar findings in his analysis of 130 stomachs in summer and autumn. *Trichosurus caninus* is also highly folivorous (Lucas, 1909). Additional dietary information is presented by Fitzgerald (1978). Rare and little-known *Wyulda squamicaudata* has been observed feeding on blossoms (Calaby, 1957).

Phascolarctos cinereus is generally pictured as among the most specialized of arboreal folivores. Its food consists almost entirely of gum leaves (*Eucalyptus*). The animal is very particular in its preference for tender shoots and young leaves (Jones, 1923; Kershaw, 1934; Sutton, 1934; McNally, 1956). Additional dietary information is presented by Eberhardt (1978).

Phalangeroids have a single large procumbent mandibular incisor on each side that occludes with 3 vertically positioned heteromorphic maxillary incisors. Both within and between phalangeroid species, the 3 upper incisors vary greatly in size and angulation (particularly the I^1). In general, during occlusion the mandibular incisor functions with the I^1 in shearing, and with the I^2 (and sometimes with the I^3) in crushing. Unlike their incisors, the premolars of phalangeroids vary greatly in number, and also probably in function. Due to the limitations of space, the various combinations of premolar number and patterns of occlusion will not be dealt with here. The great variability in both the anterior dentition and in the premolars among these animals must relate to different patterns of food ingestion and acquisition. There is considerable variation in relative incisor size among phalangeroids (Figure 11). *Dactylonax palpator* and *Dactylopsila trivirgata* are known to dig, rip, and gnaw into wood with their incisors searching for wood-boring grubs. Both species show relatively enlarged large incisors. *Petaurus breviceps* also has extremely large incisors (Figure 11). This species eats a large amount of tree sap. Access to this sap is gained by gnawing into the young branches of various trees (Troughton, 1951; Ride, 1970). Fleay (1933a) noted that on occasion captive *Petaurus* can even gnaw its way out of cages using its incisors.

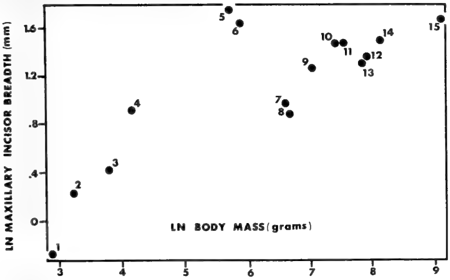


Figure 11. Maxillary central incisor size among phalangeroid marsupials. Log$_e$ sum of the maximum mesio-distal crown diameters of the maxillary central incisors is plotted against log$_e$ body mass. Symbols: 1, *Cercartetus concinnus*; 2, *Eudromicia caudatus*; 3, *Distoechurus pennatus*; 4, *Petaurus breviceps*; 5, *Dactylonax palpator*; 6, *Dactylopsila trivirgata*; 7, *Pseudocheirus peregrinus*; 8, *Pseu. lemuroides*; 9, *Pseu. corinnae*; 10, *Pseu. cupreus*; 11, *Trichosurus vulpecula*; 12, *Phalanger vestitus*; 13, *Phal. orientalis*; 14, *Phal. maculatus*; 15, *Phascolarctos cinereus*.

Unfortunately, there are very little behavioral data on food ingestion or acquisition in phalangeroids. On the basis of their relatively large incisors, it seems likely that marsupials such as *Pseudocheirus cupreus* and *Trichosurus vulpecula* engage in much more incisal biting or gnawing activities than *Pseudocheirus peregrinus* or *Pseudocheirus lemuroides*. *Cercartetus concinnus* has relatively very small incisors. Compared to species of *Petaurus* and *Distoechurus*, it probably engages in relatively little incisal gnawing or biting during the acquisition or ingestion of food.

The last lower premolar of phalangeroids is often enlarged with a serated edge (Figure 14), and it probably functions primarily during ingestion. Insects, leaves, or stems presumably must be cut into manageable pieces before mastication. When feeding on leaves, the premolars probably also function in separating leaves from branches.

When values of lower premolar shear are plotted against body weight, (Figure 12), most species cluster around the regression line. Most of the phalangeroids that are clustered around the regression line are probably either highly folivorous or insectivorous. Relative to body size *Petaurus breviceps* has an exceptionally small P_3. In 3 species the lower premolars do not contact the maxillary dentition (*Dactylopsila trivirgata, Dactylonax palpator* and *Cercartetus concinnus*). Dietary information from captive

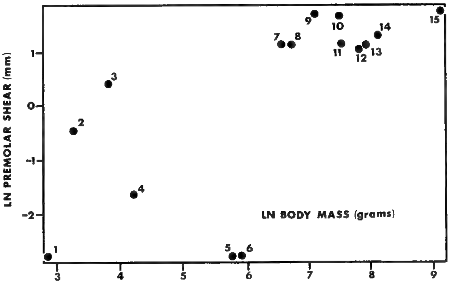


Figure 12. Premolar shear among phalangeroid marsupials. Log$_e$ summed lengths of the shearing crests on the posterior lower premolar is plotted against log$_e$ body mass. Where shearing was absent, a value of 0.05 mm was arbitrarily assigned. Symbols as in Figure 10.

and field studies suggests that *Petaurus, Dactylopsila*, and *Dactylonax* feed on soft-bodied grubs, bits of gnawed fruit, and tree sap. In each case food acquisition requires extensive incisal gnawing using the incisors but ingestive function along the premolars is probably nil. The diet of *Cercartetus concinnus* is unknown. Its incisor morphology implies little incisal gnawing while its premolar morphology indicates a diet of fruit, gum, or nectar. The most likely possibility is a diet predominately made up of either very soft fruits, naturally occurring sap (i.e., not requiring incisal gnawing for exposure), or nectar from flowers.

A principal components analysis of the molar structure of selected phalangeroids is presented in Figure 13. Data transformation was similar to that discussed above (page 9). Allometric corrections were based on body mass. The molar dimensions were chosen to reflect the development of shearing, crushing, and grinding. The first principal component generally separates species on the basis of molar and shearing-blade length and cusp height. The size of crushing and grinding surfaces has less emphasis on the result. Species which eat leaves (*Phascolarctos cinerus, Pseudocheirus peregrinus,* and *Trichosurus vulpecula*) have long shearing blades and high cusps while the gumivorous *Petaurus breviceps* has small molars with low crowns and short shearing blades. The condition of *Petaurus* is shared with *Dactylopsila trivirgata* which takes high proportions of soft plant foods and insect grubs. This contrast is visually apparent from Figure 14 comparing the dentitions of *Pseudocheirus* and *Trichosurus* with *Petaurus.*

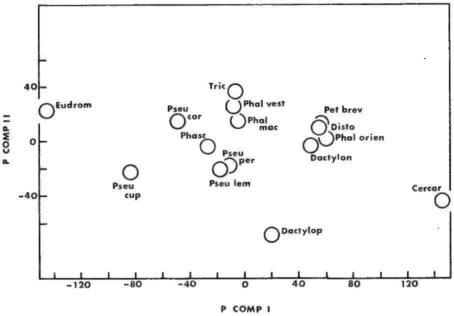


Figure 13. Principal components analysis of molar shape among phalangeroid marsupials. Frugivorous and gumivorous species are to the right. Folivorous species plus one suspected insectivorous species (*Eudromicia*) are at the center and right. Abbreviations: Eudrom, *Eudromicia*; Pseu, *Pseudocheirus*:Pseu cup, *P. cupreus*; Pseu cor, *P. corrinae*; Pseu lem, *P. lemuroides*; Pseu per, *P. peregrinus*; Phasc, *Phascolarctos cinereus*; Tric, *Trichosurus vulpecula*; Phal, *Phalanger*: Phal vest, *P. vestitus*; Phal mac, *P. maculatus;* Phal orien, *P. orientalis;* Disto, *Distoechurus;* Dactylon, *Dactylonax;* Dactylop, *Dactylopsila;* Cercar, *Cercartetus. Cercartetus.*

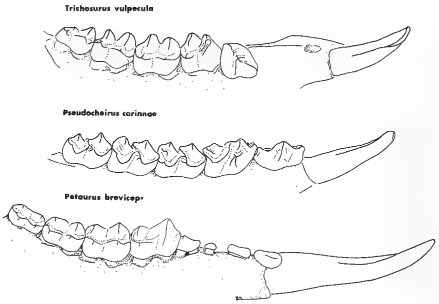


Figure 14. Lower dentitions of phalangeroid species. A, *Trichosurus vulpecula*; B, *Pseudocheirus corinnae; C, Petaurus breviceps. Pseudocheirus* and *Trichosurus* are extremely folivorous while *Petaurus* is largely a gumivore. See text for further comment.

Pseudocheirus and *Trichosurus* species differ in fundamental ways in molar construction, although both are folivorous. *Trichosurus* has rather simple 4 cusped upper and lower molars which could be easily confused with those of colobines (compare Figures 9 and 14). *Pseudocheirus* and *Phascolarctos* are convergent on a molar structure which further emphasizes shearing; many accessory crests have been added for this purpose. Crushing has been minimized by restriction of the size of the trigonid and talonid basins. Whether these differences result from habitus or heritage can not be resolved in the absence of further dietary information.

On the basis of the correlation between dental and dietary features shown for the above species, certain hypotheses can be advance for the diets of other species. Among the burramyids, *Eudromicia candata* is extremely different from *Cercartetus concinnus.* Body size would rule out a folivorous diet for *Eudromicia* and an insectivorous diet is inferred. The extremely reduced molar dentition of *C. concinnus* would be consistent with a large fruit, nectar, or gum component in the diet. The same may be said for *Distoechurus pennatus* which has molars extremely similar to those of *Petaurus* sp. *Dactylonax palpator* is more similar in molar shape to *Petaurus* spp. than to its close relative *Dactylopsila trivirgata*, implying a diet consisting in large part of gum, nectar, and fruits supplemented with insects.

The molars of *Pseudocheirus cupreus, P. lemuroides,* and *P. corrinae* have leaf-eating designs similar to

Pseudocheirus peregrinus. *P. cupreus* and *P. corrinae* have proportionally larger molars for their body size than *P. lemuroides*. This might indicate larger proportions of fibrous materials in their diet. An interesting contrast exists within the genus *Phalanger*. *P. maculatus* and *P. vestitis* have much larger molars relative to body size than does *Phalanger orientalis*. This difference would suggest that *P. maculatus* and *P. vestitus* eat more leaves than *P. orientalis*.

Summary and Conclusions

For energetic reasons, leaf-eating mammals do not usually get smaller than about 700 grams. Cellulose and hemicellulose require considerable time to digest and even ruminants cannot digest them completely. Compared to a diet of fruit, a larger amount of leaves has to be processed for a longer time to extract the same amount of energy. The smaller an animal gets, the larger becomes its energy needs per unit volume. Possibly even a bulk processor smaller than about 600-700 grams might find its digestive tract inefficient and unwieldy. Some folivorous rodents can reach much smaller sizes. This may be related to an extremely efficient masticatory apparatus. If a species could further reduce swallowed-particle size, this would speed up the digestion of food (Parra, 1978).

Molar structure reflects to a great extent the physical nature of foods chewed. This would be consistent with the notion that feeding niches are in equilibrium in most mammalian communities since a great number of generations would be required for selective alteration of mechanical designs of teeth. From our results we conclude that there is an optimal molar design for a mammal feeding on arboreal browse involving a shearing mode in food preparation. The shearing of food is accomplished by movement of the leading edges of enamel blades across one another. Such a design is often accompanied by a thinning of enamel. As tooth wear continues during life, the enamel is ruptured, leaving a pair of sharp edges for each unworn enamel ridge. Most folivorous primates tend to accentuate surfaces where food can be crushed. This strategy, which is followed also by some phalangeroids, is by no means universal among them. In some folivorous species crushing appears to be of limited importance, e.g., tree sloths and flying lemurs. Similarly crown height by itself does not always separate folivorous from frugivorous arboreal mammals.

In many respects, incisor structure responds in a predictable manner to a folivorous diet. In Figure 15 the first coordinate of a multivariate analysis of molar shape in cercopithecoids is plotted as a function of the relative size of their incisors. The correlation is quite strong; species with relatively small incisors have low first coordinate values indicating better than average development of shearing, crushing, and grinding features on the molars. Apparently, folivorous foods requiring limited amounts of incisal preparation will require at the same time comparatively large amounts of mastication. This generalization applies to anthropoids but not to prosimians or phalangeroids.

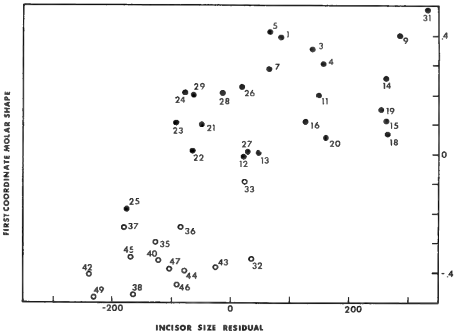


Figure 15. Relative incisor size compared with first coordinate molar shape. Symbols and numbers are as in Figure 5.

Unlike anthropoids, incisor diversity among prosimians and phalangeroids is not primarily a reflection of the proportions of leaves and fruit ingested. Instead it also reflects specialized food acquisition activities such as gum eating, bark prying and gnawing. Analysis is further complicated by the use of the anterior teeth as grooming organs. Nevertheless, there is some hint that among folivorous prosimians, the relative size of the anterior dentition may indicate the amount of leaves in the diet. *Lepilemur mustelinus* is almost completely folivorous and has lost its upper incisors. *Hapalemur griseus*, another highly folivorous form, has extremely reduced upper incisors. *Propithecus verreauxi* has a mixed fruit and leaf diet. In contrast to *H. griseus* and *Lepilemur* it has much larger upper incisors.

Compared to gum- and fruit-eating species, folivorous prosimians and phalangeroids have accentuated the amount of premolar shear. This relative increase reflects increased ingestion and mastication of fibrous foods in this region.

A balanced assessment of dental features can provide considerable information about the modal feeding strategies for species which are little known ecologically. Applications to the fossil record of mammals are currently being explored.

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Digestion of Leaves in Vertebrate Arboreal Folivores

Introduction

The combination of arboreal habitat with folivore nutrition, while affording opportunity for ecological separation of a wide range of animals, has required evolution of major adaptive changes to permit colonization of this nutritionally demanding environment. The overall nutritional requirement of all higher animals appears remarkably similar, which suggests that on the evolutionary scale there has been little chemical change in the nutritional environment or in the digestive capabilities of animals (Moir, 1968). The expansion of limited digestive capabilities has required evolution of increased complexity of the digestive system to permit utilization of a wider range of nutritional energy sources. In this way new and more "difficult" nutritional environments have been exploited and colonized by animals (Young, 1962).

The increased complexity of the alimentary tract in herbivores, involving enlargement of either the foregut or the hindgut, has been intimately associated with symbiotic interactions between the animals and the microorganisms in their guts. Gut anatomical complexity has undoubtedly evolved through such host-microbe associations and the ecological advantages they have conferred (Moir, 1968). These advantages include the capability of utilizing plant structural polysaccharides, a major source of energy unavailable to higher animals, as they lack the necessary digestive enzyme. A number of bacteria can digest cellulose, and herbivores of all types have employed these bacteria as their source of cellulolytic enzymes. The host-animal plus the bacteria compose a complex system with increased dietary range, while the bacteria concerned have benefited by adaptation to the ideal anaerobic environment provided by the stomach or hindgut of the herbivore.

Although the bacterial flora, which develops soon after birth in these different sites, is complex, the resulting fermentation is quite characteristic. In addition to bacterial cells, the fermentation products include short-chain volatile fatty acids (VFA's), principally acetic, propionic and butyric acids, together with varying amounts of gaseous products, carbon dioxide, methane, and hydrogen. The gases are waste products but the VFA's and the bacterial cells may be utilized in the nutrition of the host-animal.

In addition to affording the opportunity for utilization of structural plant materials, a microbial fermentation in the gut confers a number of advantages which have been well recognised in ruminant and ruminantlike animals. Gut microbes are capable of utilizing nonprotein nitrogen for growth. Thus, urea derived from protein catabolism in the animal can diffuse into the fermentation organ and be converted, via ammonia, to microbial protein. This high-quality protein can be a valuable supplement to low-protein food.

Besides improving dietary protein quality, this mechanism can assist in conserving water by decreasing urea excretion and formation of urine.

The bacterial flora of the rumen, because of their high numbers, turnover rate, and metabolism, rapidly adapt to new plant products. This enables the animal to colonize new plant environments including some which contain compounds which would otherwise be toxic. Finally, the bacteria can synthesize a wide range of vitamins and increase manifold the vitamin content of the ingesta to make the animal virtually independent of dietary sources of all vitamins except A and D.

The nutritional and physiological implications of a gut fermentation have been investigated most extensively in ruminants. However, these benefits might equally be expected to apply to other animals with fore-stomach fermentations, and there is increasing evidence that this is true. Although fore-stomach fermentation is best developed in the Ruminantia, it has probably evolved independently in the Tylopoda (camel, llama), the hippopotamus, the sloth (*Bradypus*), the leaf-eating monkeys of the Colobinae and in the macropod marsupials. The main advantage of the fore-stomach fermentation is that after leaving the stomach the fermentation products, including bacteria, can be digested and absorbed in the normal functional sites of the small intestine.

With a hindgut fermentation, cellulose and other plant polymers can still undergo fermentation with accompanying absorption and utilization of fermentation products. In addition there is evidence that urea can be recycled via the large gut (Houpt, 1963; Thornton, et al; 1970). However, clearly there is less opportunity for utilization of microbial protein or vitamins, which are contained mainly in microbial cells. These limitations have been overcome in some groups of animals, such as rodents and rabbits, by use of the mechanism of coprophagy, or feces ingestion. Usually this is a digestive mechanism of considerable complexity, with 2 kinds of feces being produced, and only the soft, nitrogen-rich type being eaten. By this means more efficient use can be made of the hindgut fermentation.

All higher animals, so far as it is known, possess a hindgut fermentation of some degree and presumably benefit from it to a greater or lesser extent. In herbivores, the special development of the alimentary tract, involving considerable enlargement, permits maximal use of the microbial flora in dealing with bulky plant material. The classical examples of hindgut-fermentative digestion are the horse and the rabbit. Arboreal folivores which are classed in this nutritional group include a great variety of mammals: primate indriids and noncolobid leaf-eaters; marsupial phalangers; many rodents; tree hyraxes and the colugos or flying lemur.

In many of these groups only indirect evidence for fermentative digestion is available, derived from considerations of diet and digestive anatomy; information on microbial fermentation is fragmentary or lacking. Even details of diet are not known for many arboreal animals.

In the cases of arboreal birds, amphibians, and reptiles there is no direct information on gut microbial fermentation. However, application of the criteria of diet and digestive anatomy alone would seem to preclude these classes from possession of major fermentative digestive mechanisms.

Foregut Fermentation

Colobid monkeys

Old World monkeys of the subfamily Colobinae differ from all other primates in the large size and anatomical complexity of the stomach (Hill, 1952). These differences are related to a diet consisting mainly of leaves, hence the name "leaf-eaters" commonly used to describe these primates.

Considerable literature has accumulated on the peculiarities of the gastric anatomy of the Colobinae (Hill, 1952). A gross anatomical resemblance of the stomach to the rumen of herbivorous animals has been noted, but a number of authors (Ayer, 1948; Kuhn, 1964) have stated that rumination does not occur. Although rumination is the obvious characteristic of ruminants, recent work has placed greater emphasis on the fermentative processes occurring in the rumen. The demonstration of an extensive microbial fermentation (Bauchop and Martucci, 1968) in addition to the known anatomical facts, have established that members of the Colobinae possess a highly evolved ruminantlike digestion.

The stomach of *Procolobus* has 4 parts—the sacculated and expanded presaccus and saccus, the long tubus gastricus, and the short pars pylorica (Kuhn, 1964). The saccus and presaccus in some species communicate only by narrow slits. From the esophagus, a well-defined ventricular groove (*Magenstrasse* or gastric canal) runs down the lesser curvature of the tubus toward the pyloric region. This structure may allow ingested liquids to pass directly from the esophagus to the middle compartment of the stomach. The lips of the groove are strongly muscular and have a rich nerve supply. The mucosa immediately surrounding the cardia forms a shield of dense stratified epithelium. The remainder of the mucosa of the upper stomach is of cardiac glands, and only in the terminal third of the tubular stomach do parietal cells occur. This region is followed by one of typical pyloric glands (Fig. 1). The stomach in some species is somewhat similar in form to that found in the macropod marsupials; the cecum, too, is reduced, and the small intestine is typically long (Moir, 1968).

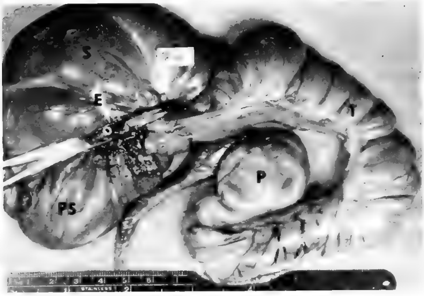

Figure 1. Stomach of *Presbytis cristatus.* PS, presaccus; S, saccus; T, tubular portion; P, thick-walled pyloric region; E, esophagus, closed by forceps.

The essential features of the Colobinae stomach is that this anatomical complexity permits excellent separation of the ingesta in the proximal regions from the distal acid pyloric region (Bauchop, 1971). The pH is thus normally maintained at a value between 5.0 and 6.7 in the langurs examined (Bauchop and Martucci, 1968) and from 5.5 to around 7.0 in the colobus monkeys (Kuhn, 1964; Ohwaki, et al., 1974), indicating excellent control of pH. The salivary glands are relatively extensive (Hill, 1952), and saliva may play a role as a buffer source. This range of pH values permits an active fermentation of ingesta by the large numbers of anaerobic bacteria present. As in ruminants, gastric contents constitute a large proportion of the body weight of these monkeys. In colobus monkeys values obtained for gastric contents were 10.5 to 20.6 percent of the total body weight (Kuhn, 1964; Ohwaki, et al., 1974) and a value of 17 percent of body weight was obtained for gastric contents of a langur monkey (Bauchop and Martucci, 1968). The large capacity of the stomach allows the accumulation of ingesta and slow rate of passage essential for extensive fermentation of plant materials.

In direct smears of stomach contents obtained from colobus monkeys, Kuhn (1964) found bacteria to be present although he did not consider that they compared either numerically or in diversity with ruminant flora. Characteristic ciliate protozoan fauna were absent. Samples obtained from 2 specimens of *Colobus polykomos* in the wild (Ohwaki, et al., 1974) also contained high numbers of bacteria and no ciliate protozoa. However, the stomach contents of these animals contained no leafy material and, although an active fermentation was present, many of the results obtained, including bacteriology, were not typical for fibrous plant fermentation.

The availability of the langur monkeys in a laboratory environment permitted Bauchop and Martucci (1968) to investigate the microbial flora of the animals in greater detail. As in the colobus monkeys, the ciliate protozoa characteristic of the rumen microbiota were not found. However, a rich bacterial flora composed of diverse types was present. Anaerobic culture counts ranged between 2×10^{10} and 1×10^{11} per gram of contents, and the ratio of anaerobic to aerobic organisms was in the range 100:1 to 1000:1, indicating the anaerobic nature of the microbial ecosystem. As langurs thrive on a leafy diet, it was significant that large numbers of cellulose-digesting bacteria were present (Bauchop and Martucci, 1968). Cellulolytic bacteria numbered 8×10^6 to 1×10^8 per gram of contents and 2 forms were isolated, a Gram positive coccus and a *Bacteroides* spp., which appeared similar to major cellulolytic bacteria isolated from the bovine rumen (Hungate, 1966). Although these results indicate that cellulose digestion is likely to be important in the Colobinae nutrition, the extent of cellulose decomposition remains to be measured.

In both langurs and colobus monkeys, major gaseous fermentation products were methane and carbon dioxide (Kuhn, 1964; Bauchop and Martucci,

Table 1.—Volatile fatty acids (VFA) in the stomach of colobid monkeys and ruminants.

		Molecular proportions					
Animal	*Concn mM/ VFA*	*Acetic*	*Propionic*	*n-Butyric*	*i-Butyric*	*n-Valeric*	*i-Valeric*
Presbytis cristatus	165	51	24	6	5	7	8
Presbytis entellus	103	50	28	14	—	5	4
Procolobus verus	181	70.5	16.7	9.9	—	2.5	—
Procolobus	219	63.9	22.8	9.8	—	2.2	—
Cattle	137	64.0	21.9	11.9	—	2.2	—
Sheep	94	58	29	7	2	1	3

1968). As in the rumen, the methane-producing bacterium *Methanobacterium ruminantium* was shown to be present in the langur stomach (Bauchop and Martucci, 1968). Fermentation studies (Kuhn, 1964; Bauchop and Martucci, 1968) revealed rate of fermentation very similar to those obtained with small ruminants (Hungate, et al., 1959). Samples of gastric contents from colobus monkeys (Drawert, et al., 1962; Ohwaki et al., 1974) and langurs (Bauchop and Martucci, 1968) contained volatile fatty acids (VFA's) similar in concentration and proportions to those formed in rumen contents (Table 1).

In ruminants the VFA's are absorbed directly from the rumen, and in ruminantlike animals, from the stomach (Moir, 1968). Although this has not been demonstrated directly in the Colobinae, Drawert, et al. (1962) found in *Procolobus verus* that the VFA concentration of the contents decreased from 230 mmoles/liter in the midstomach region to 24 mmoles/liter in the pyloric region, indicating clearly that fatty acids are absorbed directly from the stomach. The gastric concentrations of these acids represent an equilibrium between their rate of production and their absorption from the upper stomach. A constant VFA concentration was demonstrated by analyzation of gastric samples taken from a specimen of *Presbytis cristatus* (Bauchop and Martucci, 1968). After feeding fresh alfalfa, samples of gastric contents were withdrawn by stomach tube at regular intervals. Within 2 hours of feeding the VFA concentration attained a high concentration which was maintained relatively constant between 162 and 197 mmoles per liter throughout the 6.5 hours of the experiment (Figure 2). The constancy of the gastric pH at 5.6 during the course of this experiment confirmed that langurs possess an excellent mechanism for controlling, within narrow limits, the pH of their stomach contents.

A high in vitro rate of VFA production was found in fresh samples of gastric contents from both colobus and langur monkeys (Kuhn, 1964; Bauchop and Martucci, 1968). In addition in the langurs, high fermentation rates were present in samples obtained 10.5 hours after the animals were fed. This demonstrates the continuous nature of microbial fermentation in the monkeys. Using the fermentation rates obtained, Bauchop and Martucci (1968) calculated that the gastric fermentation made important contributions to the energy metabolism of these monkeys.

The ammonia concentration in the gastric contents was maintained at a high level also (Figure 2), indicative of bacterial proteolytic activity and fermentation of amino acids. The high concentration found was presumably due to the high protein content of the young leafy portions of the alfalfa, which were eaten selectively.

In ruminants, as a result of bacterial fermentations, glucose is not readily available to the animal and the blood sugar level is characteristically low. The blood sugar level of *Presbytis* spp. was found to be 62–99 mg per 100 ml (Kuhn, 1964), values comparable with tylopods but higher than in macropod marsupials or true ruminants. Although low blood sugar levels are normal in ruminants, the rate of gluconeogenesis

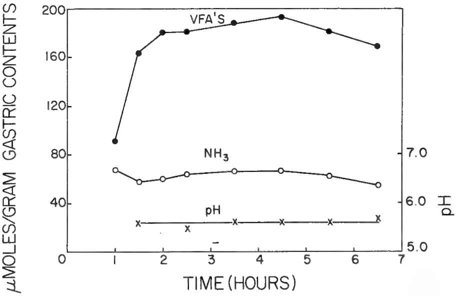

Figure 2. Changes in fermentation products in gastric contents of *Presbytis cristatus*.

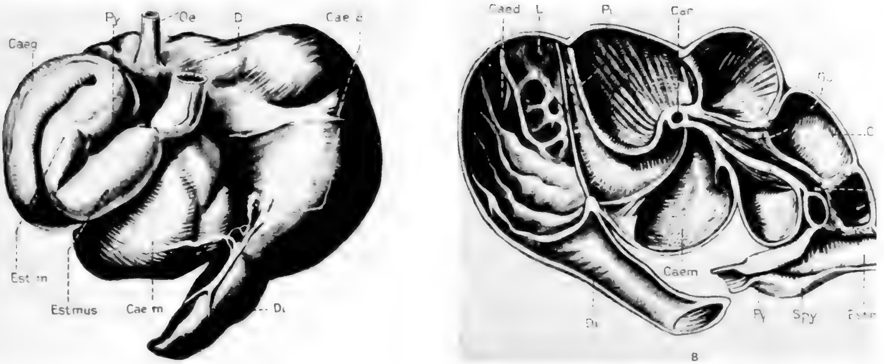

Figure 3. Stomach of *Bradypus tridactylus*. *Left:* dorsal view; *Right:* section and dorsal half. Cae d, right gastric cecum; Cae g, left gastric cecum; Ce M, central gastric cecum; Est m, central stomach; Est mus, muscular stomach; Di, diverticulum; D, duodenum; Oe, esophagus; Py, pylorus; L, division between keratinized and glandular surfaces; Car, cardia; Pi, pillar; Go, esophageal groove; Est gl, glandular stomach; Spy, pyloric sphincter. (From *Traité de Zoologie* (1956) Volume 17, page 1213. Produced under the direction of P-P. Grasse. By courtesy, Masson et Cie, Paris).

and the activity of the phosphorylating enzymes in the liver are functionally more important. In this respect the liver of ruminants is well equipped to synthesize glucose and release it into the blood. The enzymic activities in the Colobinae liver have not been examined.

An additional feature of ruminant animals is the "stearic-rich" nature of the depot fats which result from microbial hydrogenation in the rumen of dietary unsaturated fatty acids. The fatty acid composition of Colobinae lipids has not been determined although the result would be of considerable interest.

There are many gaps in our knowledge of the nutrition, digestion, and physiology of the members of the Colobinae. However, the high numbers of cellulose-digesting bacteria in the langur stomach suggest that plant structural carbohydrates serve as an important energy source. Moreover, regardless of the food ingested it is clear that microbial fermentation plays a major role in digestion. It was suggested that bacteriol biosynthetic capacity might benefit the vitamin and nitrogen economy of the host (Bauchop and Martucci, 1968). This view is supported by results of Oxnard (1966) who found that langurs (*P. obscurus* and *P. entellus*) have blood serum levels of vitamin B_{12} which are several-fold greater than those of other primates.

Although there is no direct information on nitrogen metabolism in langurs, urea recycling, via the stomach, would be expected to affect profoundly the water balance of these animals. In this regard there are a number of pertinent observations from field work. In India, langurs and rhesus monkeys frequently exist in close association, but in the dry season langurs continue to exist in areas where rhesus monkeys could not survive (Jay, 1965). In addition, in the Dharwan Forest of western India, all water sources dry up in summer but the langurs can live without drinking water for 4 or 5 months (Yoshiba, 1968). The stomach form in this group of monkeys is clearly a highly evolved ruminantlike stomach which has advanced to the point where these animals are able to invade ecological niches difficult or even impossible for other primates (Moir, 1968).

Tree sloths

Tree sloths are strictly arboreal, only rarely descending to the ground (Montgomery and Sunquist, 1975). They are herbivorous, with a diet consisting mainly of leaves, young shoots, and tender twigs.

The stomach of the Bradypodidae is extremely large and complex, unlike the relatively simple stomachs of the insectivorous members of Edentata. The replete stomach represents 20-30 percent of the body weight of the animal (Britton, 1941) and the similarity to a rumen has been noted by a number of authors (Grassé, 1955). The main body of the stomach consists of 3 chambers, well divided internally by pillars (Figure 3). It has stratified epithelium. The right or anterior chamber is extended into a large blind conical diverticulum with cardiac glands throughout. A short ventricular groove along the left chamber passes through a small chamber with cardiac and fundus glands to the pyloric region (Oppel, 1896). The general development is broadly similar to that in the camel, although the presence of pillars more closely resembles true ruminants (Moir, 1968). The large intestine is short and a cecum is absent (Britton, 1941).

In *Choloepus*, radiological studies with barium meals demonstrated that there was a slow-rate passage of food, which could remain in the stomach for 70-90 hours. A rich bacterial population is present in the stomach, but ciliate protozoa have not been observed (Denis, et al., 1967). The absence of ciliates may be worth further examination, as the specimens of *Choloepus* used were not receiving a natural diet, and ciliate protozoa may be lost under such conditions. Cellulose-digesting bacteria were shown to be present (Jeuniaux, 1962), although none of the bacteria have been identified and the extent of cellulose digestion remains to be determined.

The pH in the 3 chambers of the stomach varied from 5.2-5.8 and 6.4-6.7 in 2 animals examined (Denis, et al., 1967). In 2 cases where *Choloepus* did not eat for 1 and 2 days, the pH of the contents remained in the range 7.0-7.7, indicating the presence of a mechanism for controlling pH.

VFA's were found in different regions of the stomach in concentrations ranging from 37-95 mM, values comparable with other ruminantlike animals. Although the composition of these VFA's has not been determined, they are absorbed by the gastric mucosa and transferred to the gastric venous blood (Denis, et al., 1967) as found in other ruminantlike animals (Barcroft, et al., 1944; Moir, et al., 1956).

The blood sugar level in 2 specimens of *Choloepus* was found to be 59 and 62 mg per 100 ml (Marvin and Shook, 1963), a level intermediate between that of true ruminants and nonruminants. However, insulin administration was poorly tolerated in both *Bradypus* and *Choloepus*, even in nonfasting conditions (Britton, 1941). Ruminants, having a normal low blood sugar, can tolerate severe hypoglycemia induced by insulin injection. Additional information is needed on carbohydrate metabolism to explain such differences.

Although the available evidence is fragmentary it indicates clearly that the tree sloths possess a gastric fermentation of major importance to the nutrition of the animal. Undoubtedly further studies will reveal the several physiological ramifications of dependence upon this type of digestive mechanism.

The low body temperature of sloths (Britton, 1941) would seem to be particularly noteworthy, and the basal metabolic rate is reported to be low also (Almeida and Fialho, 1924; McNab, 1978). The lower energy metabolism could mean a lower minimum food intake or use of lower grade food. Together with the possible advantages of nitrogen conservation inherent in fore-stomach fermentation, this would confer advantages to the sloths in their nutritionally difficult ecological niche.

Tree kangaroos

About 5 species of *Dendrolagus* inhabit timbered areas in New Guinea, and 2 species occur in northeastern Queensland, Australia. Although tree kangaroos are not rare, they frequent inaccessible areas and their habits are not well known. The diet consists mainly of leaves and fruit, obtained either in trees or on the ground (Walker, 1964).

Dissection of kangaroos in the last century (see Moir, 1968) led to the recognition of similarities in the macropod marsupial stomach to those of ruminants, based mainly on size and complexity and the presence of an esophageal groove. Moir, et al. (1956), with the modern concepts of ruminant digestion, extended these observations in a study of digestion in the quokka, *Setonix brachyurus*. They established that bacterial fermentation of cellulose occurs in the fore stomach and that many other ruminant adaptations occur in this macropod. Some of these ruminantlike adaptations have been confirmed in other macropods (Tyndale-Biscoe, 1973) and, on the basis of similarities in stomach anatomy, seem probable to occur in all Macropodidae.

The macropod stomach is very large and when full can weigh 15 percent of the total body weight, a proportion similar to other ruminantlike animals. It is an elongated curved bag, deeply sacculated on the outer curvature and smooth on the inner shorter side (Figure 4). Four regions can be distinguished macroscopically, which correspond to functionally distinct parts.

The large sacculated region of the stomach is lined by an epithelium of cardiac glands, which secrete mucus but not proteolytic enzymes or acid. The pH ranges from 4.6 to 8.0 and is probably controlled by the buffering action of the parotid saliva and mucus secretions. This portion communicates with a nonsacculated thick-walled chamber which leads to the pyloric region. There is a full complement of parietal and chief cells in the well-developed epithelium and consequently there is an acid pH of 1.8-3.0. Internally, there is a well-defined esophageal groove extending from the cardia to the nonsacculated region along the lesser curvature, its length and definition varying with different species (Moir, 1968). Although some minor differences exist (Beddard, 1923), the general plan of the stomach in *Dendrolagus* is similar to other macropods. The small differences would not affect the primary fermentative function of the organ. Unfortunately, in *Dendrolagus* information is lacking on gastric microbiology and fermentation processes,

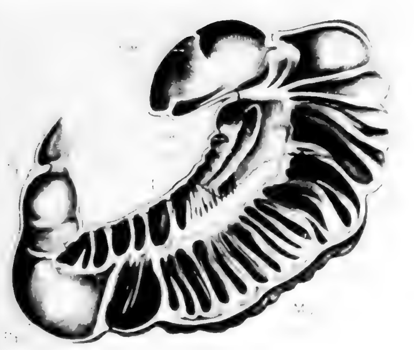

Figure 4. Stomach of macropod marsupial (*Lagorchestes leporoides*), dorsal half. Cae, gastric cecum; Car, cardia; Go, esophageal groove; L, division between squamous and glandular surfaces; Muc, surface with cardiac glands; Pgl, glandular pouch; Py, pylorus. (From Traité de Zoologie (1956) Volume 17, page 124. Produced under the direction of P-P. Grassé. By courtesy, Masson et Cie, Paris)

as well as their influence on the physiology of the animal. In other Macropodidae the highly developed fore-stomach fermentation is similar in detail and efficiency to that of the Ruminantia and confers the same advantages of nitrogen and water conservation (Tyndale-Biscoe, 1973). The low metabolic rate, common to all marsupials, presumably also confers special advantages on *Dendrolagus* in colonizing its unusal environment.

Hindgut Fermentation

Digesta entering the large gut is composed of refractory residues of the diet, undigested endogenous secretions, and cellular debris sloughed from the gut wall, as well as substances which transfer from blood, such as urea. In the case of herbivorous animals possessing only hindgut fermentations, the main substrate for fermentation will be undigested plant material. As in the foregut systems, a major consideration in assessing the nutritional contribution of the fermentation is the mass of the fermenting digesta. A number of arboreal folivores are well endowed in the capacities of their hindguts, and undoubtedly active fermentations making important contributions are present. However, details of microbiological and nutritional aspects are lacking, so comments must be limited to dietary and anatomical features, focusing attention on the more important subjects.

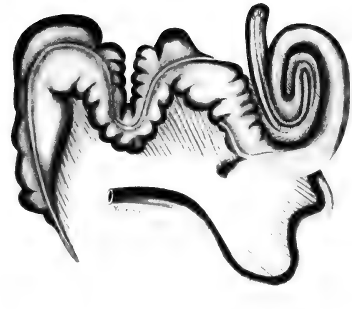

Figure 5. Cecum and colon of *Avahi laniger*, ventral view. (From *Primates. Comparative Anatomy* and *Taxonomy* (1953) Volume 1, page 591. W.C.O. Hill. By courtesy of the author).

Primate indriids

These Madagascan primates compose a family of 3 genera, *Propithecus, Avahi,* and *Indri.* They are arboreal and strictly vegetarian in the wild, feeding on leaves and buds with lesser amounts of fruit and nuts (Hill, 1953). They, thus, occupy a dietary position in the tropical forests of Madagascar similar to that of the Colobidae in Africa and Asia and the howler monkeys in tropical America (Walker, 1964).

The alimentary tract of the Indiidae is extremely capacious and complex (Hill, 1953). Although the stomach has a simple structure, it is large, presumably serving as a storage organ for the bulky diet. The intestine is relatively long; in *Propithecus* it is 9 times and in *Avahi* 14 times the body length. The whole of the posterior region of the abdomen is occupied by the coils of the enormous cecum and colon. In adult animals the greatly sacculated cecum (Figure 5) is longer than the body length. The colon is not sacculated, but the proximal portion is wide and coiled in a complex manner, with similarities to the hypertrophied spiral colon of ruminants (Hill, 1953). The importance of the cecum and colon in the Indriidae is emphasized further by the complex blood supply, with the mesenteric arteries being greatly hypertrophied and split up in a plexiform manner.

The great capacity of the large gut and the known diet of these primates would indicate a major role for fermentative digestion which could continue well into the colon. The complex coiled structure of the colon together with the excellent blood supply would provide ample opportunity for absorption of bacterial fermentation products.

Lepilemur

Two species of *Lepilemur*, both arboreal, leaf-eating animals, inhabit different wooded regions of Madagascar. The stomach is simple, although it has a large fundus, but in the hindgut, the cecum attains a remarkable size and is coiled into a spiral of 2½ turns (Hill, 1953).

New World monkeys

Many New World monkeys are primarily vegetarian, and although some gastric modifications exist, the large intestine seems likely to be the *main* fermentation site. Howler monkeys (*Alouatta*) are leaf-eaters and, in ecological terms, have been equated with Indriidae and Colobinae of the Old World (Hill, 1962; Walker, 1964). The stomach is relatively capacious and the fundus and body compose a large, subglobular sac narrowing slightly toward the tubular pyloric segment. The pyloric segment is partly or completely folded so that it lies in the dorsal wall of the lesser sac (Figure 6). Internally, strong transverse muscular pillars occur at the incisura angularis guarding the entry to the pyloric antrum. These features may provide some degree of separation of ingesta from the (acid) pyloric region sufficient to permit microbial fermentation. In this respect the great development of the salivary glands may be functionally significant.

Although the small intestine is short, *Alouatta* possesses a large intestine and cecum which are very wide. Internally, there is a very pronounced fold which forms an annulus separating the cecum from the colon. Thus the structure and capacity of the hindgut would permit the necessary stasis of digesta required for extensive fermentation.

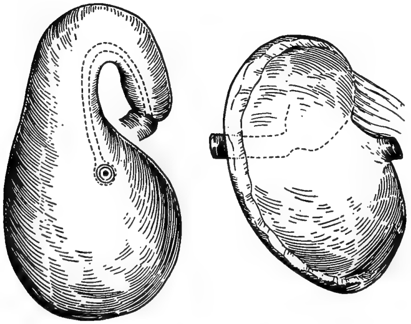

Figure 6. Stomach of *Alouatta seniculus*, ventral and cranial views. (From *Primates. Comparative Anatomy and Taxonomy* (1962). Volume 5, page 49. W.C.O. Hill. By courtesy of the author).

The form of the stomach in *Alouatta* appears significant in relation to a leafy diet and, even if primary gastric fermentation is unimportant, could permit the animal to benefit from coprophagy. There is no information on the occurrence of this digestive mechanism in *Alouatta*.

A number of other arboreal New World primates include leaves in their diets although, in common with other arboreal animals, there is a great lack of detailed information on their diet and habits. Both the woolly spider monkey (*Brachyteles*) and the spider monkey (*Ateles*) appear noteworthy. The cecum in these monkeys is extremely large and in *Brachyteles* has been described as resembling a second stomach (Hill, 1962). In *Ateles* the cecum is capacious, long, and U-shaped, and there is a well-developed sacculated colon. In addition to the obvious great fermentative capacity in the hindgut, the stomach in both *Ateles* and *Brachyteles* has a modified form. The capacity is relatively enormous, with the organ basically U-shaped and consisting of 2 tubular portions. The fundus and body of the stomach, in the first portion, are separated from the second pyloric portion by a deep incisura angularis on the lesser curvature, with a partial annular constriction surrounding the organ at the same level (Hill, 1962). Although much less highly evolved that the *Colobinae* stomach, these anatomical features alone make *Ateles* and *Brachyteles* open to speculation on the status of their gastric microbiology. In addition there is great development of the parotid glands which are more likely to affect directly conditions in the foregut than in the hindgut.

Flying lemurs

There are 2 species: *Cynocephalus volans* inhabits a number of the Philippine islands; *C. variegatus* occurs from Tenasserin and southern Indo-China to the Malay States, Sumatra, Java, Borneo, and adjacent islands (Walker, 1964). Their habitat is forested regions, and their diet consists of fruit, buds, flowers, and leaves. The digestion of these animals has not been studied systematically, although examination of stomach contents of 8 specimens revealed only green vegetable material (Wharton, 1950). Flying lemurs have a simple stomach but the large intestine is long and voluminous, and there is a capacious sacculated cecum where stasis of the digesta occurs (Grassé, 1955; Schultz, 1972).

Marsupial phalangers

Members of the Phangeridae are arboreal, and most forms are herbivorous. The koala (*Phascolarctos cinereus*) is confined to eucalyptus forests in eastern Australia and has an extremely restricted food range, being limited to a few species of *Eucalyptus*. The most extensively studied species of phalanger is the brush possum, *Trichosurus vulpecula*, common in the winter rainfall areas of Australia but with extensive distribution in other regions, including New Zealand, where it was introduced. Possums are herbivorous but thrive on a wide variety of vegetation.

The herbivorous phalangers have a small, simple stomach; in *T. vulpecula* its mass is about 3 percent of the body weight, and the pH of the stomach contents is 3-4 (Anderson, 1938). In the koala the gastric pH is 2.5-3.5 (Griffiths, 1963). The remainder of the alimentary tract, however, shows typical herbivorous development; the intestine is long and there is a large cecum (180-240 cm in the koala) which, although not grossly sacculated to the exterior, has a series of internal folds (Waring, et al., 1966). The pH in possum cecal contents was 8.5-9.0. Conditions thus exist for substantial nutritional contributions from fermentation in the hindgut of herbivorous phalangers and a rich bacterial flora has been found in the large intestine of *T. vulpelcula* (R. T. J. Clarke, 1975, personal communication). Although the extent of the fermentative contribution has not been measured there are many situations where the possum diet appears to be of low quality, which suggests that cellulose digestion may be important. The use of marker substances showed that there is a slow rate of passage of food through the possum gut (Gilmore, 1970) which, combined with a fermentative digestion can explain the high degree (80 percent) of crude fiber digestion obtained on a banana-and-carrot diet (Honigmann, 1937).

Reingestion of feces has been observed in the koala and in the ringtail possum, *Pseudocheirus peregrinus* (Waring, et al., 1966), but the extent or importance of this phenomenon is not known.

Physiological evidence, from blood sugar levels (Anderson, 1937), insulin response (Adams and Bolliger, 1954), intestinal disaccharidase patterns (Kerry, 1969), and depot lipid composition (Bolliger and Shorland, 1963), in either possum or koala, further supports the classification of these animals with simple-stomach types of herbivores.

Tree hyraxes

The genus *Dendrohyrax* is composed of 3 species, *D. dorsalis, D. validus,* and *D. arboreus*, which inhabit forests of central and southern Africa, including the islands of Fernando Po and Pemba. They spend the day in tree hollows or dense foliage and feed during the night on leaves, shoots, buds, and insects (Walker, 1964).

Hyraxes possess an extremely complicated alimentary tract (Grassé, 1955). Although the stomach does not have the complexity of ruminant or ruminantlike animals, it does possess a constriction which appears to divide it into 2 parts. The presence of a complex hindgut in hyraxes suggests that the stomach is not the primary fermentation site. This is supported by evidence from the fatty acid composition of adipose tissue, which in *D. arboreus* contains a high concentration of unsaturated fatty acids (Garton and Duncan, 1971). As the cardiac region of the stomach has few glands, the constriction could be functionally important, if coprophagy were practiced by these animals, by preventing immediate contact of ingesta with acid contents, and thus permitting more prolonged fermentation. There is no information on the occurrence of coprophagy.

The large intestine has 2 capacious ceca well separated along the colon. The second of these is further modified by possession of 2 large hornlike appendices which communicate directly with the main body of the organ. Anatomically, hyraxes thus appear extremely well endowed for extensive fermentation of plant material in the hindgut.

Rodents

Most rodents have a relatively simple stomach but well-developed ceca and large intestines, with coprophagy appearing to be a normal nutritional mechanism. In the Myomorpha, however, many genera possess a constricted stomach, with a large cardiac region lined by squamous epithelium and free of glands (see Moir, 1968), which may have functional significance in either primary fermentation or coprophagy. Energy losses associated with fermentation make fermentative digestion relatively less effective in meeting the energy requirements of very small animals (Parra, 1978). Nevertheless, this may be surmounted by selection of better quality foods. The nutritional benefits from fermentation to the vitamin, nitrogen, and water economy of the animal may be important also in many situations.

The New World porcupines (Erethizontidae) are partly arboreal and include leaves in their diet. One member, *Erethizon dorsatum*, has been investigated in more detail than the other arboreal rodents.

The cecum is only moderate in size and the mean cecal weight found was 6 percent of the total body weight, with the pH of the contents being 6.3 at the blind tip (Johnson and McBee, 1967). High concentrations of VFA's were present in cecal contents and 83 percent were absorbed directly from the organ. The composition of these VFA's was 74, 12, and 14 percent respectively of acetic, propionic, and butyric acids, values similar to other gut fermentations. It was calculated on average that they would supply 16 percent of the maintenance energy of porcupines, although the values obtained ranged from 5.5 to 33 percent of this energy requirement. Large numbers of bacteria were found also in porcupine cecal contents.

The porcupine is rarely, if ever, coprophagic; thus, the cecal microorganisms themselves are probably of little direct nutritional value. It was suggested that cecal fermentation may be of greatest importance during winter when the food range of these animals is most limited (Johnson and McBee, 1967).

Conclusion

There are many gaps in our knowledge of arboreal folivore nutrition and digestion of leaves. Ignorance of natural diets is due largely to problems of observing animals in a forest environment. The overall lack of detailed scientific studies is partly the result of a scarcity of experimental specimens. Scarcity of zoological specimens is also common. These deficiencies are due mainly to the great difficulties of adapting these animals to conditions of captivity (Roberts and Collins, 1978). Often, failures may be due to unavailability of suitable foods, but failure to appreciate the fundamental differences inherent in fermentative digestion has doubtless been involved in many cases. Such lack of understanding would be particularly pertinent to animals dependent upon a fore-stomach fermentation. The appreciation that leafy material constitutes food to an animal with a fermentative digestion, and that high starch materials are not necessarily more beneficial, is fundamental to this understanding. In the literature there are many reported attempts to adapt these difficult subjects to cereal and other high-starch diets. Sudden dietary changes of this type can upset the delicately balanced microbe-host interrelationships and ensure the failure of such endeavors. In ruminants, the deleterious effect of sudden change from fiber to grain diets are well known; doubtless similar effects are produced in other herbivorous animals.

Problems in adapting members of the Colobinae to conditions of captivity have been universal. At the National Center for Primate Biology, appreciation of the nature of the digestive processes in 2 *Presbytis* species, led to the novel use of fresh alfalfa in the diet of these monkeys (Bauchop and Martucci, 1968). This ruminant foodstuff was eaten eagerly by *Presbytis*, and its use resulted in successful adaptation.

Tree sloths, indriid primates, and certain New World monkeys also have proved difficult subjects to adapt. Better understanding of their nutrition will assist in overcoming these difficulties.

Summary

Herbivorous animals digest complex plant materials by means of bacterial fermentation in specially modified portions of the foregut or hindgut. Details of these processes were established first in ruminants where they have been studied extensively. The resulting concepts of ruminant digestion have assisted in understanding the functional importance of gut anatomy in other herbivorous animals. This knowledge has been used to evaluate mechanisms of leaf-digestion in arboreal folivores.

Evidence is presented for important foregut fermentations in colobid monkeys, tree sloths, and tree kangaroos. Lack of detailed information prevents conclusions on the function of gastric modifications in New World monkeys.

Based mainly on anatomical and dietary considerations, evidence is reviewed for important hindgut fermentations in primate indriids, *Lepilemur*, New World monkeys, flying lemurs, marsupial phalangers, tree hyraxes, and rodents. In this group of animals the possible value of coprophagy as a digestive mechanism has been discussed.

Bacterial fermentation can benefit the energy, nitrogen, vitamin, and water economy of an animal and result in profound changes in physiology and biochemistry. These aspects of fermentative digestion have been considered also in arboreal folivores.

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Comparison of Foregut and Hindgut Fermentation in Herbivores

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Introduction

The structural polymers of plants constitute the most abundant source of energy from primary producers. Higher animals cannot utilize these products directly owing to lack of the enzymes needed to hydrolize them, and only through association with bacteria can higher animals make use of structural polysaccharides. The alimentary tract of vertebrates is a site which seems particularly well fitted for the growth of microbial symbionts. All animals probably harbor bacteria, and frequently also protozoa, in their digestive tract, and these microorganisms are in many cases of benefit for the nutritional processes of the host. The benefit of the host, in general, depends on the structure of the digestive tract and on the nature of feed eaten.

Generally speaking, in the process of fermentation occuring in herbivores the following end-products are formed: volatile fatty acids (VFA) + carbon dioxide + methane + microbial cells. Methane and carbon dioxide are of no value to the host and are considered excretion products. VFA and microbial cells can be utilized by the host and the comparative magnitude of production and utilization of these products by herbivores with foregut and hindgut fermentation will be the main concern of this review.

The magnitude of any biochemical change brought about in the alimentary tract by microorganisms depends on several factors (Howard, 1967):

(1) the capacity of the alimentary canal;
(2) the concentration of microbes in the suspension, and
(3) the metabolic activity of the individual organisms.

The microbial population requires from the host a set of conditions in order to express its maximum activity. Some of these conditions are: anaerobiosis, closely controlled temperature of the digesta, retention of digesta, buffering capacity, continuous removal of end-product, supply of substrate at a given rate, etc. More important than all of the above-mentioned factors are the quality and quantity of the diet selected by the host.

Those animals with diets consisting solely or mainly of plant parts are considered to be vegetarians. Depending on their dietary habits they could be further classified as frugivores, granivores, folivores, and herbivores.

Plant tissues vary greatly in their chemical composition and availability. The main characteristic of a herbivore's diet is the predominance of structural carbohydrates (cellulose and hemicellulose) and related polymers (lignin).

Two main ways in which plants protect their leaves against herbivores and folivores are: structural, by increasing thickness of cell walls, and chemical, by depositing toxic secondary compounds in them. Toxic compounds are generally more abundant in the less fibrous plant tissues (Kingsbury, 1964; Levin, 1976; McKey, 1974).

The origin and main function of secondary compounds is still debated (Seigle and Price, 1976; Swain, 1974;). Freeland and Janzen (1974) recently reviewed the strategies used by mammals to cope with secondary compounds. There are 2 main mechanisms of detoxification; the microsomal enzymes and the microbial population of the gut. It should be noted that folivores, as opposed to terrestrial grazers, select their diets from plant tissues which are higher in secondary compounds and lower in fiber content.

Herbivores and folivores can be classified into 2 broad categories according to their digestive strategy and the part of the gut which is enlarged to accommodate microbial fermentation.

(1) Those animals with an enlarged foregut, which is the main site of microbial activity. In this case, microbial fermentation precedes gastric-intestinal digestion. This type of arrangement is present in several groups of animals as described by Moir (1968). The most conspicuous representatives of this group are the ruminants, among them: cattle, sheep, goat, giraffe, deer, antelopes, etc. Because of their direct economic importance, domestic ruminants are the most extensively studied herbivores. Other important representatives include, camelids from both the Old and New World, suiforms like hippos, macropod marsupials, sloths, and leaf-eating monkeys (see Bauchop, 1978).

(2) Those animals with an enlarged hindgut, in which gastric intestinal digestion of the diet occurs before microbial fermentation. This arrangement is present in a wide variety of animals, but is by far less understood than the ruminantlike digestion which takes place in the foregut. Some of the most important representatives of this group include equines, tapirs, and rhinos, rabbits and hares, capybara and smaller rodents, hyrax, and elephants. A group of leaf-eating primates have an enlarged cecum and colon (see Hladik, C. M., 1978). It is possible that lower vertebrates like iguanas and turtles also belong to this group (see Rand, 1978).

This classification does not imply that in a given animal there is only one site of microbial fermentation, since in ruminants there is considerable microbial activity in the cecum and colon, and in the horse, hamster, and rabbit there is significant fermentation in the stomach (Alexander and Chowdhury, 1958a; Alexander and Davies, 1963).

Capacity of the Gut

One of the main characteristics of herbivores is the large storage capacity of their gut as compared with omnivores and carnivores. This is undoubtedly related to the bulky nature of their diet and to the need of retaining the digesta for the relatively slow process of fermentation.

Parra (1973) has reviewed the values of G.I.T. content in herbivores and folivores (Table I). Most of the original determinations of gut capacity were obtained by filling the gut with water to a certain pressure. Warner and Flatt (1965) have discussed the errors involved with this technique.

There are considerable differences within species and within herbivore taxa, but the differences do not indicate any specific tendency in gut capacity for animals of comparable size with foregut versus hindgut fermentation strategies.

The total gut capacities were plotted on a log-log-scale, against body weights of the animals, as were weights of fermentation contents (rumen + cecum + colon in foregut fermentation and cecum-colon in hindgut fermentation) to compare strategies, and to establish the power function related to gut capacity and weight. There were no major differences in gut capacity (Figure I) or fermentation contents (Figure

Table 1.—Wet contents of gastro intestinal tract (G.I.T.)*

Animal	*Body wt. kg*	*Total digesta*		*Fermentation contents*		*Author*
		% BW	*g/Kg$^{.75}$*	*% BW*	*g/Kg$^{.75}$*	
FOREGUT FERMENTATION						
Cattle	546.0	13.1	630	10.0	484	Nevens, 1928
Cattle	532.0	17.2	839	14.3	697	Makela, 1960
Cattle	517.0	16.9	803	13.8	656	Makela, 1956
Cattle	371.0	18.0	791	14.4	633	Ewing, 1918
Cattle	273.0	23.9	972	17.8	728	Elsden, et al., 1946
Zebu	484.0	9.0	423			Ledger, 1968
Zebu	298.0	11.7	487			Ledger, 1968
Zebu	241.0			16.0	630	Hungate, et al., 1959
Buffalo	753.0	15.2	797			Ledger, 1968
Eland	519.0			11.9	567	Hungate, et al., 1959
Eland	508.0	13.5	641			Ledger, 1968
Water Buck	209.0	14.0	533			Ledger, 1968
Wildebeest	200.0	17.5	658			Ledger, 1968
Oryx	169.0	14.2	513			Ledger, 1968
Kongoni	134.0	13.7	467			Ledger, 1968
Topi	117.0	15.9	524			Ledger, 1968
Lesser Kudu	92.0	9.2	286			Ledger, 1968
Kob	77.0	14.7	437			Ledger, 1968
Grant's Gazelle	51.0	11.9	316			Ledger, 1968
Grant's Gazelle	49.0			10.0	265	Hungate, et al., 1959
Impala	49.0	10.7	285			Ledger, 1968
Gerenuk	31.0	8.9	212			Ledger, 1968
Thomson's Gazelle	20.0	12.8	274			Ledger, 1968
Thomson's Gazelle	24.0			14.7	326	Hungate, et al., 1959
Suni	3.70			9.1	126	Hungate, et al., 1959
Sheep	58.0	19.1	527	15.6	431	Boyne, et al., 1956
Sheep	82.0	12.1	366	10.1	304	Elsden, et al., 1946
Hippopotamus	1384.0	21.9	1335			Ledger, 1968
Camel	522.0			12.3	588	Hungate, et al., 1959
Camel	338.0			17.9	769	Hungate, et al., 1959
Langur Monkey	7.30			13.0	213	Kuhn, 1964
Langur Monkey	5.40			17.4	265	Bauchop and Martucci, 1968
Wallaby	4.50	5.6	82			Lintern-Moore, 1973
Quokka	3.16			7.7	103	Moir, et al., 1956
Sloth	4.70			15.3	225	Hartman, 1959
Sloth	3.86			14.8	209	Wislocki, 1928
HINDGUT FERMENTATION						
Elephant	2337.0			11.9	827	Hungate, et al., 1959
Horse	426.0	16.4	746	11.2	508	Elsden, et al., 1946
Wart Hog	74.0	13.4	393			Ledger, 1968
Capybara	40.5	16.5	414	12.7	319	Parra and Gonzalez, 1972
Rabbit	3.5	7.2	98	4.2	57	Slade, 1970
Rabbit	1.63	14.6	165	6.8	78	Carmichael, et al., 1945
Rabbit	1.17	17.7	184	8.6	89	Elsden, et al., 1946
Iguana	2.85	7.6	98	6.3	82	Parra, unpublished results
Guinea pig	0.683	8.0	73	6.3	57	Slade, 1970
Vole	0.0264			6.0	25	McBee, 1970
Pig	20.0	10.4	222	4.6	97	Elsden, et al., 1946
Rat	0.189	3.1	21	1.6	9	Elsden, et al., 1946

*The values shown correspond to gut fill of animals fed roughage as the main component of their diet sacrified within 6 hours after the last feeding.

Source: Parra, R., 1973

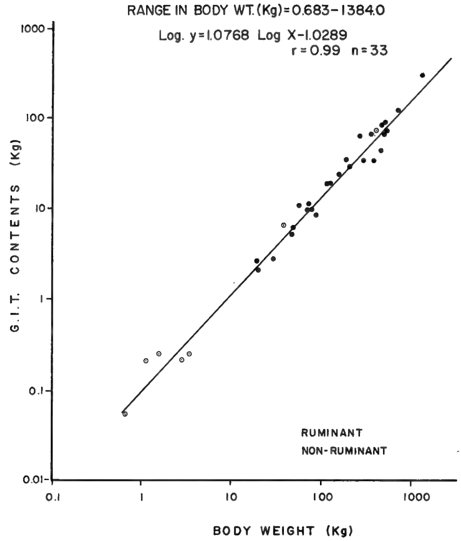

Figure 1. Log-log plot of values shown in Table 1 for total capacity of the gut (kg) and body weight (Kg) exponential equations relating total capacity of the gut (Y) and body weight (W):

All herbivores	$Y = 0.0936\ W^{1.0768}$
Ruminant	$Y = 0.0896\ W^{1.0475}$
Non-ruminant	$Y = 0.1020\ W^{1.0799}$

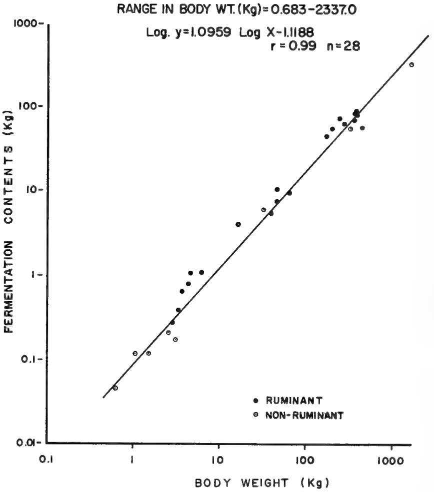

Figure 2. Log-log plot of values shown in Table 1 for fermentation contents (Kg) and body weight (Kg) exponential equations relating fermentation contents (Y) and body weight (W):

All herbivores	$Y = 0.0760\ W^{1.0959}$
Ruminant	$Y = 0.1050\ W^{1.0453}$
Non-ruminant	$Y = 0.0633\ W^{1.0922}$

2) between herbivores with foregut fermentation and with hindgut fermentation. This conclusion should not be extrapolated beyond the values studied and should be approached with caution, since they represent *wet* gut contents from animals of different stages of maturity and physiological conditions. For both ruminant and nonruminant herbivores, as size increases, the relative capacity of the gut, as percent B. W., will also increase (Table 2).

If we accept that metabolic rate is proportional to the three-fourth power of body weight (Kleiber, 1961) in inter species comparisons, it is obvious that smaller animals will have to turn over their fermentation contents at a higher rate, both because of:

(1) disproportionate energy demands on fementation contents and,

(2) the disproportionately smaller relative amounts of food-stuff available for fermentation. That smaller herbivores need relatively higher rates of turnover of fermentation contents implies widely different strategies, both behaviorally and nutritionally, in order to meet their energy requirements, this being true either for herbivores with foregut or hindgut fermentation sites. The animals are faced with a paradox, that is as their size is decreased their energy requirements per unit weight are increased and their fermentation contents per unit weight are decreased (Table I).

Table 2.—Theoretical values of gut contents and fermentation contents, in a wet basis, for ruminant and nonruminant herbivores together (from equations given in Figures 1 and 2).

Body weight (Kg.)	*Total digestive capacity (% of Body Wt)*	*Fermentation contents (% of Body Wt)*
0.1	7.8	6.0
10.0	11.1	9.5
50.0	12.3	11.0
100.0	13.3	11.8
500.0	15.1	13.8
1000.0	15.9	14.7
5000.0	18.0	17.2

Table 3.—Relative capacity of different compartments of the G.I.T. as percent of total wet digesta weight.

Animal	*Rumen-Reticulum*	*Omasum*	*Stomach abomasum*	*Small int.*	*Cecum*	*Colon*	*Rectum*
Cattle	78-69	12-6	4-2	10-7		8-5	
Sheep	73-70	2-1	8-6	9-8	8	4-3	2
Horse			8	16	15	53	8
Capybara			11	6	74	6	3
Rabbit			42-34	10-8	49-38	9-4	3
Guinea Pig			23	11	45	21	
Iguana			11	5	62	22	
Rat			11	29	33	10	17
Pig			34	18	16	28	4
Man[1]			17	66	—	17	—
Cat[1]			69	15	—	16	
Dog[1]			63	23	1	13	

Calculated from values in Table 1. Extreme values are shown when more than one report was found.

[1] Hill, 1970.

In comparing a series of animals ranging from ruminant through nonruminant herbivores and omnivores (Table 3), the differences between ruminant and nonruminant herbivores are clearly seen. There is reversal in the relative capacities of foregut and hindgut between ruminant and nonruminant herbivores. Relative midgut capacities are considerable in omnivores, while the glandular stomach of carnivores has considerable capacity.

Rate of Passage

Fermentation of the more refractory components of the diet is a slow process requiring retention of the food in a given segment of the G.I.T. Herbivores have longer retention times than omnivores and carnivores. Blaxter (1963) states, that maximal digestion occurs only if the passage of food is subjected to delay at those sites where microbial action takes place and, also, that when rate of passage is increased the depression in apparent digestibility is greater for poor quality foods than for those of high quality. It is evident that any effect of rate of passage on digestibility is going to be mainly on the fiber components of the diet, because fibrous components are those most affected by microbial action.

Rate of passage can be influenced by several factors, such as capacity and architecture of the gut, intake level, composition of the diet, rate of digestion, ration preparation, age, disease, etc. (Balch, 1961; Balch and Campling, 1965; Church, 1969).

Mertens (1973), using values from sheep and cattle, found that body weight was the variable showing the highest correlation (negative) with rate of passage.

There are thus difficulties in interpreting measures of passage of the digesta. Some of the difficulties related to the technique used have been discussed elsewhere (Kotb and Luckey, 1972).

It is generally believed that nonruminant herbivores have shorter retention times than ruminants (Moir, 1968). The differences in transit time among herbivores, omnivores, and carnivores are generally marked (Table 4) with a general decrease in time of passage in the series from ruminants through herbivores with hindgut fermentation and omnivores to carnivores. Rates of passage generally increased as herbivores become smaller. Hindgut fermentors have faster rates of passage, as compared to foregut fermentors (ruminants), even for large-size animals, like elephants and horses. These values probably overestimate the actual rate of passage of fibrous diets in these large hindgut fermentors, but on the other hand a faster rate of passage might be partly due to a lack of effect of particle size as a component of passage, since mastication is usually very efficient in hindgut fermentors (Jennings, 1965; Escobar and Gonzalez, 1972).

Mertens (1973) argues that if ruminal fill is proportional to body weight and energy demand is proportional to metabolic weight ($W^{.75}$), one should expect the smaller ruminant to need a faster rate of passage to obtain its energy requirements. Thus the rate of passage on cattle would be approximately 75 percent that of sheep. His results suggest that rate of passage for sheep may be faster than that for cattle. We can extend this argument to herbivores in general

Table 4.—Time (hrs) of appearance in feces of 5 percent and 95 percent of marker[1].

Animal	*Hours* *5%*	 *95%*
Foregut fermentation		
Cattle	20	120
Sheep[4]	18	93
Sloth[2]	?	200–300
Kangaroo	22	60
Hindgut fermentation		
Horse	15	60
Elephant	22	60
Capybara[3]	8	84
Capybara[4]	12	88
Rabbit (with coprophagy)	5	50
Rabbit (without coprophagy)	5	30
Tortoise	170	880
Omnivore		
Pig	10	40
Rat	4	24
Chicken	2	14
Goose	2	8
Turkey	2	14
Carnivore		
Fox	3	12
Mink	2	7

[1] Data compiled by Hintz, 1973.

[2] Estimated from Goffart, 1971, and Montgomery and Sunquist, 1978.

[3] Estimated from Ojasti, 1973.

[4] Gonzalez, E., et al., 1976.

(Table 4), with the advantage of dealing with a much wider range in body weight. Nevertheless we have some dramatic exceptions like the values for the tortoise and those for the sloth (Goffart, 1971; Montgomery and Sunquist, 1978).

Microbiology of the Gut

Conditions in the hindgut are similar to those found in the rumen, allowing an active microbial population to develop. Temperature of digesta are considered to be similar throughout the alimentary tract. The degree of anaerobiosis (eH) in cecal contents (Bergmein, et al., 1945) is similar to that in rumen contents (Hobson and Howard, 1969). Buffering capacity of the hindgut seems to be as efficient as that of the rumen; pH of cecum and colon contents are very close to neutrality in horse, pig, guinea pig (Alexander, 1962 and 1965), beaver (Hoover and Clarke, 1972) porcupine (Johnson and McBee, 1967), and capybara (Parra and González, 1972). The ileal "liquor" of horses and pigs resembles in its electrolytic composition ruminant saliva and possibly serves a similar function with respect to buffering the acids formed during fermentation in the hindgut of these animals (Alexander, 1962); evidence from rabbit and guinea pig (Alexander, 1965) seems to support the same conclusion.

Trying to review comparative microbiology of the gut of herbivores is a major task. I shall attempt only to make general comments on similarities and differences. Almost all the work has been done on domestic ruminants, work on nonruminant herbivores being almost nonexistent. There are several extensive reviews, some stressing a comparative approach (Bryant, 1959 and 1970; Eadie and Howard, 1963; Giesecke, 1970; Hobson, 1963 and 1969; Howard, 1967; Hungate, 1963, 1966, and 1968; Jayne-Williams and Coates, 1969; Oxford, 1964; Riis and Jackobsen, 1969; Cuthbertson and Hobson, 1960).

According to Giesecke (1970) the densities of rumen microbial populations depend mainly on:

(a) the availability of food and its quality,
(b) the feeding type, and
(c) the physiological state of the animals.

Hungate, et al. (1959) found counts of total and cellulolytic bacteria in several tropical wild ruminants to be comparable to those found in domestic ruminants. Giesecke (1970) also found comparable counts when studying European wild ruminants, although wide variations were found owing to feeding behavior and season of year. The largest variation was found with protozoa populations. In both cases, not only were the counts similar to those of domestic ruminants, but the types of microorganisms were similar as well. Microscopial observations of the quokka's (macropod marsupial) "rumen-like" forestomach showed a dense bacterial population very similar to that of the sheep's rumen under similar conditions; approximately 15 different types of bacteria were present (Moir, et al., 1956). In the large and complex stomach of the langur monkey (subfamily Colobinae), high numbers of bacteria, but no characteristic protozoal flora were found (Bauchop, et al., 1968). Viable anaerobic bacteria ranged from 7×10^{11} to 1×10^{12}/g of dry matter and cellulolytic bacteria counts of 8×10^7–4×10^8/g of dry matter.

It seems evident that all herbivores harbor comparable numbers of bacteria in their expanded compartments of the gut, furthermore it seems that the type of microorganisms are very similar. Davies (1964) examined smears of large intestine contents from horses and found many morphological types similar to those present in the rumen. Two gram-negative rods, resembling member of genus *Bacteroides*, 1 gram-negative sporeforming bacteria, and several of the unidentified cellulolytic bacteria were isolated, all resembling similar ones from the rumen. Later, Davies (1965) identified 4 types of cellulolytic bacteria, occurring in horse cecum, cecum and colon of rabbit, guinea pig, and pig. Alexander, et al., (1952) isolated gram-positive streptococci, similar to *Streptococcuss bovis*, from the horse colon. A ciliate protozoa population somewhat similar to that found in the rumen has been shown in horse colons (Adam, 1951). Studies made by Alexander and Davies (1963) and Alexander and Chowdhury (1958a) have shown high concentrations of VFA in the stomach of horses and rabbits and appreciable numbers of lactate-forming streptococci and lactobacilli present.

Bacteroides species (Ruebner and McLaren, 1958) and cellulolytic bacteria similar to *Ruminococcus* (Hall, 1952) have been found in rabbit cecum. Bonnafous and Raynaud (1968) have reported counts of 14.5×10^{11}/g of dry matter in cecal contents.

McBee (1970) has obtained culture counts of about 300×10^{9}/g of dry matter from cecum contents of vole and deer mouse. Hungate, et al. (1959) found large counts of both cellulolytic and total bacteria in cecum and colon of the elephant. According to Buisson (1923) several species of ciliated protozoa are found in the large intestine of the elephant, rhinoceros, tapir, guinea pig, chimpanzee and gorilla. Thurston, et al. (1968) found numerous ciliate protozoa in the chambers of the hippopotamus stomach.

The microbial population in a herbivore gut is mainly the consequence of its diet at any one time, both with respect to composition and numbers. So it does not seem probable that differences between ruminant and nonruminant herbivores, with regard to the efficiencies with which they digest the diet could be accounted by intrinsic differences in the microbial population. On one hand, we find similar general characteristics in the fermentation sites of both types of herbivores and, on the other hand, we must realize the microbes' tremendous capacity to adapt to changing environments (meaning mainly substrates available). If we assume one viable microbial mutation in each 10^{8} cells (Luckey, 1970), a bacterial count of 10^{11}/g of dry fermentation content and a fermentation content of 10^{4} g (gross estimate for a 400 Kg animal), then at any given time that animal harbors about 10^{7} newly mutated bacteria $[(10^{11} \times 10^{4})/10^{8} = 10^{7}]$. Coupled with a generation time of about 1 hour, this rate of mutation gives the gut's bacterial population a great potential for change.

Digestive Ability

The digestive ability of an animal is most commonly measured by digestibility trials in which some components of feed and feces are measured and compared. The Weende system of proximate analysis has been generally used for this purpose, although it is inconvenient to use, particularly regarding the separation of carbohydrates. Recently a comprehensive system of feed analysis has been proposed (Van Soest, 1966 and 1967) which essentially partitions the feed according to the availability into 2 main components: *Cell wall*, grouping all fiber components (cellulose, hemicellulose, and lignin), and *cellular contents*, including the cytoplasmatic components (sugars, starch, protein, lipids, etc.).

For the purpose of the following discussion I will deal separately with cellular contents and cell-wall components.

Cellular contents

A quantitative theory for the relationship between digestibility and feed and fecal composition has been developed by Lucas, et al. (1959 and 1961). In essence the theory states that when a chemical fraction in a feed satisfies certain critical restrictions (i.e., the fraction is a nutritive entity) there is a linear relationship between the digestible amount of the fraction in the feed (percent of fraction in feed × digestibility coefficient) and the amount in the feed (percent fraction in feed). In this linear relationship the regression slope is an estimate of the true digestibility and the intercept estimates the endogenous excretion of the component.

The data available show no consistent differences among ruminant and nonruminant herbivores in digestibility of soluble fractions (Table 5). Only ether extract in the horse seems to have a low digestibility. This might be related to the imprecision in the determination or to the fact that lipase enzyme seems to be missing from ileal juice of the horse (Alexander and Chowdhury, 1958b).

Results obtained by Van Soest (1967) for cattle and Parra, et al. (1972) for sheep show no effect of lignification on digestibility of cellular contents, the effect of lignin being restricted to the fiber components. Similar results were obtained by Fonnesbeck (1969) in horses. This evidence conflicts with the hypothesis that the availability of protein and other cell components is lowered by entrapment in lignified cells (Drapala, et al., 1947; Bell, 1971). However, less available carbohydrate was digested enzymatically by horses as the cell-wall content of the ration increased (Argenzio and Hintz, 1971), and fiber con-

Table 5.—Values of true digestibility and endogenous excretion for different fractions (Lucas test).

Animal	*Fraction*	*Slope**	*Intercept**	*Author*
Cattle and sheep	NDS[1]	98	−12.9	Van Soest, 1967
Sheep	NDS	83	−10.7	Combellas, et al., 1971
Horse	NDS	100	−12.7	Fonnesbeck, 1969
Cattle	Protein	92	−3.87	Lucas, 1959
Sheep and goats	Protein	95	−3.72	Lucas, 1959
Sheep	Protein	80	−1.60	Combellas, et al., 1971
Horse	Protein	80	−3.30	Slade and Robinson, 1970a
Horse	Protein	90	−2.61	Lucas, 1959
Horse	Protein	82	−3.20	Fonnesbeck, 1969
Capybara	Protein	87	−2.50	Gonzalez and Parra, unpublished results, 1972
Guinea pig	Protein	94	−5.50	Slade and Robinson, 1970a
Rabbit	Protein	92	−5.00	Slade and Robinson, 1970a
Swine	Protein	96	−4.08	Lucas, 1959
Cattle	Ether extract	100	−1.19	Lucas, 1959
Sheep and goat	Ether extract	95	−0.93	Lucas, 1959
Horse	Ether extract	70	−0.68	Lucas, 1959
Horse	Ether extract	75	−1.2	Fonnesbeck, 1969
Swine	Ether extract	99	−1.10	Lucas, 1959
Horse	Soluble CHO	100	−5.1	Slade and Robinson, 1970a

* From equation $Y = -a + bx$
a = endogenous fraction in g/100 g intake
b = true digestibility in %
[1] Neutral Detergent Solubles.

tent depressed the digestibility of all other nutrients to a much greater extent in the horse than in ruminants (Olsson and Ruudvere, 1955; Olsson, 1969). This lowering of digestibility of other nutrients as fiber increases might be partly due to the fact that as fiber increases, the soluble components of the diet (protein, starch, fat) decrease and usually the level of intake is also reduced, producing a marked reduction in the intake of solubles, followed by a logical drop in the *apparent* digestibility of the fraction.

It can be concluded that there are no major differences in the digestive ability of ruminant and nonruminant herbivores, regarding cellular contents. Cellular contents are almost entirely available to the animal regardless of the lignin content of the fiber. It is evident that sites and means of digestion of cellular contents can vary greatly in the two types of herbivores (Table 6). In ruminants most of the cellular contents are fermented before reaching the site for enzymatic digestion in the midgut. In nonruminant herbivores the tendency is for enzymatic digestion to occur first and to predominate with a consequent higher efficiency in the utilization of cellular contents (Argenzio and Hintz, 1971).

Cell-wall components

It is difficult to make valid comparisons of the ability of various herbivores to digest fiber components. The number of comparative trials, in which different animal species are fed the same diet are limited, and even the validity of this approach is questionable. There have been several reviews (Hintz, 1969b; Vander Noot and Trout, 1971; Olsson, 1969) comparing domestic ruminants with horses and rabbits. There is a total lack of information regarding other nonruminant herbivores. All of the reviews conclude that nonruminant herbivores show lesser ability to digest fiber components than ruminants, but no satisfactory explanations are offered.

For ruminants, lignin is the most important factor in reducing digestibility of the fiber (Van Soest, 1967; Deinum, 1971; Parra, et al., 1972).

In general (Figure 3), nonruminants digest fiber to a lower extent than ruminants. However, the superiority of ruminants in digesting fiber is marked only when considering nonruminant herbivores of small size (rabbit, vole, etc.). Large nonruminant herbivores (horse, pony, zebra, capybara) digest fibrous food nearly as well as ruminants.

Table 6.—Site of digestion (as percent of total digestion).

Animal	*Diet*	*Chemical fraction*	*Fore gut***	*Middle gut*	*Hind gut*	*Author*
Sheep	Hay	Pentosans	71.0	0	29.0	Marshall, 1949
Sheep	Hay	Cellulose	70.0	0	30.0	Gray, 1960
Sheep	Hay ad-lib	Cellulose	90.0		10.0	Waldo, 1970
Sheep	Hay ad-lib	Hemicellulose	69.0		31.0	Waldo, 1970
Sheep	Hay-chopped Low intake	Cellulose	94.3	2.7	3.0	Beever, et al., 1972
Sheep	Hay-pellet Low intake	Cellulose	76.9	6.0	17.1	Beever, et al., 1972
Sheep	Hay-chopped Hi intake	Cellulose	92.7	2.0	5.3	Beever, et al., 1972
Sheep	Hay-pellet Hi intake	Cellulose	72.8	−2.4	29.6	Beever, et al., 1972
Sheep	Hay-chopped Low intake	Hemicellulose	91.3	0.8	7.9	Beever, et al., 1972
Sheep	Hay-pellet Low intake	Hemicellulose	68.0	8.8	23.2	Beever, et al., 1972
Sheep	Hay-chopped Hi intake	Hemicellulose	84.5	7.8	8.7	Beever, et al., 1972
Sheep	Hay-pellet Hi intake	Hemicellulose	65.0	1.4	33.6	Beever, et al., 1972
Sheep	Alfalfa hay	NDF	86.8		13.2	Hogan and Weston, 1967
Sheep	Wheaten hay	NDF	81.2		19.8	Hogan and Weston, 1967
Ponies	Hay:grain 1:0	NDF		29.1*	70.9	Hintz, et al., 1971a
Ponies	Hay:grain 3:2	NDF		23.0*	77.0	Hintz, et al., 1971a
Ponies	Hay:grain 1:4	NDF		28.0*	72.0	Hintz, et al., 1971a
Capybara		Cellulose		15.0*	85.0	González and Parra***
Ponies	Hay:grain 1:0	Nitrogen		58.3*	42.7	Hintz, et al., 1971a
Ponies	Hay:grain 3:2	Nitrogen		52.8*	47.2	Hintz, et al., 1971a
Ponies	Hay:grain 1:4	Nitrogen		55.6*	44.4	Hintz, et al., 1971a
Horse	Corn diet	Nitrogen		6.5*	93.5	Reitnour, et al., 1969
Horse	Oat diet	Nitrogen		30.7*	69.3	Reitnour, et al., 1969
Horse	Barley diet	Nitrogen		31.5*	68.5	Reitnour, et al., 1969
Ponies	Hay:grain 1:0	Available CHO		50.8*	49.2	Hintz, et al., 1971a
Ponies	Hay:grain 3:2	Available CHO		55.3*	44.7	Hintz, et al., 1971a
Ponies	Hay:grain 1:4	Available CHO		72.0*	28.0	Hintz, et al., 1971a
Sheep	Alfalfa	Sol. CHO	82.0			Hogan and Weston, 1967
Sheep	Wheaten	Sol. CHO	89.0			Hogan and Weston, 1967
Sheep	Hay-chopped Low intake	O.M.	64.4	29.4	4.2	Beever, et al., 1972
Sheep	Hay-pellet Low intake	O.M.	56.2	33.7	10.1	Beever, et al., 1972
Sheep	Hay-chopped Hi intake	O.M.	61.9	32.7	5.4	Beever, et al., 1972
Sheep	Hay-pellet Hi intake	O.M.	57.3	26.0	16.7	Beever, et al., 1972
Sheep	Concent. Diet	D.M.	69.0	17.0	14.0	Topps, et al., 1968
Sheep	Hay	D.M.	67.0	22.0	11.0	Topps, et al., 1968
Ponies	Hay:grain 1:0	D.M.		33.0*	67.0	Hintz, et al., 1971a
Ponies	Hay:grain 3:2	D.M.		34.7*	65.3	Hintz, et al., 1971a
Ponies	Hay:grain 1:4	D.M.		45.4*	54.6	Hintz, et al., 1971a

* Relative digestion of both foregut and middle gut (as percent of total).

** Includes rumen, reticulum, omasum, and abomasum.

*** Unpublished information, 1972.

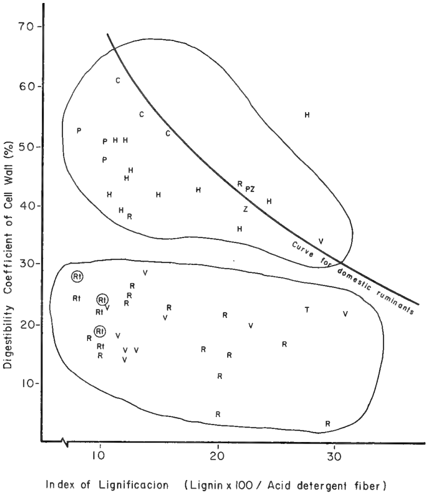

Figure 3. Relationship between lignification (lignin × 100 ÷ acid detergent (fiber) and digestibility of cell-wall components. Forage was the only or main component of the diet in all cases. The meaning of symbols and the source of the data are as follows:

H	Horse. Fonnesbeck (1968); Hintz, personal communication (1973).
Z	Zebra. Hintz, personal communication (1973).
PZ	Przewalski's Horse. Hintz, personal communication (1973).
C	Capybara. González and Parra, unpublished results.
P	Pig. Keys, et al. (1970)
R	Rabbit. Ingalls, et al. (1965); Mertens, personal communication (1973); Proto (1963).
Rt	Rat. Keys, et al. (1970).
Ⓡⓣ	Rat (cecum inoculated with rumen fluid). Keys, et al. (1970).
V	Vole. Keys and Van Soest (1970); Keys, et al. (1970).
T	Tortoise. Hintz, personal communication. (1973).

Curve for domestic ruminants (Goering and Van Soest, 1970).

There are several possible factors that contribute to the differences noted above. A faster rate of passage for nonruminant herbivores would decrease digestion of fibrous food, and smaller nonruminant herbivores have the higher passage rates. Prins and Geelen (1971) and Short, et al. (1974) argue the same to explain the differences between large and small ruminants in their ability to digest fiber.

The importance of retention time of the digesta for obtaining a maximum of the potential available in the fiber is brought into focus by Figure 4. Both Figure 4 and Table 7 show that different sources of fiber require different retention times for extracting maximum benefit from them.

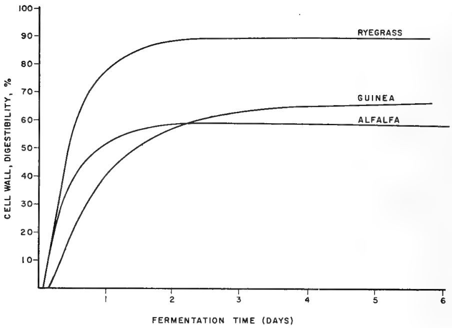

Figure 4. Curves showing the progress of fiber digestion with time. These values were obtained by in-vitro methods, using inoculum from a cow's rumen. They represent a temperate grass (Ryegrass), a tropical grass (Guinea), and a legume (Alfalfa).

Another possible contribution to a lower fiber digestion in nonruminant herbivores might be based on the composition of the substrate reaching the fermentation site. In the case of hindgut fermentation the substrate reaching the cecum and colon has been deprived of most of the soluble components, because the enzymatic digestion occurs ahead of them, leaving only the more refractory material which would have a slower digestion rate. In addition, nutrients essential for maximal microbial activity might be deficient in the substrate because they were absorbed before reaching the hindgut (Mehren and Phillips, 1972).

On the other hand, the hindgut fermentors might gain advantage through the pre-treatment of fiber with gastric pepsin at a low pH, causing a partial solubilization of the hemicellulose, acting on the hemicellulose-lignin linkage, or both. This has been observed in "in vitro" experiments with cecal fluids of capybara and horses (González and Escobar, 1975; Koller, [1974] personal communication) and "in vivo" experiments with swine and rats (Keys, et al., 1969). This pre-treatment of fiber seems also to increase its rate of fermentation (Parra, [1976] unpublished results).

Small nonruminant herbivores, which digest a lesser proportion of each unit of fiber, digest equivalent or a higher total amount of fiber per unit time due to a higher rate of turnover of digesta. If quantity and quality of forage available is not limiting, they will presumably select materials of high nutritive value which can have much faster fermentation rates.

Table 7.—In vitro dry matter digestibility (DMD) of different substrates (incubated in nylon bags inside goat's rumen).

Substrates	*Maximum DMD %*	*Time for reaching Max DMD Hrs.*	*DMD at 4 hrs., as % of max DMD*
Honeysuckle leaves	89	8	98
Mature mixed forbs	49	72	80
Immature Elbon Rye	94	32	75
Mature woody twigs	33	96	72
Mature mixed grass	57	168	27

Source: Short, et. al. (1974).

Large herbivores digest fiber to a greater extent than small herbivores; the differences between foregut and hindgut fermentors are obscured by size considerations (cf. Figure 3).

Results from our laboratory indicate no difference in digestive ability of ruminant (sheep) and nonruminant herbivores (capybara) of similar size, when fed forages (González and Parra, 1975; González and Escobar, 1975; Parra, 1976.)

Site of digestion

From the relative capacities of the different segments of the G.I.T. (Table 2) it can be predicted that in ruminant and ruminantlike animals most of the digestion will be carried out in the foregut and the opposite should occur in nonruminant herbivores. In the case of ruminants, almost all of the digestion of structural carbohydrates is carried out through fermentation in the rumen, and a major part of the soluble components of the diet are also fermented in the foregut. In nonruminant herbivores enzymatic digestion of most of the solubles occurs in the fore and middle gut and the digestion of cell-wall components is completed in the cecum and colon. This pattern can be modified to a considerable extent by manipulating the compositions of the diet or its physical characteristics in both ruminants and horses (Beever, et al., 1972; Hintz, et al. 1971a, 1971b).

The importance of hindgut fermentation in ruminants has not been established, but under certain conditions it might be more important than commonly believed, particularly in fermenting the bacterial cell wall, which is not digested in the abomasum and small intestine (Mason and White, 1971; Mason and Milne, 1971).

The contribution of foregut fermentation in some nonruminants is not understood, although, as mentioned before, it might be considerable. Another problem which is not usually appreciated in nonruminant herbivores is the fast rate of passage through fore and middle gut and its effect, if any, on the efficiency of digestion in these compartments of the G.I.T. According to Alexander (1955), digesta pass through the ileum of the horse within 3 hours after ingestion, and in capybara an estimate of turnover time for digesta in stomach and small intestine is of 2.5 hours (Parra, [1972] unpublished data).

End-products of Fermentation and Their Utilization

By far the main products of bacterial fermentation are volatile fatty acids of which acetic, propionic, and butyric are found in largest quantities. The most common way of measuring fermentation activity is to determine concentration of VFA in the contents of a portion of the gut at a given time after a meal. The concentration of VFA is an indicator of fermentation activity and has been used to estimate fermentation rates in ruminants (Giesecke, 1970; Leng, 1970). Weston and Hogan (1968) found that the total quantity of VFA in the rumen, rather than its concentration, was closely related to its production rate.

The following discussion will be restricted to VFA, its concentrations in the digesta and rate of production in ruminant and nonruminant herbivores. Most of the available information is on VFA production in the foregut of domestic ruminants, with little information on hindgut production of VFA in nonruminant herbivores. The concentration of VFA in the tract of herbivores and the proportion of the individual acids depend on several factors, such as composition of the diet, level of intake, time after last meal, physiological condition of the animal, etc. The variability caused by these factors causes great difficulty in making valid comparisons between different species.

The high concentration of VFA in the cecum of nonruminant herbivores (Table 8) indicates the importance of the hindgut as a fermentation site. Elsden, et al. (1946) showed minor differences in VFA concentrations between ruminant and nonruminant herbivores, and there are individual values for cecum-colon concentrations reaching those found in the rumen. However, the tendency is for higher VFA concentrations in animals with foregut fermentation. The shorter retention time of fibrous material in the hindgut of nonruminant herbivores particularly in the smaller animals, reduces the amount of fermenta-

Table 8.—Volatile fatty acid concentration (micro mole/g of dry digesta).

Animal	*Diet*	*Rumen or stomach*	*Ce-cum*	*Colon*	*Author*
Cattle*	variable	919 (1274-565)[1]			Church, 1969
Sheep*	variable	892 (1268-427)[1]			Church, 1969
Deer*	alfalfa + corn	816			Short, 1963
Presbytis cristatus[2]	leaves	766			Bauchop and Martucci, 1968
Presbytis entellus[2]	leaves	883			Bauchop and Martucci, 1968
Sloth (choloepus)	fruit + leaves	1156			Denis, et al., 1967
Horse	straw + mangolds		970		Elsden, et al., 1946
Horse	hay:conc. 1:0		640	260	Hintz, et al., 1971b
Horse	hay:conc. 3:2		698	296	Hintz, et al., 1971b
Horse	hay:conc. 1:4		564	160	Hintz, et al., 1971b
Rabbit	bran + oats + mangold		320		Elsden, et al., 1946
Rabbit	mixed diet, low fiber		227		Hoover and Heitmann, 1972
Rabbit	mixed diet, hi fiber		219		Hoover and Heitmann, 1972
Wild rabbit[3]	mossen and lichen		368	291	Henning, et al., 1972
Wild rabbit[4]	mossen and lichen		317	226	Henning, et al., 1972
Porcupine	natural	89	511	338	Johnson and McBee, 1967
Beaver	natural		498	419	Hoover and Clarke, 1972
Guinea pig	commercial		380		Hagen and Robinson, 1953

* For rumen content assumed: sp. gravity = 1.039
D.M. in sheep = 14%
D.M. in cattle = 12%

[1] Mena of extremes and range.
[2] Leaf-eating monkeys.
[3] Measured at daytime.
[4] Measured at nighttime.

tion and thus the ratio of VFA to gut content. In addition, the composition of the substrate reaching the cecum and colon has already been subjected to enzymatic digestion, leaving mainly the fibrous portion of the diet and little of the solubles, which are more readily fermented.

Perhaps a more convenient measure of fermentation activity would be the rate of production of acids. The difficulties associated with this measurement (Hungate, 1966; Leng, 1970) are evident by the very scanty information available. The values (Table 9) are variable, and as a whole do not seem to indicate any specific tendency for ruminants as compared to nonruminants. Perhaps the most important effect is that of body size, tending to show faster rates of fermentation in smaller animals, but again the data available lacks consistency. As animals become smaller, the relative size of their fermentation contents becomes smaller too. If a decrease in size means an increase in energy requirements and a decrease in fermentation capacity per unit of body weight, the animal will have to turn over its digestive contents faster and must increase the fermentation rate. Hungate et al. (1959) and Short (1963) have given evidence to support this point of view. This could only be accomplished by selecting a diet in which readily fermentable components will predominate. In small nonruminant herbivores, the selection of a high-quality, low-fiber diet will diminish the importance of the hindgut in supplying energy for the animal, since most of the digestion will be completed before reaching the hindgut. On the other hand, in the case of the small highly selective ruminant, most of the diet would be fermented at a very fast rate in the foregut. Microbial digestion of food invariably reduces the efficiency of utilization of digested energy by animals because of energy losses associated with methane production, heat of fermentation and poor utilization of absorbed VFA (Blaxter, 1963; Black, 1971).

From the above considerations it can be postulated that, if selection of diet is allowed, the small herbivores will be better off by having a hindgut fermentation strategy as compared to the ruminantlike type of strategy. Based on the information given above we can calculate the expected fermentation rate per gram of dry fermentation contents required to gener-

Table 9.—Fermentation rate (micromoles of VFA/g of dry digesta/hr).

Animal	*Rumen*	*Cecum*	*Colon*	*Author*
Lactating cow	240 (304–146)			Hungate, et al., 1961
Cattle (Zebu)	125	37	45	Hungate, et al., 1959
Deer	93			Short, 1963
Camel (female)	92	46	32	Hungate, et al., 1959
Camel (male)	59	69	56	Hungate, et al., 1959
Grant's gazelle	233	45	58	Hungate, et al., 1959
Thomsom's gazelle	142	42	42	Hungate, et al., 1959
Eland	70	53	53	Hungate, et al., 1959
Suni	629	79	64	Hungate, et al., 1959
Langur monkey	475			Bauchop and Martucci, 1968
Quokka[1]	135			Moir, et al., 1956
Rabbit (low fiber diet)[2]		205		Hoover and Heitmann, 1972
Rabbit (hi fiber diet)[2]		175		Hoover and Heitmann, 1972
Porcupine		184		Johnson and McBee, 1967
Pig (low fiber diet)[3]		345		Farrell and Johnson, 1970
Pig (hi fiber diet)[3]		271		Farrell and Johnson, 1970

[1] Assume 15% D.M. in forestomach content.

[2] Assume 20% D.M. in cecal content.

[3] Assume 15% D.M. in cecal content.

Table 10.—Theoretical calculations of the fermentation rate needed to supply the energy requirements for maintenance.

Body Wt. (Kg)	*A Fermentation contents (FC)* (Kg)*	*B Energy requirements** (Kcal/day)*	*B ÷ A × 1000 Kcal/g of FC*	*Fermentation rate*** mole/g dry FC/hr*
0.1	0.006	24.9	4.20	4137
1.0	0.076	140.0	1.80	1773
10.0	0.950	786.8	0.80	788
100.0	11.800	4424.0	0.40	394
500.0	69.000	14798.0	0.20	197
1000.0	147.000	24892.0	0.17	167

* From: $Y = 0.0760W^{1.0959}$.

** From: Maintenance Requirements = $2 \times 70W^{.75}$.

*** Assume: % DM in Fermentation Contents = 15% 290 Kcal/mole of VFA mixture.

ate the energy needed daily to meet maintenance requirements (basal heat expenditure + activity). From the values shown in Tables 9 and 10 we can postulate that for animals below 10 kg of body weight a foregut fermentation strategy seems difficult to maintain (if all energy is to be derived from VFA) and hindgut fermentation is a more viable alternative.

There are several arboreal folivores (sloth, leaf-eating monkeys, leaf-eating marsupials) and a few herbivores of small size (1-5 kg of body weight) that challenge the above generalization. Arboreal folivores have limitations on body size determined by the environment in which they forage. It can be argued that the limitations imposed by the abundance of secondary compounds in their diet makes a foregut fermentation a more desirable strategy, as it has been postulated that it is a more efficient detoxification mechanism than the hindgut fermentation strategy (Freeland and Janzen, 1974; Foose, 1974), even though foregut fermentation is not the best alternative for meeting the energy demands of small-size vegetarians.

In some of the small folivores, especially in the case of the sloth, a group of specific features are also present:

(a) low metabolism and hence low maintenance requirements. In the sloths (*Bradypus* and *Choloepus*) and in marsupials, respectively, metabolic rates are only 50-47 percent (Goffart, 1971) and 73 percent (Blaxter, 1972) that of rodents, artiodactyls, and perissodactyls. Partial evidence (Grand, 1978) indicates that a leaf-eating monkey (howler) has a reduced muscle mass, which may suggest lower basal metabolism, since it has been shown that maintenance of muscle tone represents a major portion of basal heat expenditure. This lower metabolic rate changes the demands on the fermentation contents to supply the required energy for maintenance.

(b) In sloths we find an extremely large forestomach chamber and a prolonged retention of the digesta in it (Goffart, 1971; Montgomery and Sunquist, 1978), and

(c) fermentation activity may be affected by the low body temperature that usually accompanies low metabolic rate in homiotherms and changing body temperature typical of poikilotherms.

Utilization of Fermentation Products

Fermentation can only be of use to the host if it can utilize some of the end-products. VFA, microbial cells, and ammonia can be utilized by the ruminant (Hungate, 1966), but the details of utilization of these products by nonruminant herbivores is largely unknown.

Absorption and utilization of volatile fatty acids

Dobson and Phillipson (1968) have proposed a model for the relationships among production, absorption, metabolism, and transport of VFA in ruminants. They describe a loss from the lumen side as absorption and its appearance on the blood side as transport. If we ignore accumulation within the epithelium, then the amount of acid absorbed will equal the sum of the amounts transported and metabolized.

The absorption of VFA from the foregut of ruminants has been extensively studied (Dobson, 1961; Annison, 1965; Dobson and Phillipson, 1968; Stevens, 1970; Fell, 1969; McDonald, 1969). There are estimates of 76 percent of ruminal VFA, being absorbed from the rumen, 19 percent from the

It is evident that nonruminant herbivores can absorb VFA from the hindgut and that the main difference between absorption from the rumen is in the rate of epithelial tissue metabolism of fatty acids.

omasum and abomasum and 5 percent passing into the small intestine (Weston and Hogan, 1968).

Absorption of VFA from the hindgut of nonruminant herbivores is important, so that the VFA can be utilized as an energy source, and to maintain acidity conditions within a tolerable range for the microbial population of cecum and colon. The information available for nonruminant herbivores is very limited.

Ørskov, et al., (1970) suggest that VFA absorption is inefficient in the sheep's cecum, however Williams (1965) and Ward, et. al., (1961) showed considerable absorption of VFA from the ruminant's cecum. Drawert, et al., (1962) suggested considerable absorption of VFA from the forestomach fermentation chamber (Tubus gastricus) of a leaf-eating monkey. The classical work of Barcroft, et al. (1944) demonstrated the absorption of VFA from the rumen of sheep and cows, the cecum of rabbits and pigs, and the colon of horses, by determining the concentrations of VFA in the veins draining those organs. Recent reviews have indicated a considerable capacity of the horse hindgut in absorption of VFA (Alexander, 1963; Mehren and Phillips, 1972).

Baker, et al. (1970) have shown VFA absorption from cecal infusions in horses. Stevens (1970) and Giddings and Stevens (1968) have studied absorption of VFA from cecal epithelium of horses and from rumen epithelium. They conclude that equine cecal epithelium metabolizes VFA at a much lower rate that does rumen epithelium, but shows little difference in its absorption or transport of acetate and butyrate. They suggest that the differences between these epithelial tissues is in the rate at which they metabolize acetate or butyrate, not in relative differences in permeability to these fatty acids.

McBee (1970) indicates efficient absorption of VFA from the cecum of a wide group of rodents and the rabbit, and suggests no preferential absorption of any of the 3 main acids (acetic, propionic, and butyric) and probably little, if any, metabolism of absorbed acids in cecal wall. Johnson and McBee (1967) have shown that 83 percent of the VFA produced in the porcupine's cecum was absorbed there and that 64 percent of the VFA entering the colon was absorbed there, so very little was excreted. Yang, et al., (1970) in rats, Hagen and Robinson (1953) in guinea pigs, and Phillipson (1947) in dogs, have shown VFA absorption from the large intestine.

Dobson (1961) demonstrated that VFA absorption from the rumen depended, among other things, on the concentration of the acids and this is probably true for the cecum.

It has thus been shown that the VFA produced by fermentation in the hindgut of nonruminant herbivores can be absorbed. Are these fermentation products utilized by the host's tissues? In general, volatile fatty acids are utilized less efficiently than is glucose following absorption (Blaxter, 1971).

Horino, et al. (1968), proposed that any species should eventually evolve an insulin secretory response mechanism to that nutrient or type of nutrient which represents the major metabolic or energetic substrate for that particular organism. They found an insulin response to intravenous injection of propionate and butyrate, but not of acetate, in sheep and cows. The response to glucose was smaller than that to VFA. They also found no insulin response to propionate or propionate-and-butyrate injections in rat, rabbit, and pig. According to the authors, this is an indication of VFA not being a primary energy substrate for these small nonruminant species. There are no indications on the diets fed to these animals.

Argenzio and Hintz (1971, 1972) have studied tolerance times and plasma insulin response to intravenous VFA and glucose injections in ponies, as indicators of the ability of an animal to metabolize a substrate in the presence of the primary metabolic substrate. They found contradictory results with ponies. They did not find an insulin response to injections of VFA and a response to glucose similar to that of man, indicating a regulatory system for VFA and glucose in ponies which is markedly different from that in ruminants. However, the percentage of CO_2 derived from glucose in ponies fed an alfalfa-beet pulp ration or in fasted ponies was very similar to ruminant values, suggesting that a large fraction of the total energy supply came from VFA. Table 11, from these authors, indicates a flexible arrangement for ponies, resembling nonherbivores or herbivores, according to the diet eaten.

How much does VFA contribute to the total energy requirements of the ruminant and nonruminant herbivore? Ruminants obtain most of their energy from the products of fermentation (Table 12), and the values shown for small hindgut fermentors are considerably lower than those for foregut fermentors. It might be a consequence of the diets selected by small size nonruminant herbivores, which makes them less dependent on fermentation for obtaining the energy required. In the case of large nonruminant herbivores (like equines), however, VFA is the most important source of energy when the animals are eating diets high in fiber.

Table 11.—Interspecies comparison of parameters of glucose metabolism[°].

Species	*Diet*	*Entry rate*	*% CO_2 from glucose*	*% Glucose to CO_2*
		$g/hr/kg^{0.75}$		
Sheep	Fed	0.26	9.6	32
	Fast	0.19	9.6	32
Man	Postabs.	0.31	33.8	63
	Fast 64 hr	0.21	21.3	57
Dog	Fast 16 hr	0.32	14.0	41
Pony	Fed, oats	0.35	15.8	53
	Fed, alf.-beet pulp	0.25	9.2	38
	Fast 72 hr	0.18	8.8	30

[°] Taken from: Argenzio, R. A., and Hintz, H. F. (1972).

Utilization of microorganisms

The discussion to follow will be concerned with the production of microbial protein and its fate in ruminant and nonruminant herbivores. Microbial protein is of high biological value (Bergen, et al., 1967; Hoogenraad, et al., 1970; Mason and Palmer, 1971).

Herbivores are dependent, to a variable extent, on the products of microbial action for their supply of nutrients. These products become available to the ruminant host-animal by absorption from the fermentation site or by passage to, and absorption from the intestines either with, or without, further enzymatic action. Ruminants also benefit from digestion of their symbiotic bacteria and protozoa in the abomasum and small intestine with subsequent absorption of the soluble components of the cytoplasm of these microorganisms (Cuthbertson and Hobson, 1960). Hungate (1968) indicated that rumen microorganisms can provide a large part of the nitrogenous food needed by the host.

Much less is known about the fate of the microbial population of the hindgut fermentors. Since the fermentation site is located beyond the sites of active enzymatic digestion, there are doubts about the efficiency of utilization of the microbes. There seem to be 2 types of strategies in nonruminant herbivores—one is that of coupling hindgut fermentation with coprophagy and the other is not clearly understood although it does not involve reingestion of feces (Moir, 1968).

There are almost no estimates on the extent of microbial growth in the hindgut of nonruminant

Table 12.—Energy from volatile fatty acids° ((Kcal from VFA/2 × 70 Kg$^{3/4}$) × 100)

Animal	Site of fermentation Foregut %	 Hindgut %	Author
Cattle and Sheep	70–80		Church, 1969
Sheep	57–79 [1]		Seeley, et al., 1969
Sheep	77 [1]		Bergman, et al., 1965
Goat	37–46		Stewart, et al., 1958
Deer	25		Short, 1963
Langur monkey	>100		Bauchop and Martucci, 1968
Horse [a]		Large	Argenzio and Hintz, 1972
Horse [b]		Small	Argenzio and Hintz, 1972
Rabbit		12 [a]	Hoover and Heitman, 1972
Rabbit		10 [b]	Hoover and Heitman, 1972
Rabbit		8	McBee, 1970
Porcupine		19 (6–39)	Johnson and Clarke, 1972
Beaver		19	Hoover and Clarke, 1972
Beaver		18	Currier, et al., 1960
Rat		9	Yang, et al., 1970
Pig		15–28	Friend, et al., 1964
Pig [a]		8	Farrell and Johnson, 1972
Pig [b]		5	Farrell and Johnson, 1972

° Values calculated from information available in literature
[1] Total VFA/Metabolizable energy
a High fiber diet
b Low fiber diet.
Source: Parra, R., 1973.

herbivores. Slade (1970) showed rates of microbial cell production in the cecum of guinea pig and rabbit (3.55 to 7.53 and 5.19 to 4.42 mgm of microbial cells/g of dry cecal contents/hr, respectively), and Slade, et al. (1973) for the cecum of the horse (4.50 mg/g dry cecal contents/hr.), comparable to those reported for sheep rumen (4.3 mgm/g dry rumen content/hr) by Al-Rabbat (1970).

A regeneration cycle of proteins, of vital importance for ruminants, has been proposed by Houpt (1970). An equivalent cycle for nonruminant herbivores has been recently proposed by Slade, et al. (1970; Figure 5). Several authors have supported this idea of the recycling of urea from and to the cecum of nonruminant herbivores (Houpt and Houpt, 1971; Houpt, 1963; Phillipson, 1964; Nelson and Tyznic, 1971), but Reitnour and Treece (1971) showed evidence against the recycling hypothesis.

An indicator of the activity and importance of the microbial population in herbivores is the ability to utilize nonprotein nitrogen (NPN) sources for microbial protein synthesis. The ability of ruminants to utilize NPN has been extensively studied and reviewed (Briggs, 1967). A classical experiment by Virtanen (1966) demonstrated the possibility of high milk production in cows fed on protein-free rations. There is contradictory evidence on the ability of nonruminant herbivores to make use of synthetic forms of nitrogen in their ration. Several authors reported a negative value of urea as a protein replacement: Olcese and Pearson (1948) and King (1971) in rabbits; Cody and Caffrey (1967) and Reitnour and Treece (1971) in horses; Matsumoto (1955) in rats; Slade and Robinson (1970b) in guinea pigs; Hoefer (1967) in pigs and Featherson (1967) in chickens. But, on the other hand, there are several reports showing an increased nitrogen retention when NPN was added to low protein diets and comparable efficiencies of N utilization when NPN replaced protein sources (Hintz and Schryver, 1972; Houpt and Houpt, 1971; Nelson and Tyznic, 1971; Slade, et al., 1970, all in horses; Houpt, 1963; Yasui and Nagata, 1968; Slade and Robinson, 1970b, all in rabbits; Matsumoto, 1955, in hamsters).

Although most of the recent evidence points to the utilization of NPN by nonruminant herbivores, it is unclear how this utilization is achieved and its significance to the host. Hintz and Schryver (1972) indicate the need to determine whether the increased N retention is a result of synthesis of nonessential amino acids

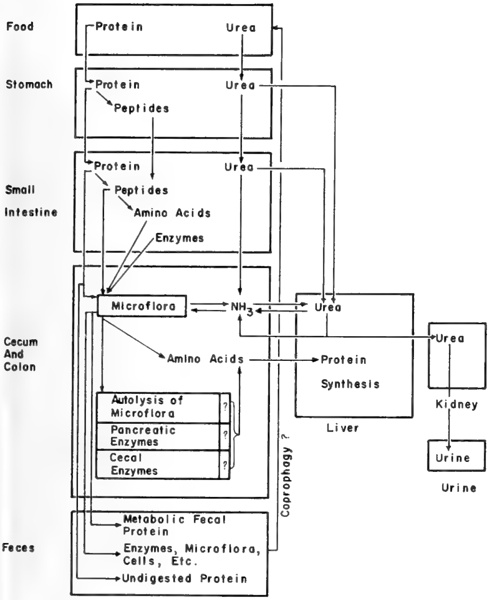

Figure 5. A proposed Nitrogen cycle for nonruminant herbivores. Source: Slade, et al. (1970).

by the liver or is due to absorption of amino acids synthesized by the intestinal microflora. Houpt and Houpt (1971) suggested lower rates of urea utilization in rabbit and horses as compared to sheep, probably due to less intensive and extensive microbial activity in nonruminant herbivores. Reitnour and Salisbury (1972), in experiments with cecally infused protein in horses, indicate that N is absorbed, but in a form that is little utilized by the animal. In this experiment a considerable amount of protein was infused into the cecum over a short period of time. The amount of protein present in the cecum might have been far beyond the abilities of the microbial population to utilize it, and most of it was liberated as ammonia and lost to the animal. Nelson and Tyznic (1971) suggested that urea addition to diets low in protein results in a stimulation of cecal microbial protein synthesis.

Houpt (1963) proposed the following hypothesis: (a) endogenous urea moves from body fluids into the cecum where it is hydrolyzed with formation of ammonia, (b) part of the ammonia is absorbed and used in hepatic synthesis of nonessential amino acids, and part is used in microbial synthesis of both essential and nonessential amino acids and (c) cecal microbial protein is either reingested by coprophagy and subsequently digested and absorbed in the foregut or, in the case of noncoprophagous animals, microbial protein becomes available for absorption from the large intestine, presumably after death and disintegration of microorganisms release their contents (Houpt and Houpt, 1971). It is of interest to note that urease activity in cecal contents is high (Hintz, et al., 1970; Hecker, 1971), contrary to the suggestion of Alexander and Davies (1963).

Ørskov, et al., (1970) suggest that the microbial protein formed in the cecum of the sheep is not utilized. In nonruminant herbivores the information available is quite scarce. Those animals which practice coprophagy seem to have a good mechanism for utilizing microbial protein and vitamins (Hintz, 1969a; Kwong and Barnes, 1969; Hotzel and Barnes, 1966), reingestion of feces being essential for maximum efficiency of utilization of some of the products of hindgut fermentation. In the case of nonruminant herbivores which have not adopted coprophagy as a mechanism, the state of knowledge is even more obscure. Baker (1942) proposed autolysis of microbes during passage through the colon as a most likely mechanism for release of microbial protoplasma and subsequent absorption. Bonnafous and Raynaud (1970) indicate that 71 percent of the microorganisms and nitrogen in cecal contents of rabbits disappear along the proximal colon in the day-type feces, but this is not observed in the night-type feces. This suggests an important retention of proteins for the host. They suggest a double mechanism for maximum efficiency in extracting microbial protoplasm, one by coprophagy of night feces and another by lysis of the microbial population of day feces. The mechanisms involved are unknown. Slade, et al., (1971) injected ^{15}N-labeled washed cell suspension, prepared from cecal contents of horse, into the cecum of live horse and monitored the labeled-N in blood taken from the cecal vein. They obtained 2 peaks showing increased labeled lysine, essential amino acids, nonessential amino acids, ammonia, and urea. The first peak (60 min) suggests rapid absorption of free amino acids and ammonia from the cecum, while the second peak (4 hrs) suggests hydrolysis and absorption of labeled microbial protein. This work supports the idea that nonruminant herbivores are capable of utilizing microbial protein originating in the large intestine to supply essential amino acids which may be lacking in the diet. The values for endogenous excretion for ruminant and nonruminant herbivores (Table 5) do not show marked differences. Since the true digestibility of cellular contents (protein soluble carbohydrates, etc.) is almost complete, it is evident that fecal cellular contents are almost all of endogenous origin (Jarrige, 1963; Van Soest, 1967). Furthermore, most of this endogenous fraction is of bacterial origin (Mason, 1969; Virtanen, 1966). The endogenous fractions (calculated according to Lucas test, Table 5) are similar for ruminant and nonruminant herbivores, indicating similar extents of utilization of microbial cells by both groups of herbivores.

Nonruminant herbivores, which are not coprophagous, can thus utilize the microbial protein (microbial cells) in a useful manner to the host.

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Adaptations of Tissue and Limb Segments to Facilitate Moving and Feeding in Arboreal Folivores

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Introduction

The central topic of this analysis is the relation between anatomical structure and motor behavior in arboreal folivores. Body weight is one biological property which focuses this problem of form and function. At the same time, from an analytical point of view, weight is a transitional device for studying the growth and metabolism of the individual and the economy of the species.

Each analysis of body weight has its own orientation and bias, whether biochemical and physiological (McNab, 1971, 1974, 1978; Goffart, 1971; Passmore and Draper, 1964), functional (Grand, 1977), veterinary anatomical (Huntley, 1971; Ledger, 1963, Palsson, 1955), paleoanthropological (Turnbull and Reed, 1974), or ecological (Eisenberg and Thorington, 1973; Lamprey, 1964; Kruuk and Turner, 1967; Foster and Coe, 1968; Sachs, 1967). A methodology devised to analyze locomotor adaptation and first applied to primates and carnivores (Grand, 1977) has been used with representative mammalian herbivores. The first level of description considers the proportions of skin, muscle, and bone to total body weight; the second deals with the body as a series of linked segments and shows how weight is distributed to tail, foot, calf, etc. around the body's center of gravity.

As an introduction to both method and interpretation, data are given on a pair of terrestrial herbivores, the agouti (*Dasyprocta*) and young kangaroo (*Macropus*), since they admit of comparisons between animals of the same weight but of diverse motor pattern and lineage. Adaptations to terrestrial movement serve as a perspective for studying arboreal animals and locomotor problems in the canopy. In greater detail, the howler monkey and the two- and three-toed sloths are then described. The contrasts (tailed vs. tailless, primate vs. edentate) enhance the similarities which will be outlined.

Finally, "corrected" body weight is discussed as a methodological and philosophical problem, and its application to comparative physiology and ecology is explained.

Methodology

The animals used in this study are listed in Table 1 which includes their age, sex, and body weight and the preservation technique used before dissection.

Table 1.—Specimen List.

Species		Sex	Age	Body Weight (kg)	Preservation
ROCTA AGUTI		-	ADULT	2.25	FROZEN
HOTIS PATAGONA		M	ADULT	5.00	FROZEN
HOTIS SALINICOLA		M	ADULT	1.62	FROZEN
PUS SP.		-	INFANT	3.234	FROZEN
A IGUANA		-	ADULT	2.07	FROZEN
TTA CARAYA*:	No. 3467	-	ADULT	3.50	FROZEN
	No. 2110	M	ADULT	6.15	FROZEN
PUS INFUSCATUS		F	ADULT	3.60	FROZEN
EPUS HOFFMANI:	No. 1	F	ADULT	4.692	FRESH
	No. 2	-	ADULT	4.498	FROZEN

ER SPECIMENS FROM GRAND, 1977, PART 1.

Because of the limited availability of animals, individuals are assumed to be representative of their genera. By including published observations on these species and by adding members of other groups, I tried to compensate for this difficulty.

Since the dissection method has been described elsewhere (Grand, 1977), only the sequence of procedures is given here. To obtain the relative composition of tissues, one side of the animal was dissected free of each of the major tissues: the *skin*, the *muscle* in 4 groups (forelimb, hindlimb, back extensor, remaining or "other"), limb and truncal *bone*. Dividing total body weight into the weight of each tissue gives the percent Total Body Weight (TBW) of that tissue. To obtain the relative weight of the segments, each segment (tail, foot, calf, thigh, etc.) on the other side was disconnected and weighed. Dividing total weight into the weight of each segment gives the percent TBW or relative weight of that segment. Each segment was then broken down into skin, muscle, and bone, and the weight of each of these tissues was divided by the total weight of the segment to arrive at its compositional profile. The reconstruction of truncal tissues was a similar, somewhat more complicated procedure. Some functional muscle groups were also weighed to determine their proportions within the segment. Data are provided in the tables to facilitate comparison with other dissection methods.

The stomach and intestines, liver, and a *Bradypus* fetus were dissected free and weighed. Dividing TBW into each element gives percent TBW of that component.

Note that "light" and "heavy" applied to tissues and segments are always relative terms.

Observations

Tissue composition of the whole body (Figure 1). In all specimens used in this study, skin constitutes from 8 percent to 16 percent TBW. The 3 sloth specimens average 15.5 percent TBW; Britton's observations (1941b) give 20 percent TBW. Heavier body segments have relatively lighter skin covering than smaller segments; larger, heavier animals have relatively less surface area than smaller ones. (This latter phenomenon is not apparent in the similarly sized animals used here.) This is based on the fact that whereas weight (both of segment and of body) increases by the cube, surface area increases by the square (Thompson, 1969).

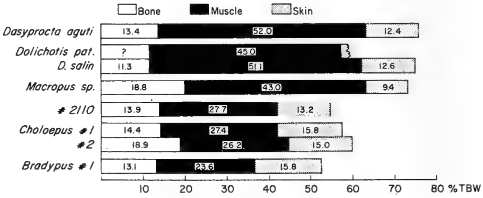

Figure 1. Bar graph of tissue composition.

Muscle varies more, has a greater effect on total weight and physiology, and is more sensitive to locomotor differences than skin and bone. Muscle constitutes over 40 percent TBW in the kangaroo, over 50 percent in the agouti, cavy, and jackrabbit. By contrast with these terrestrial forms, muscle ranges

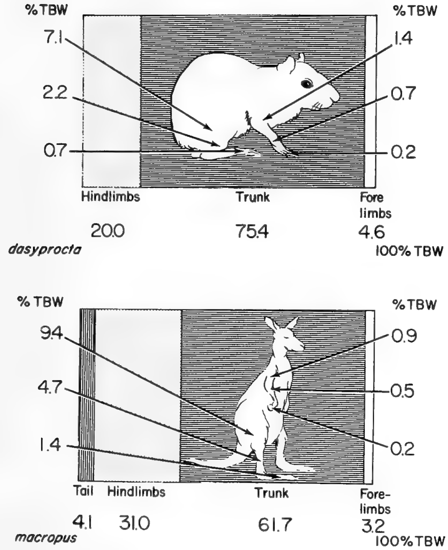

Figure 2. Terrestrial forms-segment figures. A. *Dasyprocta*. B. *Macropus*.

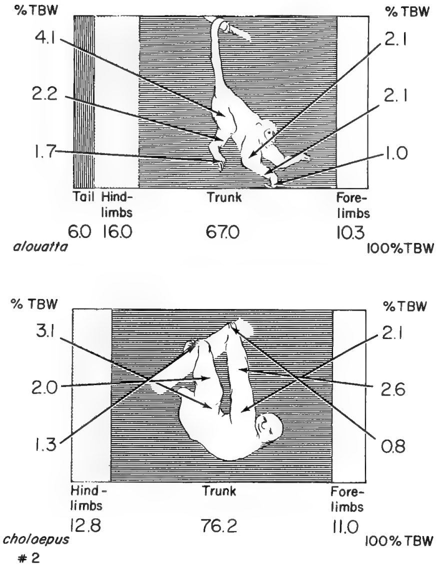

Figure 3. Arboreal forms-segment figures. A. *Alouatta*. B. *Choloepus*.

from 23.5 percent to 27.5 percent TBW in the howler monkey and sloths. In the two *Choloepus*, it averages 26.7 percent TBW; in the *Bradypus*, 23.6 percent TBW. Britton and Atkinson (1938) give 25 percent TBW for *Bradypus* (see Table).

Bone varies from 11 percent to 19 percent TBW; Britton (1941b) estimates 20 to 25 percent TBW for the sloth. The concentration of bone in tail and hindlimbs of the kangaroo should be noted.

The weight of stomach and intestines varies from 6 percent to over 30 percent TBW. Unfortunately, these data are difficult to compare with published observations. Dissection procedure as well as terminology differs: offal, abdominal viscera, stomach and intestines, wet or dry weight, and surface area (Moir, 1968; Hladik, 1967). Nevertheless, the high percentage corresponds with Beebee's (1926) report of 37.8 percent (abdominal viscera in *Bradypus*) compared with 25 percent (in *Dasyprocta*). Britton (1941b) notes 25 percent TBW (stomach and intestines in *Bradypus*).

Segmental distribution of weight (Figures 2 and 3).—This biomechanical method provides a transition to locomotor analysis. In addition, it illustrates the bone-skin-muscle distribution about the body core.

In *Dasyprocta aguti*, the agouti (Figure 2A), 20 percent of the TBW is concentrated in the hindlegs, 4.6 percent in the forelegs. The tail is vestigial. At 7 percent TBW, the thigh is the heaviest segment; at 0.7 percent or less, the feet, forearms, and forepaws are the lightest.

Most of the weight (75 percent TBW) is concentrated in the trunk and head. The composition of tissues follows: skin 9 percent TBW, truncal bone 10 percent TBW, stomach and intestines, heart and lungs, 23 percent TBW. Beebee (1926) gives 25 percent TBW for the abdominal viscera. The back extensors are the dominant muscle constituents at 12 percent TBW. The viscera and back extensor components differ significantly from the sloth trunk (Figure 4).

The inverse tapering of limb tissues from proximal to distal is common to all animals. Muscle constitutes over 80 percent of thigh weight, but drops below 20 percent of foot weight. Bone contributes 10 percent to thigh weight, over 50 percent to foot weight.

In *Dolichotis patagona* and *D. salinicola*, the patagonian and dwarf cavies, the forelimbs, which protrude from the trunk at the elbow, are long and light like the feet and calves whereas the thighs are

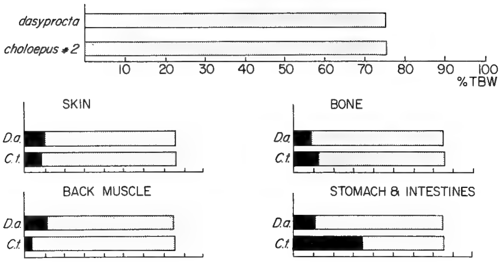

Figure 4. Bar graph-trunk composition. *Dasyprocta* trunk = 75.4 percent TBW. *Choloepus* #2 trunk = 76.2 percent TBW.

quite massive. The muscle of the hindlimb tapers from 90 percent in the thigh to 15 percent in the foot, but the bone tapers inversely from 10 percent in the thigh to 60 percent in the foot. The same pattern is seen in the greyhound and jackrabbit (Grand, 1977). As in these other high-speed forms, the back extensor muscles as well as the shoulder-elbow muscles are quite large.

Macropus sp., the young kangaroo is shown in Figure 2B. Each hindleg is over 15 percent TBW, each forelimb 1.5 percent, and the tail 4 percent TBW. Thus, the tail and two legs constitute almost 35 percent TBW. Twelve percent of the body's muscle is in each leg, about 1.5 percent in each foreleg.

The remaining 61.7 percent TBW is concentrated in trunk and head. About 6 percent TBW is in the back muscle, about 5 percent in the guts.

Iguana iguana, the iguana is analyzed in Tables 2 and 3. This animal is included partly because its terrestrial/arboreal flexibility are unique for the sample and partly because other data on reptiles are not comparable to these data on mammals. The forelimbs and hindlimbs protrude from the central body mass, the former 7 percent, the latter over 16.5 percent TBW. The trunk and tail are the structural origin of the sinusoidal locomotor pattern; the chain of truncal extensor and tail muscles represent about 13 percent TBW. The tail is about 75 percent muscle, and if this muscle is included in the percentage of body muscle, then the total value rises from 33.4 percent to 41.4 percent TBW.

Alouatta caraya, the howler monkey, is shown in Figure 3A. In distribution of weight, the hindlimbs constitute 16 percent of weight, the forelimbs 10 percent. The gradients from thigh-calf-foot (4.1 percent to 1.7 percent) and upper arm-forearm-hand (2.1 percent to 1.0 percent) are more moderate than the steep thigh-calf-foot (7.1 percent to 0.7 percent) gradients in the agouti. The hands and feet are somewhat heavier, the thighs and upper arms lighter than in most quadrupedal monkeys. These weight features between segments can be decomposed into functional muscle groups within the segments. Although the adductors, rotators, and pronators are large, segment weight is reduced by relatively lighter propulsive and antigravity muscles (hamstrings, quadriceps femoris, gastrocnemius, triceps). The invertor and digital flexors of calf and forearm are relatively large. The overall hindlimb dominance is characteristic of quadrupedal monkeys.

Muscle constitutes 30 to 35 percent of the hands and feet. These intrinsic muscles of palm and sole produce finger movements and cause the tissue balance which is characteristic of most monkeys. Muscle is less than 20 percent in the terrestrial forms. In the howler, bone constitutes 30+ percent of the hands and feet; in terrestrial species, over 50 percent.

The wrist and hand can be further analyzed. As the elevated and elongated "heel" of the hand, the hypothenar eminence functions during the early contact phase of weight bearing. This complex is composed of ulna, ulnar carpals, fifth metacarpal, and binding ligaments. Within the palmar friction skin, two sets of creases are apparent, one transverse which facilitates finger flexion against the palm, the other longitudinal through digits #2 and #3, which is the main axis of prehension. The main plane of motion, which runs from hypothenar eminence through the longitudinal crease to digits #2 and #3, is controlled at the wrist by ulnar flexors and radial extensors (Grand, 1968). The thumb is turned upon its long axis to line up with digit #2. Convergence of the distal touch pads is poor.

At 6+ percent TBW, the tail is heavier than that of all other primates except for its own close relatives. The tail which is 40 to 50 percent muscle as compared to less than 30 percent in others, has an extraordinary range of mobility and is integrated into all body postures of horizontal and vertical movement, as well as terminal branch feeding. If tail muscle is included in the percentage of body muscle, then the total value rises from 25.6 percent to 27.7 percent TBW.

Choloepus hoffmanni and *Bradypus infuscatus*, the two-toed and three-toed sloths are analyzed in Figure 3B and Tables 2 and 3. The forelimb and hindlimb segments are 10.6 percent and 13.2 percent TBW, respectively, in the two *Choloepus*; the segments are equal at 11.8 percent TBW in *Bradypus*. In both genera this balance contrasts with the tendency to hindlimb dominance of other mammals.

The weight gradient within one limb from proximal

Table 2.—Tissue Composition.

	Dasyprocta aguti		*Dolichotis patag.*		*D. salinicola*	
	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW
Skin	138.7	6.2	250.0	>3.9	101.4	6.3
Muscle						
fore	115.0		285.2		87.6	
hind	231.3		576.6		145.2	
back	132.1		350.4		100.4	
other	107.5	26.0	236.2	22.6	79.4	25.6
Bone						
fore	16.5		47.8		13.0	
hind	33.2		83.8		17.8	
trunk	202.0	13.4	> 282.9	>8.5	120.6	11.3
Body Wt. (kg)	2.25		6.4 (est.)		1.614	

	Macropus sp.		*Iguana iguana*		*Alouatta no. 2110*	
	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW
Skin	151.5	4.7	85.5	4.1	458.4	7.5
Muscle						
fore	52.7		86.6		274.9	
hind	378.3		129.1		313.6	
back	150.8		53.0		83.8	
other	115.9	21.6	77.0	16.7	112.0	12.8
Bone						
fore	19.7		25.9		95.6	
hind	123.0		29.0		98.5	
trunk	323.0	18.8	174.7	13.7	467.1	13.9
Body Wt. (kg)	3.234		2.07		6.15	

	Bradypus infusc.		*Choloepus no. 1*		*no. 2*	
	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW	Tissue Wt. (gm)	% TBW
Skin	284.5	7.9	369.5	7.9	337.3	7.5
Muscle						
fore	183.2		230.3		231.3	
hind	123.3		209.2		183.0	
back	33.1		56.0		64.0	
other	84.2	11.8	145.1	13.7	110.7	13.1
Bone						
fore	60.1		63.0		80.8	
hind	45.6		68.0		83.4	
trunk	259.0	13.1	415.0	14.4	520.0	18.9
Body Wt. (kg)	3.6		4.692		4.498	

Table 3.—Segment Weights.

	Dasyprocta aguti		*Dolichotis salinicola*		*Macropus sp.*		*Iguana iguana*	
	Segment Wt. (gm)	% TBW	Segment Wt. (gm)	% TBW	Segment Wt. (gm)	% TBW	Segment Wt. (gm)	% TBW
Forepaw	5.5	**0.2**	3.1	**0.2**	7.0	**0.2**	12.5	**0.6**
Forearm	15.0	**0.7**	8.7	**0.5**	17.3	**0.5**	25.0	**1.2**
Upper Arm	32.5	**1.4**	25.2	**1.6**	28.5	**0.9**	36.5	**1.8**
Foot	16.1	**0.7**	9.0	**0.6**	45.0	**1.4**	22.7	**1.1**
Calf	49.9	**2.2**	30.0	**1.9**	153.2	**4.7**	48.9	**2.4**
Thigh	160.0	**7.1**	92.0	**5.7**	304.7	**9.4**	98.8	**4.8**
Tail	-		-		132.8		390.0	**18.8**
Body Wt. (kg)	2.25		1.614		3.234		2.07	

	Alouatta caraya			*Bradypus infusc.*		*Choloepus hoffmani*		
	#3467	#2110				#1	#2	
	Segment Wt. (gm)	Segment Wt. (gm)	Av. % TBW	Segment Wt. (gm)	% TBW	Segment Wt. (gm)	Segment Wt. (gm)	Av. % TBW
Hand	34.6	46.5	**0.9**	38.0	**1.1**	33.6	37.2	**0.8**
Forearm	72.2	133.0	**2.2**	96.4	**2.7**	104.7	118.0	**2.4**
Upper Arm	75.0	145.8	**2.2**	75.1	**2.1**	96.8	96.1	**2.1**
Foot	57.8	84.7	**1.6**	45.2	**1.3**	54.6	60.2	**1.2**
Calf	78.0	132.0	**2.2**	76.5	**2.1**	101.3	89.6	**2.1**
Thigh	143.4	247.5	**4.0**	89.1	**2.5**	163.2	141.6	**3.3**
Tail	211.3	333.7	**5.7**	-		-	-	
Body Wt. (kg)	3.5	6.15		3.6		4.692	4.498	

segment to distal is not as steep as in terrestrial forms partly because of heavy calf and forearm, and partly because the sloths have lightened both thigh and upper arm. Neither genus has a significant tail; it is vestigial in *Choloepus*. It is not so much a shortened segment in *Bradypus* as a sacroiliac buttress, presumably related to burying fecal materials.

The proximo-distal tapering of tissues is like that of the preceding forms: thigh and upper arm are primarily muscular, with low bone-skin components; the hands and feet are primarily bone. However, the largest and most emphasized functional muscle groups differ from those of both the howler monkey and the terrestrial forms, and these groupings correlate directly with truncal suspensory posture and range of motion at each of the limb joints. Hip and knee, shoulder and elbow exhibit substantial ranges of motion (Lucae, 1883). The hip has no ligament of teres, the shoulder has a weak clavicle. Elbow and knee are at rest in full extension, and this position is a basic component of suspensory posture. Ankle and wrist have broad ranges of vertical rotation and key elements of suspension (Böker, 1937). At the more distal joints of each limb, however, the bony components fuse and the digital rays are reduced (Lucae, 1883; Jouffroy, et al., 1961; Vassal, et al., 1962). At the distal interphalangeal joints flexion-extension is retained, and hooklike claws and digital flexor muscles are elaborated. The trunk itself is extraordinarily flexible, through lumbar torsional mobility and through extreme lumbosacral and cervical flexion (Lucae, 1883; Slijper, 1946).

Correlated with each of these joint motion features is a series of muscular adjustments: large cervical and lumbar (truncal) flexors, expanded anterior longitudinal ligament, reduced dorsal extensors; large adductors and rotators of hip (adductors, quadratus femoris) and shoulder (pectorales, brachioradialis, scapulohumeral); small retractor and antigravity muscles (hamstrings, quadriceps femoris, gastrocnemius, latissimus dorsi, triceps). The digital flexors are the dominant components of the calf and forearm. See also: Miller, 1935; Jouffroy, 1971.

Seventy-five percent of body weight is concentrated in the trunk and head. The tissue analysis of the trunk in Figure 4 shows the major differences with the agouti. Skin, truncal bone, and limb musculature are about the same in both forms except that the upper arm is a free segment in the sloth but incorporated within the trunk in the agouti. The back extensor muscles, however, are a bit over 2 percent TBW, and the flexors are relatively large. Lucae (1883) noted this disproportion between truncal extensors and flexors. The viscera (lungs, heart, liver, guts) constitute almost 40 percent of total weight. Beebe (1926) observed that the abdominal viscera equal 37.8 percent TBW in the three-toed sloth, Britton (1941a) that stomach and intestines equal 25 percent TBW. Gut size has altered lung position (Böker, 1937) and may explain the peculiarly expanded pelvic basin. The fetus and placenta were 13 percent TBW in *Bradypus*; a newborn, without placenta, constituted 8.6 percent TBW (Britton, 1941a). In a *Choloepus*, the newborn, without placenta, was 6.9 percent TBW (Britton, 1941a).

A characteristic feature at the junction of trunk and proximal limb segments, the rete mirabile, forms an arteriovenous network (Straus and Wislocki, 1932) which is also found in the elbows and knees. The hair pattern is reversed on the trunk and limbs, parting ventrally and meeting dorsally. The ascribed function is water drainage to accommodate the habitual suspensory posture.

Striking similarities with the potto and slow loris should be noted: reduced percent of body muscle; balanced proportions of forelimb and hindlimb segments; reduced or vestigial tail; elevated calf and forearm weight because of the enlarged digital flexor muscle; expanded range of truncal motion, reduced vertebral spines and articular processes, and increased truncal flexor muscles with corresponding decrease in extensors; arteriovenous networks at shoulder and elbow, hip and knee (See Grand, 1977).

Discussion

My discussion is limited to 2 aspects of these data: (1) the correlation between the components of body weight on the one hand and motor pattern and physical environment on the other; (2) the reassessment of weight as a physiological and ecological standard.

First, the data show that mammalian folivores differ in tissue composition and weight dispersal to limbs and tail. To terrestrial forms, the ground offers a resistant, continuous, undulating surface for their activity. These properties favor the evolution of rapid acceleration, higher speeds, and longer transport distances. These skills have adaptive value in foraging and avoidance of predators. As a result, structural convergences have appeared among the agouti and cavy, the jackrabbit, and the kangaroo: (1) a high proportion of body muscle; (2) major concentrations of muscle in back and thigh and increased parasagittal trunk flexibility; (3) reduced muscle and a concomitant increase of bone in forepaws and feet; (4) reduction of weight in distal segments and of palmar and plantar surfaces; (5) segment elongation below knee and elbow; (6) proximal packing of limb muscle which, along with (4) and (5), elevates the center of limb mass; (7) increased parasagittal mobility of proximal limb joints with reduction of rotator and adductor muscles.

Canopy dwellers, on the other hand, have been subjected to quite different selection pressures. Consideration of the mechanical properties of the canopy focuses our attention upon the structural and motor adaptations made by the howler monkey and sloth.

We begin with the purely physical image of a 10-lb (4 kg) mass moving 100 feet horizontally and 10 feet vertically through the canopy (Figure 5). Mechanical work (foot/lbs.) is estimated by body weight (the object's resistance to motion) times the distance moved. Theoretically, this is a fairly easy calculation but it becomes difficult to apply. Nevertheless, motion sequences can be graded according to their degrees of energy expenditure. By reducing vertical displacement, the canopy offers a natural short-cut to horizontal motion. An animal moving the same distance over the ground must move his body mass up the side of the ravine. In vertical ascent, an animal moves against his own full weight; in vertical descent, muscle controls the fall, but gravity assists. Furthermore, animals vary in their ability to perform these movement sequences. In one other area, canopy-dwellers can reduce energy costs below those of terrestrial forms. To avoid predators, an arboreal form can use his climbing skill to attain a safe perch where the predator cannot follow or attack. These potentials

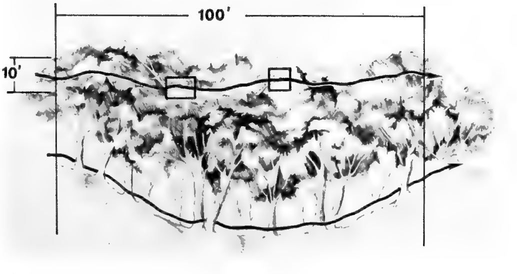

Figure 5. Canopy structure.

for reduced effort underscore McNab's conclusion (1978) that arboreal forms have lower rates of basal metabolism and do not achieve the multiples of this basal rate that terrestrial forms generally do.

Body mass and support surface demonstrate 2 different postural relations. If the animal is above the branch, his fingers and toes require muscular input to achieve counterpressures against the curved surface. Muscle is also necessary to keep the limb columns vertically upright. However, since the columns are not truly straightened, rotational muscles operate at each joint pair. In forward movement, muscular effort levers the body forward through these angled columns. These are the theoretical costs of posture and motion. To these inefficiencies in coping with small branches must be added the fact that every muscular action elicits an equal and opposite reaction.

If the animal is below the branch, the body mass is connected to support surface through relatively straightened joints. Alignment reduces joint strain and permits the elaboration of various passive anatomical mechanisms. Suspensory ligaments replace muscles, bones are curved, joint pairs fused. The hooklike foot of the sloth is a classic example of this adaptation. Below-the-branch movement has 2 other theoretical advantages: gravity damps body oscillations and potential energy during the early swing phase often substitutes for muscular impulse (Figure 6).

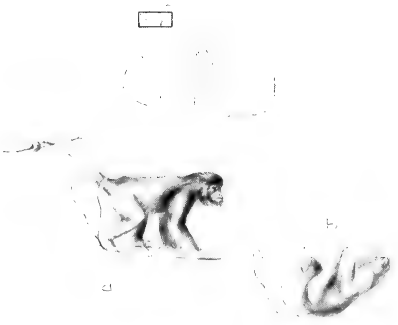

Figure 6. Balance above and below the support. A. *Alouatta*. B. *Choloepus*.

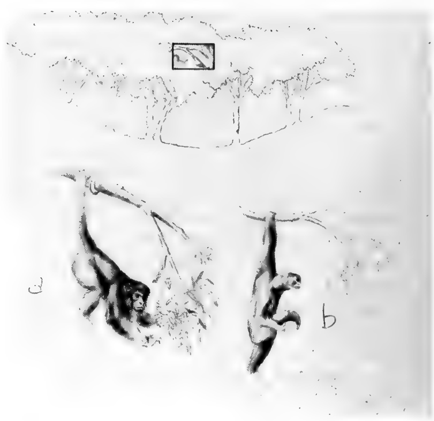

Figure 7. Feeding and descent techniques. A. *Alouatta*. B. *Bradypus*.

Two other properties of the canopy serve as barriers to movement and feeding. First, the branches are sensitive to absolute weight and deform downward (NOT up) under increasing strain. The farther from the axis of rotation the object moves, the greater the strain becomes. Second, open space surrounds each branch and, as a consequence, the greater an animal's reach immediately about his body, the greater his security and stability. Two functional situations, feeding and descent, reveal how the howler monkeys and sloths solve these mechanical problems.

During terminal branch feeding by *Alouatta*, the point of tail contact is near the base of the branch (Figure 7A). Deformation is reduced and the food bends down in front of the animal. If he moves along the top of the branch, the point of strain is farther out and the leaves and fruits bend away from him (Grand, 1972). The tail prehensility also increases space utilization and body weight dispersal among small branches.

Suspensory posture suggests another adaptation to leaf or fruit foraging. To obtain these immobile foods, an animal is not disadvantaged by either the truncal sway or the rotations which occur as a reaction to forward reaching. The animal's finger pads need not converge precisely, nor wrist and elbow exhibit good coordination. By contrast, an insect-eating relative of the howler monkey, the cebus (*Cebus capucinus*), does not (or cannot) forage suspended from his tail, and he has a hand that is noted for its dexterity and precision. One wonders at this point whether mobile foods, such as insects, acted as a selection pressure for finger precision and against selection for a prehensile tail and an unstable, suspensory trunk. The immobile fruits and leaves may permit the evolution of the prehensile tail and a less dextrous hand in howler, woolly (*Lagothrix*), and spider (*Ateles*) monkeys.

In vertical descent, suspension from tail or limb enables the animal to drop into a lower branch cluster with minimal strain, and branch deformation allows an ever closer proximity to the target (Figure 7B). The sloth further reduces the strain by a slow transfer of weight and by great flexibility of body and limb. An animal positioned above the branch, however, must jump down into the target branches and thereby generates rapid strain and great force. To solve identical problems of branch deformation and space control, the gibbon (*Hylobates*) has evolved a convergent set of motor behaviors (Grand, 1972, and in prep.).

Thus, the correlates of canopy movement are a reduction in the scope of motor activity, reduced musculature, increased use of passive anatomical mechanisms, increased body flexibility, and emphasis on specific muscle groups.

The second aspect of these data is the reassessment of body weight as a standard for physiology and ecology. Most investigators are aware of the components of weight when confronted by extreme adaptations like the sloth. Inert gut material and the metabolically less active tissues represent over 35 percent of the sloth's weight. In computing metabolic activity or standing crop biomass, the scientists have "corrected" or "adjusted" body weight for greater accuracy. In this manner, dress weight, offal, viscera, etc., have been used. None of these schemes, however, is completely adequate because none determines precisely HOW or functionally WHY weight is organized. Three examples from our data help to demonstrate this.

Both kangaroos and howler monkeys have tails of substantial size and weight (4 percent and 6+ percent TBW, respectively) which, however, differ functionally and anatomically. The kangaroo uses his tail on the ground to stabilize and to increase step length. Within the canopy, the howler uses his tail for moving and feeding. The tail of the iguana which is three times the weight of the howler tail apparently functions in balance as a counterweight. Agouti, cavy, and sloth possess comparable skills in their respective environments, but are tailless.

At 75 percent TBW, the truncal mass of the agouti and sloth is equal. Some components, like skin and truncal skeleton, are about equal. Others, however, are quite different. The weight in the back extensor muscles of the agouti is elevated, a marked locomotor adaptation, whereas the weight of the sloth gut is elevated, a basic nutritional adaption. If the relative weights of truncal mass in the 2 forms are tabulated, the results fail to distinguish these differences and to evaluate them functionally.

The mechanisms of muscle reduction differ substantially in the sloth and howler monkey. In the former, increased gut weight is accompanied by a reduction of truncal extensor, palmar, and plantar muscle. This correlates with a threefold physiological and behavioral reduction: of daily movement, basal metabolism, and metabolic scope (Sunquist and Montgomery, 1973; Montgomery and Sunquist, 1978; McNab, 1978; Britton and Atkinson, 1938). In the howler monkey, inert gut contents have (probably) increased, but the amount of muscle in back, tail, hands, and feet has remained the same as in its closest relatives (*Cebus, Ateles, Lagothrix*).

Body weight is thus neither a unitary nor an elemental biological quantity. How the species evolved 60–70 percent of weight to transport the remaining 30–40 percent (guts, teeth, sex organs) and whether the amount of musculature and the locomotor technique of the ancestors were the same must be determined. Corrections for physiological scaling or ecological computation can then be made. Functional analysis is not ancillary to these other studies; it is preliminary.

Summary

The proportional composition of locomotor tissues (skin, muscle, and bone) and the distribution of weight to limb segments and trunk are given for mammalian folivores (marsupials, primates, rodents, edentates) of divergent motor style. Although skin, muscle, and bone constitute over 65 percent of the total body weight in these animals, the relative proportion and regional disposition of these tissues vary considerably. Most differences in limb, back, and tail musculature can be correlated directly with motor pattern. Segmental distribution of body weight is also related to gross function. These data demonstrate that (1) components of weight reflect locomotor and feeding adaptations, (2) evolutionary pressures operate divergently on tissue and limb segment characteristics in different animals, (3) selection pressures operate convergently for economy of motion and conservation of effort, and (4) from the functional anatomical point of view, body weight is not a unitary biological property.

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Locomotion, Posture, and Habitat Utilization in Two Sympatric, Malaysian Leaf-Monkeys (*Presbytis obscura* and *Presbytis melalophos*)

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Introduction

Although arboreality may impose some broad restrictions on an animal's locomotion (Grand, 1978), an arboreal setting also provides opportunity for considerable locomotor diversity. No group of vertebrates shows a wider range of locomotor adaptations to arboreality than do living primates. While the diversity of primate locomotor abilities is well documented (Napier and Napier, 1967), attempts to relate this diversity to ecological parameters, such as forest strati-

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fication or substrate characteristics, have been largely theoretical or speculative (e.g., Avis, 1962; Napier and Napier, 1967; see review by Stern and Oxnard, 1973). An understanding of the ecological factors associated with locomotor behavior is necessary for understanding either the present diversity of the Order, or the evolution of primate locomotor behavior.

In absolute numbers, biomass, or taxonomic diversity, leaf-monkeys of the genus *Presbytis* are the most successful higher primates of south and southeast Asia. They are also the most important mammalian folivores in these regions. This paper describes the locomotor and postural behavior of 2 sympatric leaf-monkeys from peninsular Malaysia, *Presbytis obscura* and *Presbytis melalophos,* and relates differences in locomotion and posture to the use of forest strata and the arboreal supports within those strata.

Methods and Results

These results are based on observations made in West Malaysia in June–September 1973 and July 1974–March 1975. Incidental data were also collected in June–September 1972. Most of the observations were made in forested areas on the Lima Blas Estates, Selangor (see Bernstein, 1967, for a description of the site). Additional observations were made in the Krau Game Reserve, Pahang (Chivers, 1974; Curtin and Chivers, 1978), and Bubu Forest Reserve, Perak. Total contact time (including time spent filming) was over 500 hours for *P. melalophos* and over 300 hours for *P. obscura.* This study is restricted to the behavior of adult individuals. Further details of data collection are presented in the sections devoted to specific results.

All tests of significance were performed on the raw measurements. In Table 1 these measurements have

Table 1.

	Presbytis melalophos				
TRAVEL (*N* = 731)	*Quadrupedal walking and running*	*Leap*	*(hop)*	*Climbing*	*Arm swinging*
Percent of observed bouts	20.7	42.5	25.0	8.4	3.4
			67.5		
$\bar{x}$ distance per bout (m)	3.78	4.32	4.42	2.45	1.80
Meters per km of travel	196	460	275	53	15
FEED (N = 235)					
Percent of observed bouts	35.5	10.6	20.9	30.1	.9
$\bar{x}$ distance per bout (m.)	2.29	2.76	3.17	1.93	—
Meters per kilometer	346	124	286	244	
	Presbytis obscura				
TRAVEL (*N* = 348)	*Quadrupedal walking and running*	*Leaping*	*Climbing*		
Percent of observed bouts	50.6	40.2	9.2		
$\bar{x}$ distance per bout	5.67	3.18	2.58		
Meters per Km of travel	660	287	53		
FEED (*N* = 235)					
Percent of observed bouts	68.6	15.0	16.4		
$\bar{x}$ distance per bout	2.84	1.39	1.55		
Meters per kilometer	810	90	100		

been converted to percentages for easier comparison. Figures 2–7, and 10 are rendered from tracings of 16mm cine films taken with a Beaulieu R16B camera at speeds between 24 fps and 64 fps.

Diet

Presbytis obscura and *Presbytis melalophos* differ considerably in diet. *P. obscura* eats predominately leaves and leaf-parts, whereas fruit and seeds make up the larger portion of the diet of *P. melalophos.* Because of their high biomass densities (Curtin and Chivers, 1978), both species are important folivores.

Foraging patterns

A troop of *P. melalophos* forages as a cohesive group. Generally, members of a troop sleep, rest, and move from food source to food source as a single unit. By contrast, a troop of *P. obscura* may sleep together in the same or adjacent trees and often forage or rest together in early morning or late evening; however, for most of the day, the troop divides into smaller foraging parties which often spend long periods of time in a single tree. (Curtin, personal communication; Curtin and Chivers, 1978; personal observation).

Utilization of forest strata

A cross section of Malaysian rain forest suggests 3 structural levels. The main canopy is a horizontally continuous stratum containing most of the large trees. It provides a network of large boughs and branches upon which quadrupedal animals can travel horizontally. The understory may be vertically continuous with the main canopy, but is discontinuous horizontally. The trees of the understory are smaller and available supports are less stable than those of the main canopy. Horizontal movement within the understory requires that an animal (1) ascend to the main canopy, (2) descend to the ground, or (3) possess some locomotor method (fly, glide, leap) of crossing discontinuities in the forest. Emergents form the uppermost stratum. These giant trees, up to 60 meters high, are separated from one another horizontally, and their canopies are often separated vertically from the main canopy. Progression into, from, or between emergents entails climbing up or down the trunks from the main canopy or making long leaps. Within an emergent, large boughs connect different parts of the tree. Because absolute vertical height of different strata may vary considerably from forest to forest and is meaningless in hilly areas, habitat utilization is more easily analyzed in terms of these more consistent structural units.

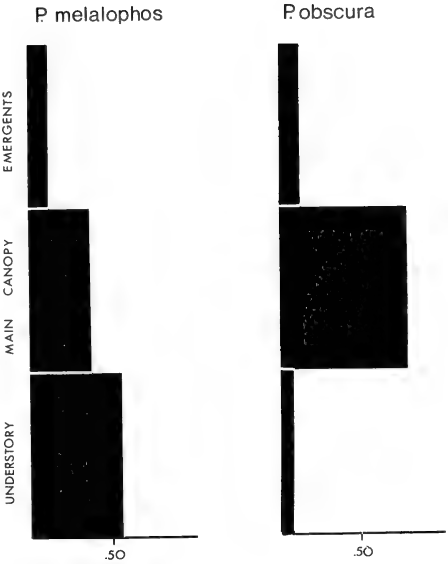


Figure 1. Distribution of feeding observations for *Presbytis melalophos* and *Presbytis obscura* in different structural levels at the Krau Game Reserve, Pahang, Malaysia.

The distribution of feeding observations for the 2 species in the Krau Game Reserve is presented in Figure 1. To prevent biases due to observer presence, only first sightings have been included. Sightings of *P. obscura* were primarily in the main canopy and to a lesser extent in the emergents. *P. melalophos* ranges throughout all levels, but spends more time foraging in the understory than does *P. obscura*. Observations in other localities indicate a similar pattern. The locomotor and postural differences described below can be interpreted as adaptations to utilization of these different structural levels.

Locomotor behavior

The locomotor activities of the 2 leaf-monkeys can be divided into 4 categories on the basis of limb usage:

QUADRUPEDAL WALKING AND RUNNING (*Figure 2*) continuous, usually horizontal progression using 4 limbs in alternating regular, or nearly regular sequences.

LEAPING (*Figure 3*) progression between discontinuous supports using rapid extension of the hindlimbs for propulsion. Landing usually involves both arms and legs. A series of consecutive leaps is described as hopping (Figure 4).

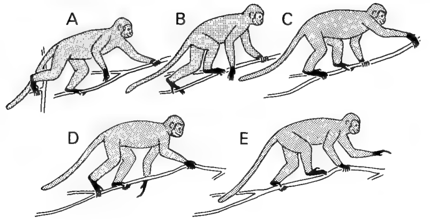
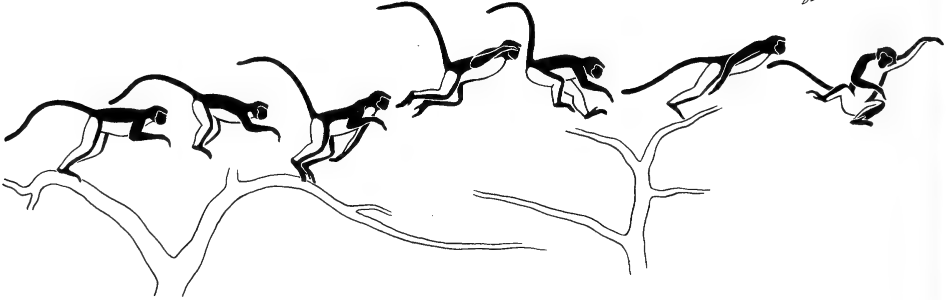


Figure 2. *Presbytis obscura* walking quadrupedally along a branch.

Figure 3. *Presbytis melalophos* leaping.

Figure 4. *Presbytis melalophos* hopping.



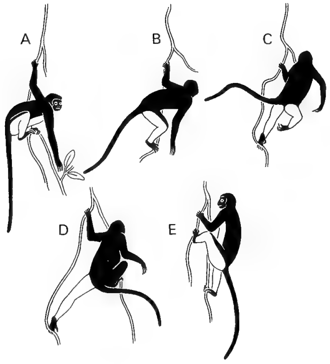


Figure 5. *Presbytis melalophos* climbing up a small vine.

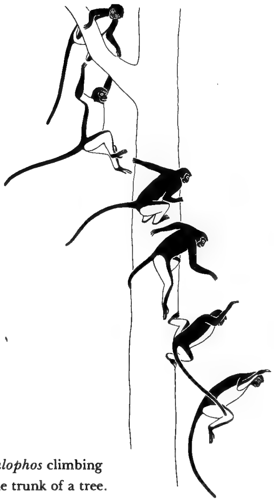


Figure 6. *Presbytis melalophos* climbing down the trunk of a tree.

Figure 7. *Presbytis melalophos* progressing bimanually along a bough following a leap. Note the extensive trunk rotation.

CLIMBING (*Figure 5,6*) continuous progression, often vertical, involving various combinations of 3 or more limbs. Arms are used primarily to pull the body up while hindlimbs push.

ARMSWINGING (*Figure 7*) bimanual progression.

Observations were made by following adult individuals during daily activities and recording the sequence of individual locomotor bouts (modified after Prost, 1965), the distance traveled during the bout, and the size of the substrate providing support. A sample of traveling behavior might be recorded as follows:

Quad—5 meters—bough
Leap—10 meters—branch to branch
Rest
Quad—6 meters—branch

Arboreal supports were grouped into 3 categories on the basis of estimated diameter—bough (≥ 10 cm), branch (<10 cm, >2 cm), and twig (≤ 2 cm). For analysis, observations were divided into 2 categories on the basis of associated activity: (1) *locomotion during travel,* movement to and from sleeping trees or between food sources; and (2) *locomotion during feeding,* movement during a feeding session, within a single food tree or group of trees and vines.

The percentage of bouts of different locomotor patterns and the average distance traveled per bout are given in Table 1. The 2 species show significant differences in the relative use of locomotor patterns during travel (Figure 8) (χ^2 test, $P < .05$). Quadrupedal walking and running account for over 50 percent of the observations of *P. obscura,* but only 20 percent in *P. melalophos.* Leaping and hopping account for 67 percent of the bouts of *P. melalophos,* but only 40 of those for *P. obscura.* Climbing is equally common in the 2 species; only *P. melalophos* progresses bimanually.

In *P. melalophos,* bout lengths are similar for

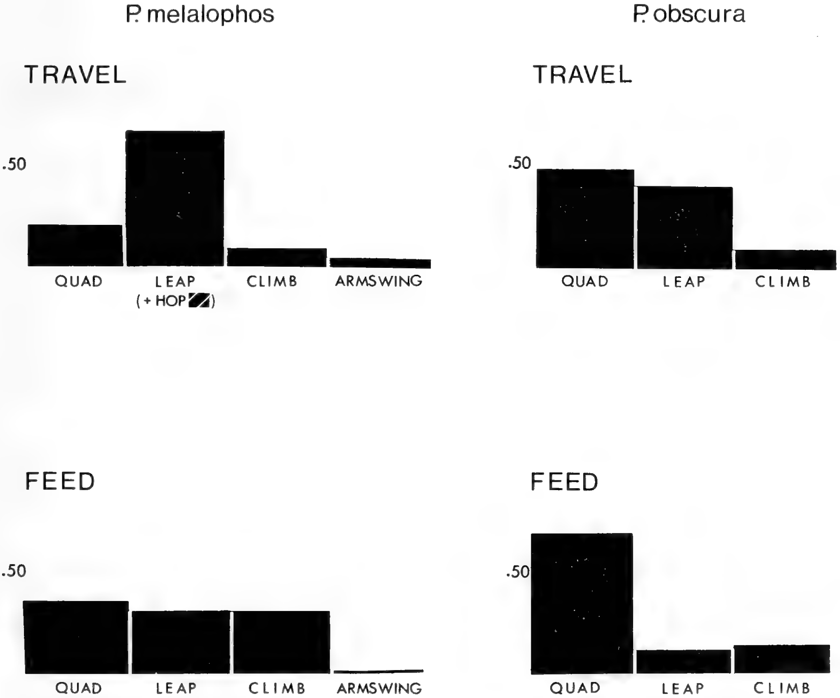


Figure 8. Bout frequencies of different locomotor patterns in locomotion during travel and locomotion during feeding.

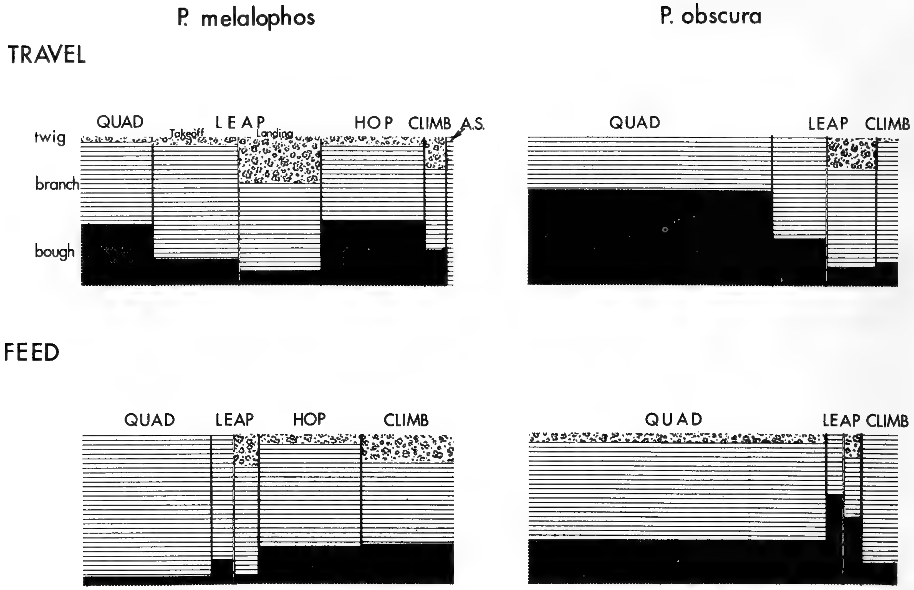


Figure 9. Distribution of locomotor patterns on different-sized supports in locomotion during travel and locomotion during feeding. Horizontal axis shows the contribution of different patterns in each kilometer of progression; vertical axis gives the proportion of that distance that is moved on different types of supports. In *P. melalophos* hopping is separated from other forms of leaping. For leaping, take-off supports and landing supports are shown separately.

quadrupedal walking and running or leaping and hopping; climbing and armswinging bouts are shorter. Quadrupedal bouts of *P. obscura* are significantly longer than bouts of any other locomotor activity of either monkey. This reflects the extensive utilization of continuous main canopy supports by that species. The leaps of *P. obscura* are shorter than those of *P. melalophos*.

In both species, the relative use of locomotor patterns during feeding is significantly different from that during travel (χ^2 test, $P < .05$). Both use more quadrupedalism and climbing and less leaping. In *P. melalophos* the use of bimanual progression during feeding is negligible, and hopping is more common. Individuals of *P. melalophos* tend to hop between different parts of a large feeding tree, and climb or move quadrupedally within smaller regions of the tree. For all locomotor patterns, bout distances are significantly smaller in locomotion associated with feeding than in travel (t test, $P < .05$). The scale of distances involved in feeding sessions is smaller than that in travel; the former takes place within a tree, the latter within a home range.

One can calculate from the percentage of bouts and the average bout distance, the contribution of each pattern of locomotion in an average kilometer of progression (Table 1, Figure 9). Since cost of locomotion for a given species is a function of the distance traveled and manner of progression, rather than speed or time spent moving (Taylor, *et al.*, 1970), this approach should be appropriate for analyzing energy expenditure. This type of analysis further contrasts the locomotor differences between the 2 leaf-monkeys by emphasizing the patterns with long bout distances—leaping in *P. melalophos,* and quadrupedal walking and running in *P. obscura.*

Locomotion and support size

The size of the substrate providing support was estimated for each locomotor bout. The distribution of locomotor patterns on supports of different size is shown graphically in Figure 9. Two major patterns are apparent. First, *Presbytis obscura* travels predominantly on boughs; *P. melalophos* travels on or between branches. Second, both species move on smaller supports in locomotion associated with feeding than in travel. Locomotion during feeding must take place among the smaller branches where food (fruit, leaves, flowers) is located; travel may potentially occur on a variety of available supports.

The 2 species show a number of similarities in the details of support use. Leaping occurs on smaller supports than does quadrupedal walking and running, except during feeding in *P. obscura* when the monkeys are moving between the boughs of large trees. Takeoff supports are larger than landing supports. Climbing is primarily among branches.

Feeding postures (Figure 10)

Feeding postures were sampled at 2 minute intervals during feeding sessions. Posture, limb use, and support size was recorded for each observation. Feeding postures were divided into 2 categories—seated postures (Figure 10:A,B,C,F,E,H) and hanging postures (Figure 10:D,E). Seated postures are used predominantly by both species (Figure 11): *P. melalophos* uses suspensory postures more frequently than does *P. obscura*.

The distribution of seated feeding postures on different supports is shown in Figure 12. Both species sit mainly on branches; *P. obscura* shows a tendency to sit on boughs while *P. melalophos* uses the smallest supports more than does its congener.

Summary of results

Presbytis obscura restricts its feeding activities largely to the main canopy and emergents, where it travels predominantly by quadrupedal walking and running along large boughs. In contrast *P. melalophos* feeds more in the discontinuous understory where it travels more by leaping and hopping between smaller supports. Movement, support use, and postural behavior during feeding are more similar in the 2 species than is locomotion during travel. The differences between species are, nevertheless, consistent, with *P. obscura* moving more quadrupedally, and using more seated postures on larger supports than *P. melalophos*.

Discussion

The results above illustrate how the locomotor and postural behavior of 2 sympatric leaf-monkeys can be related to differences in utilization of structural regions of a Malaysian rain forest. In this section I would like to discuss briefly several other aspects

Figure 10. Feeding postures of *Presbytis melalophos* (A-E) and *Presbytis obscura* (F-H).

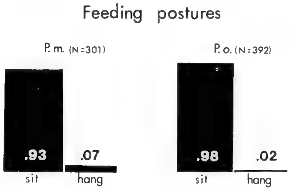


Figure 11. Relative use of different feeding postures by *Presbytis melalophus* and *Presbytis obscura*.

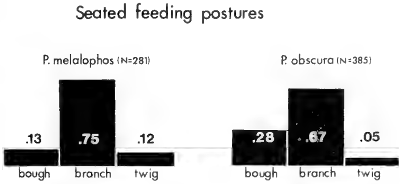


Figure 12. Distribution of seated feeding postures of *Presbytis melalophos* and *Presbytis obscura* on different-sized supports.

of the relationship between locomotor adaptation and habitat utilization.

Ontogenetic differences in locomotion and posture

The results above are based totally on the behavior of adult individuals and thus provide a restricted view of the role of locomotion and posture in habitat utilization. Locomotor and morphological differences (e.g., weight, limb proportions, muscle proportions) between immature and adult individuals of the same species are often as great as the differences between adults of different species. The different locomotor and postural abilities of young animals permit them to utilize different aspects of the habitat from adults of the same species (e.g., Clutton-Brock, 1973). This diversity of abilities within a single troop or population should be an important consideration in evaluating the effect of a particular species on the available resources.

Diet and foraging

The diet and foraging strategies of the 2 leaf-monkeys can be related to their locomotor differences only in a very general way. The ability of *P. obscura* to eat mature leaves and unripe fruit which other animals apparently cannot digest (Chivers and Curtin, 1978) probably permits their more sedentary habits. By contrast, the greater mobility of *P. melalophos* presumably derives from their greater reliance on fruit and new leaves which may be more widely scattered and temporally restricted in availability. Similar differences between sympatric colobine species, in which the more folivorous species is less mobile, have been noted by other workers (Ripley, 1967 for *P. entellus* and *P. senex* in Sri Lanka (Ceylon); and Clutton-Brock, 1974, for *Colobus badius* and *Colobus guereza* in East Africa). Whether these differences are related primarily to the differential distribution of food sources (Clutton-Brock, 1974) or whether they also reflect energetic constraints imposed by leaf-eating (McNab, 1978) cannot be determined at present. Too little is known of either the spatial and temporal distribution of palatable foods in Malaysian forests or the physiology of leaf-eating monkeys to distinguish causal relationships from associations.

Aside from these general patterns of mobility, comparative data suggest that among forest primates broad correlations between diet and particular locomotor activities are unlikely. Among sympatric Malaysian species, there are no apparent trends. Of the 2 colobines, the more folivorous (*P. obscura*) is the more quadrupedal; however, the long-tailed macaque (*Macaca fascicularis*) is more quadrupedal than either leaf-monkey, and probably more frugivorous (Curtin and Chivers, 1978). Similarly, *P. melalophos* is more frugivorous than *P. obscura* and also uses more bimanual progression; however, the siamang (*Symphalangus syndactylus*) uses more bimanual progression than either leaf-monkey and is largely folivorous (ibid.).

Anatomical Adaptations

In the results above, I have concentrated on the associations between locomotor behavior and habitat utilization in the 2 leaf-monkeys. No mention has been made of the problem which is fundamental to the study of primate locomotion. Do these locomotor differences reflect the behavioral flexibility of a single morphology to different environmental conditions; or do the two species show morphological adaptations in their musculo-skeletal anatomy that can be related to the locomotor differences? In view of the locomotor flexibility that has been attributed to extant primates, either interpretation is reasonable. As discussed elsewhere (Washburn, 1944; Fleagle, 1977, in press). *P. melalophos* and *P. obscura* show numerous differences in muscle mass distribution, arrangement of individual muscles, skeletal proportions, joint mobility, and details of skeletal morphology that can be related to their differences in locomotor behavior. The presence of such morphological differences in animals as behaviorally flexible as primates emphasizes the importance of differences in habitat utilization in the natural selection of locomotor morphology.

Conclusions

Many workers (e.g., Avis, 1962; Napier, 1966, 1967; Napier and Napier, 1967; Stern and Oxnard, 1973) have stressed the need to relate primate locomotor behavior to support use and forest stratification. However, there has been little detailed evidence for such associations. The results of this study provide evidence of detailed differences in locomotion and posture that are associated with differences in the use of arboreal supports and structural levels within the Malaysian rain forest. The general level of locomotor activity seems to show an association with diet; the more folivorous species is less active. However, there is no evidence for association between any particular locomotor activity and diet. The presence of numerous morphological differences between the 2 species suggests that differences in habitat utilization such as those described here can have an important effect in the evolution of locomotor morphology.

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Feeding and Associated Positional Behavior of Black and White Colobus Monkeys (*Colobus guereza*)

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Introduction

The present study began in September 1974 and quantitative data collection began in November 1974. Data collected from November 1974 through March 1975 are reported here. It is hoped that field work will be continued until a complete annual cycle has been covered, and this is a preliminary report on one aspect of a field study which is in progress. The study is aimed at collecting quantitative data on positional (postural and locomotor) behavior, its relationship to habitat structure, its association with maintenance and social activities, and its temporal variation and variation between different age-sex classes. Data are being collected on a troop of vervet monkeys (*Cercopithecus aethiops*) and a troop of a species of black and white colobus monkey, the guereza (*Colobus guereza*). This report concentrates on some aspects of the feeding behavior of the guerezas. Useful supportive information on colobus monkeys is contained in the papers of Ullrich (1961), Schenkel and Schenkel-Hulliger (1967), Marler (1969 and 1972), Leskes and

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Figure 1. Mature acacias in northern part of home range. Trees reach up to 30m in height. Ground cover is mainly grass as a result of scrub clearing. Guerezas come to the ground here mainly to play or progress to other parts of the home range.

Acheson (1971), Groves (1973), and Morbeck (1974 and 1975). More specific information on feeding behavior is available from the studies of Clutton-Brock (1974a), Dunbar and Dunbar (1974), Oates (1974, 1977), Struhsaker and Oates (1975), and McKey (1978).

The Study Area

The study site is an area of riparian acacia forest on the shore of Lake Naivasha in the Rift Valley of Kenya, East Africa, at an altitude of 1884 m above sea level (Figure 1). A grid of 30-by-30-m quadrats was mapped over an area within which the guereza troop ranges, and the position of all trees over 3 m high within each quadrat was plotted. Fever trees (*Acacia xanthophloea*) form 58 percent of such trees, pepper trees (*Schinus molle*) 16 percent, fig trees (*Ficus vallis - choudae*) 13 percent, and 15 other species of trees the remaining 13 percent. The peppers and most of the trees in the last group are domestic trees grown wild. They originated in an orchard and garden that were maintained in the study area up to about 30 years ago (D. Iceley, personal communication).

The northern two-thirds of the study area, which includes the base of a lava ridge running parallel to the lake, contains mostly mature trees ranging from about 10 to about 30m in height, while the southern third consists mainly of regenerating acacias reaching a maximum of about 7 m in height. Ground cover consists of low bushes, creepers, and vines in the southern half of the area, and meadow, resulting from clearing to provide grazing for cattle, in the northern half. There is a mean of 60 trees over 3 m tall per ha, although there is considerable variation in different parts of the area, with densities ranging from 0 to 242 trees per ha.

Virtually no rain fell during the period reported on here, although the long rains of 1974 continued until the beginning of October and the vegetation was still comparatively lush in November. Considerable drying out of the thicker ground cover, however, had occurred by March 1975. The acacias flowered in September and October 1974, and immature fruits were beginning to form in late October. The pods had dried and the seeds were hard by the beginning of March 1975. Flowering of the figs preceded the start of the study period and trees were bearing unripe fruit throughout the period reported on.

The Study Troop

The guereza home range is 4.8 ha, estimated from those quadrats which they occupied during the recording of quantitative data. Individuals have been observed outside this area during periods of casual observation, and a final estimate of home range size will no doubt be larger. About five ha, however, is probably a good estimate of the most extensively used part of the complete home range.

The guereza troop is a large one, consisting of 19 animals at the time of writing. The troop includes 2 adult males and 3 adult females, 4 large juvenile males and 3 large juvenile females, 2 small juvenile males and 2 small juvenile females, 2 female infants, and 1 infant of undetermined sex. This troop size is equal to the largest of the troop sizes reported in Groves's (1973) survey of the literature for black and white colobus monkeys. The guereza density is considerably higher than that of the guerezas studied by Oates (1974, 1975) and Dunbar and Dunbar (1974). However, the preliminary estimate of home range size is probably low, and final estimates of density may be lower. There are 15 trees per animal for the study troop, about 2 trees per animal more than the maximum given for a number of guereza troops by Dunbar and Dunbar, who suggest that density estimates *per se* may be equivocal, but that estimates of (especially food) trees per animal might have more meaning.

While there are other guereza troops in the same general area, there are no contiguous troops. The nearest troops are about 3 km away in an acacia forest beside a lake in a volcanic crater; they are out of visual and auditory contact with the study troop. Another troop lives several kilometers away along the lake shore and is in auditory, but not visual, contact with the study troop.

Table 1.—Percentage of time spent feeding and in progression associated with feeding at different times of the day.

Progression associated with feeding is defined as progression taking place between feeding bouts, or followed by a feeding bout.

	Hour of day													
	06–07	*07–08*	*08–09*	*09–10*	*10–11*	*11–12*	*12–13*	*13–14*	*14–15*	*15–16*	*16–17*	*17–18*	*18–19*	*Average*
Feeding	9.1	28.0	45.0	38.3	20.8	37.1	21.3	22.5	26.0	22.1	44.2	39.7	36.9	30.0
Progression Associated with Feeding	0.2	0.3	0.6	0.5	0.2	0.5	0.2	0.1	0.4	0.4	0.5	0.5	0.5	0.4
Total	9.3	28.3	45.6	38.8	21.0	37.6	21.5	22.6	26.4	22.5	44.7	40.2	37.4	30.4

Recording Methods

The data reported here were gathered by making a spoken recording of a particular animal's activities over a half-hour period in order to provide quantitative time budget information. The particular animal which was observed during each period was chosen by locating all animals of the required age-sex class and then selecting 1 on the basis of a rotating schedule of first-located, second-located, and so on (depending on how many animals there were in that age-sex class) in order to minimize visibility biases in selection. Recording periods were started on the hour or half-hour to prevent uneven sampling from within hourly periods. The variables recorded included time of day, age-sex class, weather conditions, positional activities, social or maintenance activities, support utilization, food plant utilization, height above the ground, and other variables related to particular activities. Longer activity periods were timed with a stopwatch in the field, shorter periods were timed during transcription of the records onto checksheets. During the 5-month period 162½ hours of records were made, equal numbers of records being made for each hour of the day, and nearly equal numbers for each age-sex class.

Because of the preliminary nature of this report some data will not be presented here, or will be mentioned only briefly. These include data concerning activities other than those associated with feeding, detailed descriptions of positional activities and feeding techniques, quadrat occupancy, use of individual trees or trees of a particular species, and height above ground at which different activities are performed. It has not been possible to carry out statistical tests of significance of differences in the data presented here, so only the more marked features of the data will be commented on. Data for all hours of the day and for all age-sex classes have been lumped for the analyses presented below, except for the data in Table 1.

Results

Feeding.

Ripley (1970) has characterized the feeding activities of another predominantly leaf-eating colobine monkey, the gray langur (*Presbytis entellus*), as consisting of a series of bouts during which an animal sits and gathers food, possibly making some postural changes but not making any gross movements. A number of bouts, between which an animal makes short moves to new locations, make up a feeding interval. An animal moves across a tree or between trees in the time between feeding intervals. Several feeding intervals make up a feeding period, at the end of which an animal will rest or make a major move. This basic pattern seems to be common to most arboreal herbivorous primates. The major differences among species seem to relate to variations in the length of feeding bouts and intervals and the duration of periods of progression between bouts and intervals.

For the guereza troop not much progression occurred in association with feeding; it accounted for only 0.4 percent of all activities on a time basis (Table 1). Feeding per se accounted for 30 percent of all activities. This is relatively low compared to the amount of time many other primates spend feeding. Thus, vervet monkeys ranging in the same area during the same time and feeding largely on the same food plants as the guerezas spent 47 percent of the time feeding. Olive baboons (*Papio anubis*), ranging mainly on the ground at a nearby site (Rose, 1977), also spent 47 percent of the time feeding. If progression associated with feeding is included, these

Table 2.—Frequency of feeding bouts of different durations.

This table is based on the 897 bouts which both started and terminated within the half-hour recording periods, and is, therefore, biased towards excluding some bouts of longer duration.

	Duration of Bout in Minutes													
	0–1	*1–2*	*2–3*	*3–4*	*4–5*	*5–6*	*6–7*	*7–8*	*8–9*	*9–10*	*10–11*	*11–12*	*12–13*	*13–14*
Number of bouts	223	248	156	89	52	44	31	17	12	4	9	5	5	1
Percentage of Total Bouts	24.9	27.7	17.4	9.9	5.8	4.9	3.5	1.9	1.3	0.4	1.0	0.6	0.6	0.1
Percentage of Total Time	4.7	15.8	16.5	13.2	9.9	10.3	8.5	5.4	4.3	1.6	4.0	2.5	2.7	0.6

figures become 48 and 64 percent for vervets and olive baboons, respectively.

The pattern of variation in the time the guerezas spent feeding throughout the day (Table 1) is fairly typical of most arboreal primates in that there are 2 main peaks of feeding activity during the day. One of these occurred between 8 and 10 o'clock in the morning and the other during the last 3 hours of the day. Animals only spent about 2 percent of feeding time on the ground. The guereza feeding pattern was characterized by relatively long bouts and intervals, by very short periods of progression between bouts and intervals, and by feeding periods separated by relatively long periods of resting. All troop members tended to start and finish feeding periods at about the same time, although the timing of bouts and intervals seemed to be related to food availability and distribution in the immediate vicinity of individual animals. Just under half the feeding bouts were longer than 2 minutes (Table 2). Bouts lasting between 1 and 2 minutes occurred more frequently than any other. About half of the feeding time, however, was made up of bouts lasting longer than 4 minutes. This situation contrasts with that of vervet monkeys, in which bouts lasting for less than a minute make up nearly half of all bouts and also occur more frequently than other bouts. About half of their feeding time is made up of bouts lasting less than 2 minutes.

Support utilization

Branches used during feeding and associated progression were classified into 9 types on the basis of size and grade. The problem with a size classification in the context of positional behavior is that branch size is relative to the size of the animal active on it. Branch sizes are therefore defined in a way which attempts to take this into account. A small branch was one which deformed appreciably when an animal was on it. A medium-sized branch was one on which an animal placed its hands and feet in line during quadrupedal progresstion. Medium-sized branches ranged from about 2 cm to about 8cm in diameter. A large branch was one on which an animal could perform positional activities more or less as it would on the ground. The 3 categories of horizontal, sloping, and vertical branches each include branches within 30-degree ranges between the true horizontal and vertical.

Medium-sized branches were used for nearly three-quarters of the time spent feeding (Table 3). Just over two-thirds of the time was spent on horizontal branches, with almost all of the rest of the time being spent on sloping branches. On such branches, animals could adopt stable postures and still be within reach of terminal sprays of leaves. However, stable postures could still be adopted on small-sized branches, especially if they were horizontal. The degree to which particular types of branches were used must depend to a certain extent on the fre-

Table 3.—Percentage of feeding time spent on different support types.

Criteria used for size of branches are given in the text.

	Horizontal	*Sloping*	*Vertical*	*Total*
Small	16.1	8.2	<0.1	24.4
Medium	51.2	21.1	<0.1	72.3
Large	0.8	2.5	0.0	3.3
Total	68.1	31.8	0.1	

quency with which branches of different types occur within the habitat. This information is not yet available.

Positional activities

There is a spectrum of postural and to a certain extent locomotor activities, and division of this spectrum into discrete categories tends to disguise this fact. Data collection methods were used which treat positional activities as a spectrum, but a complete exposition of these methods and the results obtained from them is beyond the scope of this report. However, the categories reported on all represent the activities within the spectrum which are regularly used during feeding and its associated progression.

Sitting was by far the most frequent activity during feeding (Table 4). Animals sat on branches close to food sources, usually with 1 or both of the ischial callosities resting on the branch. The feet either rested on the branch, took grips, or were propped against nearby branches to stabilize the posture. One hand sometimes gripped a branch to provide additional support, but more frequently both hands were used for food gathering. The tail usually hung straight down (Figure 2).

Manipulation during food gathering and in other situations has been studied in detail by Morbeck (1975 and personal communication), and only a brief account will be given here. Animals gathered leaves directly from a branch, usually by gripping them between the flexed fingers and the palm or the base of the reduced thumb, and then pulling. The other hand was sometimes used to grip or pull in the branch from which leaves were taken. A stripping technique was occasionally used. Animals plucked leaves with their mouths in some situations, particularly when they were supporting themselves with one hand and were holding the leaf-bearing branch with the other. Small, round objects such as fig fruit were sometimes gathered with the hand, the second and third digits gripping the object against the base of the reduced thumb. The hand was frequently ulnar deviated and the forearm fully pronated during this type of manipulation. However, plucking with the mouth was more usual with small, round objects.

Postures other than sitting were used very rarely (Table 4). Bipedal standing was used to pull down branches from an overhead position (Figure 3). Tripedal standing, in which the free hand gathered food, usually occurred after a bout of locomotion, prior to sitting. Suspension was occasionally used by younger animals among small branches, but only briefly. Feeding in a lying posture occasionally occurred during periods of resting.

Table 4.—Percentage of feeding time spent in different positional activities.

	As a percentage of time spent in feeding postures	*As a percentage of time spent in feeding and progression associated with feeding*
Sit	99.9	98.6
Bipedal Stand	<0.1	<0.1
Lying	<0.1	<0.1
Suspension	<0.1	<0.1
	As a percentage of time spent in progression associated with feeding	
Quadrupedal Walk	47.8	0.6
Climb up	19.9	0.2
Climb down	16.3	0.2
Leap [1]	15.4	0.2
Quadrupedal Run	0.5	<0.1
Tripedal Walk	0.1	<0.1
Suspension	<0.1	<0.1

[1] Leaps are arbitrarily given a duration of one second.

Locomotor activities accounted for only 1.3 percent of all activities associated with feeding (Table 4), indicating a very conservative pattern of movement associated with feeding. Quadrupedal walking was the most frequently used locomotor activity. The distinction between quadrupedal walking and quadrupedal running is made on the basis of speed of progression (Hildebrand, 1966). Guerezas use galloping and bounding gaits at all speeds of progression. Climbing and leaping were other locomotor activities used with relative frequency.

Progression between feeding bouts was usually by quadrupedal walking with some leaping. Such progression often involved an animal making its way fairly slowly and carefully across masses of small branches. Progression after a feeding interval usually involved a combination of quadrupedal walking, climbing, and leaping. An animal made its way some distance toward the center of a tree and then moved peripherally again to a new food source, or moved between trees. Progression before or after a feeding period usually involved a combination of quadrupedal walking, climbing, and leaping. Such

Figure 2. Guereza sits feeding on medium sized horizontal branch. The posture is stabilized by foot grips and one hand grip while leaves are gathered with the free hand.

Figure 3. Guereza stands bipedally on sloping medium-sized branch of fig and gathers fruit with free hand.

progression was usually a troop activity involving a series of fairly short moves separated by short periods of resting, and usually involved a major change of location.

Progression preceding or following a feeding period involved the use of habitual pathways through the canopy along which troop members traveled one after the other. These pathways were mostly made up of medium-sized branches with a minimum of gaps that required crossing by leaping. There were usually a number of available pathways along branches, but they all tended to converge on leaping sites where the characteristics of the takeoff and landing sites were well known to the animals through frequent use. There were only 3 sites within the home range that required leaps of more than about 3 m to be made, and even these were easily negotiated by the youngest troop members capable of independent progression (Figure 4).

Leaps occurred on average nearly 7 times per hour of feeding and progression associated with feeding. Horizontal or sloping branches were favored both as takeoff and landing sites (Table 5). Medium-sized branches were favored for both takeoff and landing, although small-sized branches were used fairly frequently (Table 6).

Food plant use

About half the feeding time was devoted to acacia leaf, with unripe acacia fruit and unripe fig fruit forming other staples (Table 7). Leaves of a variety of other plants made up the rest of the diet. These other plants were rarely used as the main food source during any particular day but were used at the end of a feeding period devoted to 1 of the 3 main food sources or at the most were used during a feeding period toward the end of the day.

Figure 4. Three guerezas rest during a group progression along a habitual pathway. Animals tend to move one after the other along the same pathways during major changes of location. This pathway leads up a large diameter sloping branch from a feeding site close to the ground.

Table 5.—Percentage of 340 leaps made between supports of different grades.

	Take-Off				
Landing	*Horizontal*	*Sloping*	*Vertical*	*Ground*	*Total*
Horizontal	31.0	14.4	0.0	0.6	46.0
Sloping	20.9	26.5	0.0	0.9	48.3
Vertical	0.9	0.6	0.3	0.3	2.1
Ground	2.7	0.6	0.3	0.0	3.6
Total	55.5	42.1	0.6	1.8	

Table 6.—Percentage of 340 leaps made between supports of different sizes.

	Takeoff				
Landing	*Small*	*Medium*	*Large*	*Ground*	*Total*
Small	15.2	17.8	0.6	1.2	34.8
Medium	11.8	42.0	1.8	0.6	56.2
Large	0.6	2.4	2.4	0.0	5.4
Ground	1.2	2.1	0.3	0.0	3.6
Total	28.8	64.3	5.1	1.8	

Table 7.—Percentage of monthly feeding time spent feeding on different food plant parts.

	Nov.	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Average*
Acacia Leaf	0.0	32.6	76.2	66.1	59.1	51.0
Unripe Acacia Fruit	68.1	8.4	9.3	8.9	0.0	16.4
Unripe Fig Fruit	17.8	35.4	2.1	7.8	14.8	14.6
Other Leaf	14.1	23.6	12.4	17.2	26.1	18.0

There was considerable variation in the degree to which various types of food were used during the 5-month period (Table 7). The main factor influencing this variation was probably the availability of unripe acacia fruit pods. Flowering and fruiting of the acacias were nearly synchronous, both for different parts of the same tree and for different trees. Immature fruit pods began to form in mid-October, when the guerezas began feeding on them while continuing to feed on a acacia leaf, which had been the main food source during September. By the beginning of November most acacias bore large numbers of green pods up to 10 cm in length. The pods themselves were still fleshy and contained soft, green, developing seeds. During November the guerezas spent about two-thirds of their time feeding on acacia pods, and had completely stopped feeding on acacia leaves. In the next 3 months the acacia pods gradually hardended, as did the seeds. No pods were eaten after they had reached full maturity and began to dry out. The relatively low levels of utilization of acacia pods from December through February represent the use of more mature green pods, but also the selection of younger pods from parts of trees or individual trees that were slightly out of phase with the majority of acacias in the habitat. Animals seemed to be much more selective when feeding on acacia pods during these months than they had been in November.

Acacia leaves were taken again in December, when animals spent about one-third time gathering them.

The guerezas spent about three-fourths of their time at this food source in January, although less time was spent taking leaves in February and March. While guerezas are selective in their choice of acacia leaves, they take all except the most mature leaves. The acacias produce new leaves all the time, perhaps owing to constant water availability related to the riparian nature of the habitat.

Unripe fig fruit was available throughout the 5-month period, and the extent to which this food source was used seems to have been in part dependent on the extent to which acacia leaf and fruit was used. Oates (1974) also found that the utilization of fig fruit by guerezas did not correspond closely to its availability but seemed to be dependent on the availability of more favored food items. The use of other food plants also varied somewhat from month to month, but not to the extent to which that of fig fruit varied. These plants may, therefore, form a supplement to more staple food sources, and the degree to which they are used may depend on the relative availability of both the staples and of the supplements themselves.

Discussion

Perhaps the most obvious point to make about guerezas, thought to be leaf-eating monkeys, is that they are also to an extent frugivorous. Indeed, nearly one-third of feeding time was spent gathering and eating fruit during the period reported on. The inclusion of fruit in the diet has been noted by most of the authors who have worked with either the African or Asian leaf-eating monkeys.

The guereza troop which is the subject of this report is perhaps rather odd in that it is both large and isolated. While there are areas contiguous with the study site which could support guerezas, the troop showed no signs of splitting, or even utilizing these areas as an intact troop. The guereza density may be high, but there would seem to be adequate food sources within the home range to support the present population. During the period reported on, a troop of 16 vervet monkeys were also utilizing both fig and acacia fruit, and a number of bird species were also actively taking fig fruit. The fact that acacia leaves, which were the major food source, were produced with minimal seasonal variation may also be important. The age-sex profile of the troop would seem to indicate that the troop is flourishing within its present habitat.

The biphasic pattern of diurnal feeding activity shown for the period reported is not confined to leaf-eating primates, arboreal primates, or even the primate order (Clutton-Brock, 1974b; Rose, 1974). Although diurnal temperature change seems to be a likely factor in producing a biphasic pattern, the actual factors responsible for the pattern in a particular time may be varied (Clutton-Brock, 1974b). The pattern of activity on any day may depart somewhat from the overall pattern. Thus, in different species and populations, and perhaps in the same population at different times, the peaks of a biphasic pattern may occur at different times of the day. Three peaks, 1 peak, or a continuous feeding pattern may also occur, indicating that the causation of different patterns may be somewhat complex.

Despite a fairly typical pattern of diurnal variation in the amount of time spent feeding, guerezas spent relatively small amounts of time feeding when compared with some other primates. Guereza feeding times observed by Oates (1974, 1977) and Dunbar and Dunbar (1974) are similar to or lower than the estimates of this study. Clutton-Brock (1974b) observed similar feeding times for the red colobus monkey (*Colobus badius*).

A number of features of guereza life in general, as well as of feeding behavior in particular, point toward a strategy of energy conservation. These include the relatively small amounts of time spent feeding, a tendency to use a minimum of locomotion in association with feeding, and the use of relatively long feeding bouts. This pattern seems to be associated with the utilization of a small number of food plant species, and a concentration on 1 or 2 species as major food sources for most of the year. Dunbar and Dunbar (1974) observed guerezas utilizing a fairly wide range of food plants in a more diverse habitat. Even so, 7 species provided 80 percent of the diet, and time spent feeding was relatively low. Guerezas spent the majority of nonfeeding time resting, and day journeys are short. The duration of social interactions seems to be short, and the frequency of occurrence of at least the next 3 months the acacia pods gradually hardended, as did the seeds. No pods were eaten after they had reached full maturity and began to dry out. The relatively low levels of utilization of acacia pods from December through February represent the use of more mature green pods, but also the selection of younger pods from parts of trees or individual trees that were slightly out of phase with the majority of some interactions, such as agonistic interactions (Oates, 1974), is low. This type of energy-conserving pattern contrasts with the pattern found in the omniherbiverous, mainly ground-living baboons. In baboons, a more or less continuous diurnal feeding pattern is usually evident, large amounts of time are spent feeding, feeding bouts are relatively short, much progression is associated with feeding, a large number of food plants are used, and a concentration on a particular food plant species only occurs at certain times of the year. Only some of nonfeeding time is spent resting, social interactions last for relatively long periods of time and are frequent (Rose, 1977).

While the guereza pattern of energy expenditure seems to be conservative, the question of energy acquisition would seem to be equivocal, and the mass of food ingested may not necessarily be low despite the relatively small amounts of time spent gathering it. An animal concentrating on a small number of individual food plants and feeding in relatively extended bouts might be able to gather as much or more food than an animal gathering food from a large number of individual food plants, feeding in bouts of short duration, and spending considerable time moving between food sources. It is possible that some of the features mentioned above are related as much to the ruminantlike digestive physiology of guerezas as to strictly energetic factors. Thus, the pattern involving periods of fairly concentrated feeding separated by extended rest periods may be a means of rapidly accumulating a mass of substrate which can be fermented over a period of time, before the whole process is repeated over again. This would then contrast with a pattern of more or less continuous digestion of relatively small amounts of food taken in over relatively long periods of time. The guereza pattern might, therefore, relate to digestive efficiency in relationship to particular food types rather than to a specifically low-energy turnover pattern. As with so many problems, the final answer might well be in terms of a compromise between the two (and possibly more) possibilities. While there are similarities in digestive physiology between leaf-eating monkeys and ruminants, these similarities are not necessarily reflected in overall feeding patterns. Thus, not all resting periods follow periods of feeding. Guerezas habitually spend most of the first 2 hours of the day resting in the sun before settling down to the first concentrated feeding period of the day. There is also no evidence that regurgitation and remastication of food take place during the extended resting periods.

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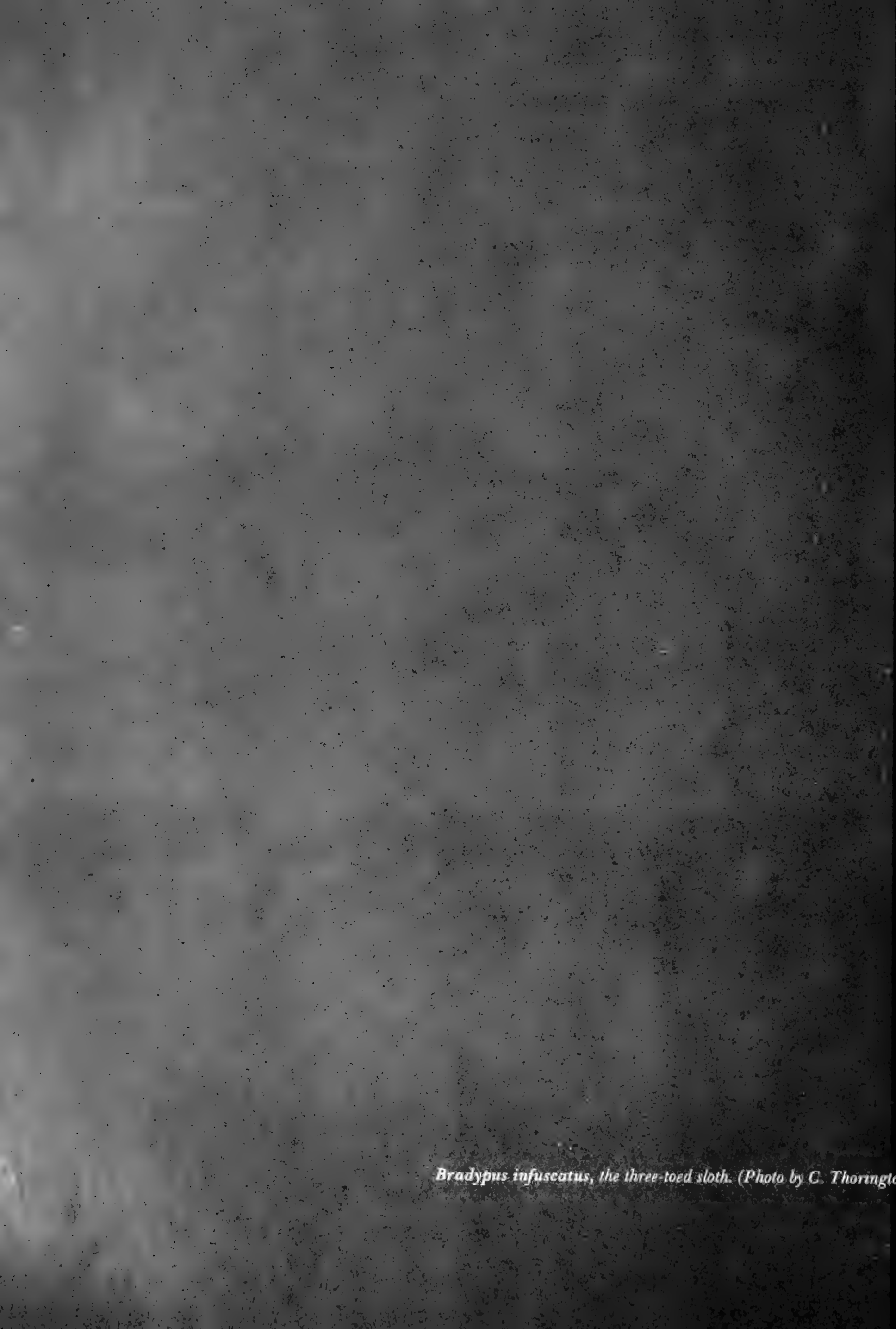
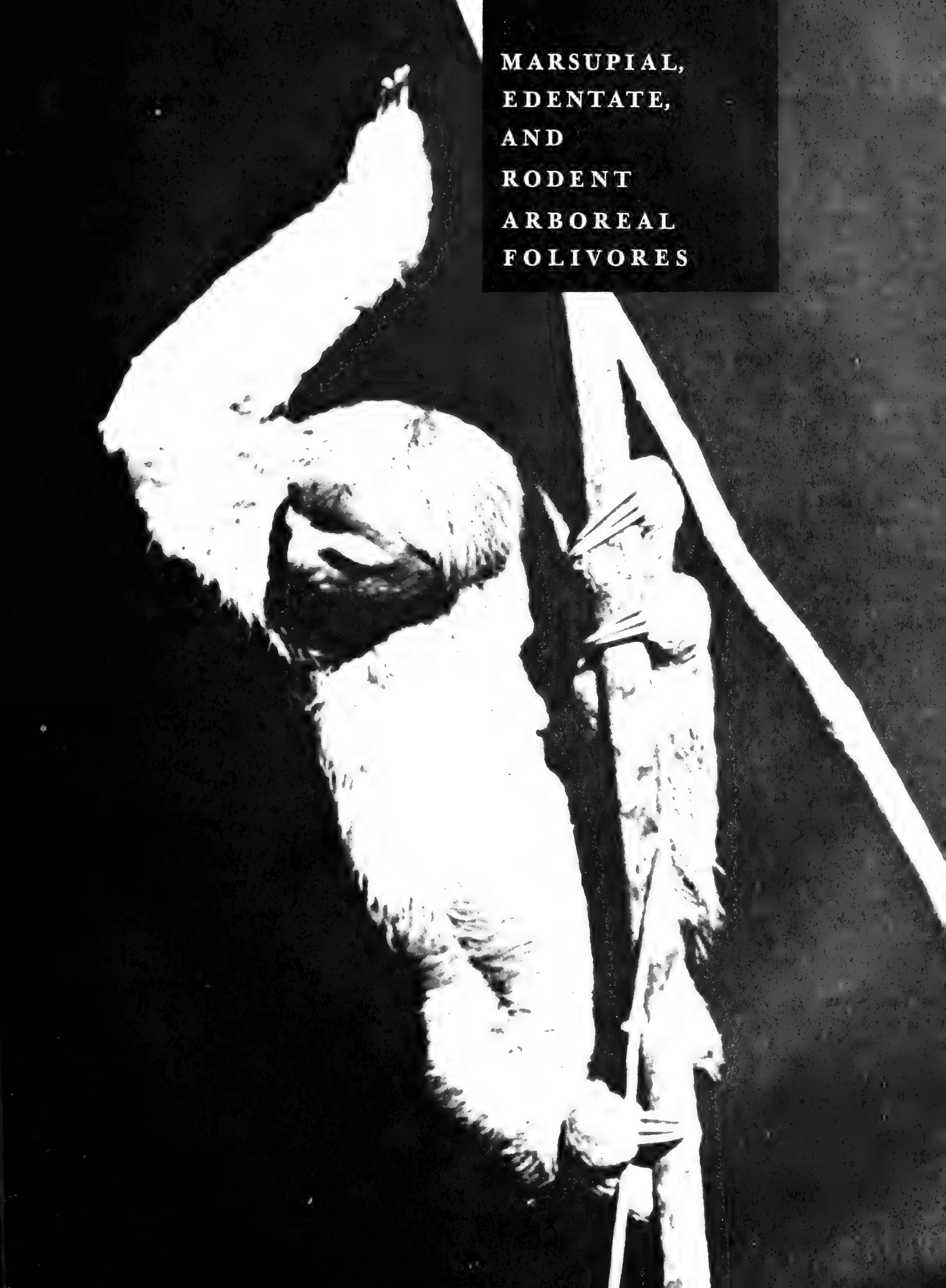


Bradypus infuscatus, the three-toed sloth. (Photo by C. Thorington).

MARSUPIAL, EDENTATE, AND RODENT ARBOREAL FOLIVORES



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Habitat Use and Home Range of Radio-tagged Opossums *Trichosurus vulpecula* (Kerr) in New Zealand Lowland Forest

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Introduction

The Australian brush-tailed opossum *Trichosurus vulpecula* (Kerr), introduced into New Zealand about 1840 (Pracy, 1962), has become a widely distributed pest. It was introduced into the Orongorongo Valley near Wellington about 1893–94, where the Department of Internal Affairs and the New Zealand Forest Service studied control techniques (Pracy and Kean, 1949, Batcheler et al., 1967), foods (Mason, 1958), and the behavior of penned animals (Kean, 1967) from 1946 to 1962.

In 1966 M. C. Crawley of the Ecology Division, Department of Scientific and Industrial Research, initiated a long-term, live-trapping study of the density, reproduction, home ranges, and movements of the same population of opossums (Crawley, 1973; B. D. Bell, in preparation). In 1969 radiotracking techniques were developed (Ward, 1972) to give a better measure of the home range and to determine how the animals used the habitat in this area, which is similar to much lowland forest occupied by opossums in New Zealand (Batcheler et al., 1967). Radiotelemetry is particularly useful for studying the opossum, which is nocturnal and mainly arboreal.

This paper describes the results of radiotracking 4 opossums for 2 years from September 1970 to August 1972. A comparison of the home ranges of these animals, determined by tracking and by live-trapping, will be published elsewhere.

Study Area

The 14-ha study area around the Ecology Division Field Station in the Orongorongo Valley, southern Rimutaka Range, North Island (Figure 1), lies 90–180 m a.s.l. on the east bank of the Orongorongo River and 11 km from its mouth. The study area is hilly and covered mainly with dense, mixed evergreen broadleaf podocarp forest with an upper canopy at 25–35 m in which *Metrosideros robusta* and *Dacrydium cupressinum* are dominant (Robbins, 1958). A middle stratum at 12–25 m is mainly *Knightia excelsa, Elaeocarpus dentatus,* and *Laurelia novaezealandiae.* Small trees and shrubs reaching 12 m—chiefly of *Melicytus ramiflorus, Hedycarya arborea,* and *Pseudowintera axillaris*—make up a lower stratum. Epiphytes, lianas, and tree ferns (*Cyathea* spp.) are abundant. On the drier eastern slopes of the study area *Nothofagus truncata* with some *Nothofagus solandri* is dominant. The mean annual rainfall at the field station is 2443 mm.

On this area a 30-by-30-m grid is marked on the ground with steel pegs. In a central area 150 m square, all trees with a breast-height diameter (dbh) exceeding 10 cm have been identified and numbered with metal tags; those over 30 cm dbh are also mapped. Hence, any point on the ground can be plotted to ± 1 m even at night, which was essential for recording locations of radiotracked opossums.

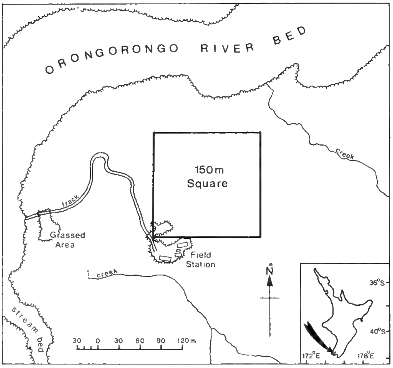

Figure 1. General map of study area.

Materials and Methods

Radiotracking equipment

The radiotracking system was described by Ward (1972). Transmitters based on the design of Cochran and Hagen (1963), powered by a Mallory RM 12 mercury cell and weighing 55–60 g, were fitted to 4 opossums. Each transmitter had its own frequency in the 27-MHz band, and animals were located with a portable, directional loop aerial and a modified citizens band 2-way radio telephone. This unit was used as a homing device, enabling the operator to approach each animal closely. It was not used to fix the animal's position by triangulation because the peculiarities of signal propagation in dense forest made this inaccurate (Ward, 1972). Great care was taken not to disturb the animals which had become accustomed to the observer and could be approached to within 2–3 m without apparent concern.

Choice of animals

The 4 opossums were selected on 3 criteria. First, they were animals frequently recaptured in the live-trapping study, which allowed regular checks on their weight and the renewal of transmitter power packs. These were changed every 3 months, the animals being tranquilized with succinylcholine chloride (Scoline) (Taylor and Magnussen, 1965). Second, the ranges of the selected animals had to lie on the 150-m square (Figure 1) where all the large trees were tagged and mapped, so that the tree species being used, and their positions, could be determined at night. As the study progressed, however, many trees outside this area had to be identified and plotted. Third, their home ranges had to be sufficiently discrete to avoid disturbing one animal when locating another—a precaution eventually found unnecessary.

The 4 animals selected were females 144 and 293, first caught as adults in November 1966 and May 1969 respectively; male 291, which was 1 year old when first captured in April 1969; and male 329, which was first caught as an adult in December 1969. Females 144 and 293 and male 329 were fitted with transmitters at the end of August 1970; male 291 one month later. When first radiotagged, both females were carrying a pouch young, which they successfully raised to independence, and they each reared a young during 1971. In 1972, however, only ♀ 293 bred successfully. The 4 opossums were weighed when first recaptured

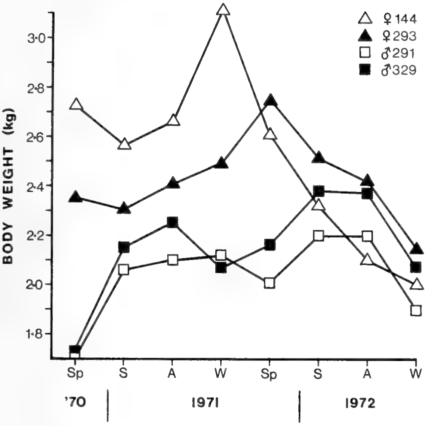

Figure 2. Seasonal (mean monthly) weights of each animal.

in each monthly (4-night) trapping period. The seasonal means of these monthly weights (Figure 2) showed that all the animals varied in weight during the 2 years, the males being particularly light when first fitted with a transmitter. The 2 females lost weight steadily during the second year, their condition declined and ♀ 144 died 2 months before the end of the study. The 2 males lost weight in the final winter but only ♂ 291's condition declined. These weight changes followed the general trend of the population (B. D. Bell, in preparation).

Tracking routine

A 10-m-high dipole aerial at the field station received signals from all parts of the study area. The onset and cessation of the opossums' activity was determined by listening for variations in signal strength caused by movement of the transmitter. Once active, the animals were located with the portable receiver hourly throughout the night, starting on the hour, for 3 successive nights each month from September 1970 to August 1972. At the start of each hourly session, standard weather observations were made by means of simple indices. The 4 animals were always located in the same order, the time required averaging 20 to 25 minutes, but varying from 10–60 minutes depending upon their relative positions. They were also located in the early morning and late afternoon in order to identify den trees and check for movement during the day.

Tracking success

The total number of nights each opossum was tracked during the 2 years (Table 1) was from a maximum of 72 for 3 of the animals to 69 for ♂291. Nights were usually missed in groups of 3 (i.e., a 3-night tracking week) and were caused chiefly by early failure of mercury cells, water getting into transmitters during wet weather, and animals removing the transmitter when an earlier method of attachment was being used. Also shown in Table 1 is the total number of locations made during the active period. These locations fall into 5 classes; the one in which the animal could be located accurately and associated with a particular tree or part of a tree was designated T and constituted the largest class. In approximately 12 percent of the locations, an animal's position could be placed vertically above a point on the ground, accurate to 2–3 m, but the species of tree occupied could not be determined. This type of location, designated UT, often occurred when an animal was in densely tangled understory. Animals on the ground formed the third class of location, G.

About 8 percent of the signals were of even strength over an area up to 25 m square. This happened when the animal was high in the canopy, or above it in an emergent tree, and the canopy scattered the signal. The center of such an area was accepted as the location, designated A. On rare occasions, signals of even strength were recorded over a much larger area and could not be plotted; these gaps were designated NP. The percentage of active locations in each category is shown in Table 1, together with the number of times an animal was sighted while being located.

Analysis of data

The results are frequently treated seasonally as spring (September-November), summer (December-February), autumn (March-May), and winter (June-August). For convenience the two 12-month periods, although not calendar years, are referred to as the first and second year. All observations were recorded in the field on a tape recorder. Each night's locations were plotted on translucent drafting foil and home-range areas measured with a compensating polar planimeter. The frequently used term "active period" refers to the time from when the animals first became active, usually before sunset, to when activity ceased at the end of the night, and includes any periods of inactivity which occurred during the night. The methods of analysis are described where appropriate.

Table 1.—Two-year totals of tracking nights and locations (active period only) for each opossum and the proportions of the locations appearing in each category.
(T = identified tree; UT = unidentified tree; G = ground; A = approximate locations; NP = unsuccessful locations).

		♀144	*♀293*	*♂291*	*♂329*
Number of nights tracked		60	66	64	66
Number of locations (active period only)		632	722	704	713
Percentages of locations in the categories	T	67.1	77.1	50.9	55.1
	UT	8.1	6.5	15.3	18.4
	G	18.7	6.4	21.2	18.8
	A	5.7	9.6	11.6	6.3
	NP	0.4	0.4	1.0	1.4
Number of sightings		174	115	222	213

Measurement of home range

Much more detailed information can be obtained about home range, and in a much shorter period, by the use of radiotracking rather than live-trapping. The effect of time on range size can be determined in detail and a finer analysis can be made of range use by radiotracking.

In this study the area traversed by an animal in a night was taken as the shortest unit for analysis of home range. All locations were used in measuring the nightly range, including 1 location for the den site at dusk and 1 for the den used next day. The method of measurement was that devised by Harvey and Barbour (1965) for determining home-range areas of *Microtus ochrogaster*. This method, unlike the traditional minimum-area method (Dalke, 1942), objectively reduced or excluded those areas within a polygon which the animal never visited. It required one-quarter of the range length (Stickel, 1954) to determine the perimeter of the range. Working clockwise, if 2 outer points were more than one-quarter of the range length apart, they were not connected. Instead, the boundary was drawn from the first point to the next outermost point within the distance of one-quarter of the range length. Locations further than this distance from any other point were excluded from the main home-range area, but were connected to the nearest point by a straight line given a nominal width of 1 foot so that all fixes were eventually included. This method is used here with 2 modifications: half, rather than a quarter, of the range length proved more suitable, because the shorter measure often failed to create any area at all, and a width of 1 m seemed more appropriate for the lines connecting outlying locations to the central area. Both minimum area and range length and width were also calculated, the former for comparison with other published results and the latter for some analyses, but also because linear dimensions are often more easily visualized than proportions of a hectare. The term "core area" designates the most intensively used portion of the home range (cf. Kaufmann, 1962).

Results

Nightly range and excursions

Table 2 shows for both years the mean nightly ranges of each animal, measured by the modified minimum area method. In the first year, ♀293 occupied a significantly smaller nightly range than ♀144 and ♂291 ($p < 0.05$), and also a smaller nightly range in the second year than ♀144 ($p < 0.05$) and both males ($p < 0.001$). Female 293 also had a significantly smaller nightly range in the second than in the first year ($p < 0.01$).

The lengths of the animals' nightly ranges shown in Figure 3 provide a poor index of home-range area because the ranges varied in shape from circular to linear, but Figure 3 does make clear the occasional long excursions undertaken by each animal. In Figure 4 these excursions are mapped diagramatically from the geometric center of activity (Hayne, 1949) of the annual range of each animal. To compare the distance of these excursions to the nightly range size, a circle equal in area to the mean nightly range of each animal for each year determined on dry nights only (see following) is described about the center of activity of the respective annual range. These excursions are discussed later.

Table 2.—Mean and standard error of the nightly, 3-nightly, seasonal, and annual home ranges of each animal for each year, and the 2-year ranges.

Opossum	*Year*	*Mean nightly range* (m^2)	*Mean 3-nightly range* (m^2)	*Mean seasonal range* (m^2)	*Mean annual range (ha)*	*2-year range (ha)*
♀144	1	818 ± 141	2821 ± 404	5221 ± 490	.978 ± .054	2.50
	2	615 ± 184	2938 ± 466	4805 ± 894		
♀293	1	459 ± 91	1512 ± 359	4362 ± 912	.846 ± .567	1.75
	2	129 ± 20	590 ± 111	1268 ± 170		
♂291	1	822 ± 112	3258 ± 329	10212 ± 2676	1.490 ± .716	4.66
	2	677 ± 127	2849 ± 413	10010 ± 1546		
♂329	1	758 ± 122	2133 ± 280	5188 ± 1185	1.189 ± .350	2.15
	2	849 ± 98	2293 ± 249	4870 ± 692		

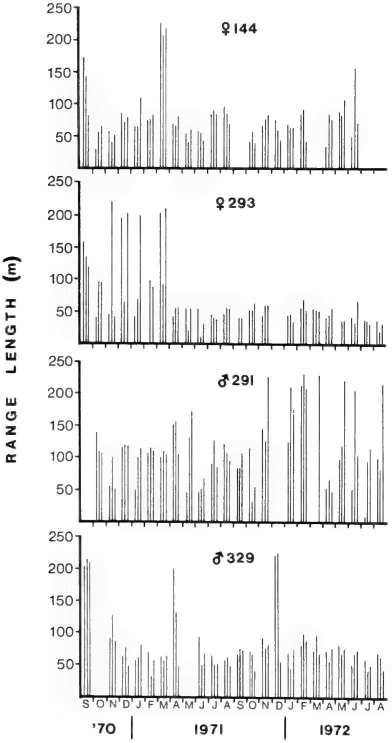

Figure 3. Range lengths of the nightly home ranges as indicators of excursionary activity.

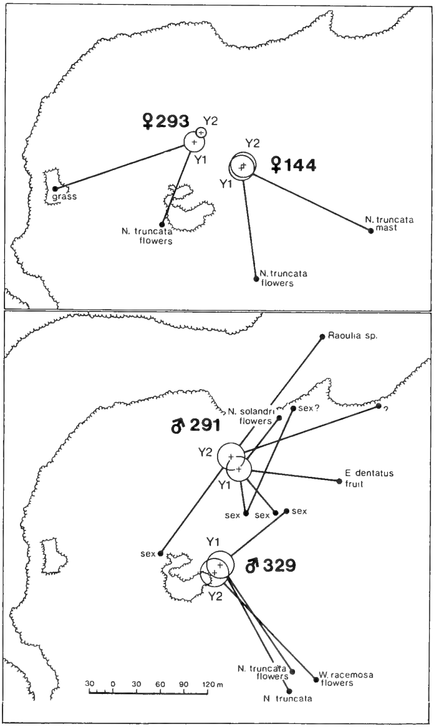

Figure 4. Direction, distance, and cause of the excursions undertaken by each animal, with the mean nightly range size of each year inscribed about the respective annual centers of activity.

Table 3.—Number of fine, dry tracking nights, and nights in the categories of precipitation used to measure the influence of wet weather on nightly range for each year.

Weather category on nightly range	*Year 1*	*Year 2*
Fine and dry	18	20
Raining <50% of night	8	10
Raining >50% of night	9	5
Nights not classified	1	1
Total	36	36
Fine and dry	18	20
Canopy dripping <50% of night	5	5
Canopy dripping >50% of night	9	7
Nights not classified	4	4
Total	36	36

Influence of rain on nightly movement

It was noticeable while locating the opossums that they restricted their movements during wet weather. To verify this, their nightly ranges were compared on completely dry nights with nights when it rained for < 50 percent and > 50 percent of the time, and nights when the forest canopy was dripping for < 50 percent and > 50 percent of the time. This accommodates the considerable differences in the apparent duration and intensity of rainfall under the forest canopy and in the open; light rain scarcely penetrates the forest, yet the canopy may drip for hours after prolonged heavy rain. The numbers of nights in each class in each year are shown in Table 3, and also those which did not fit, e.g., when no rain fell but the vegetation was wet.

The Mann-Whitney U test was used for all comparisons, and the 2 years are treated separately (Table 4). Tests on ♀144's ranges in the second year were limited by small sample sizes. Compared with dry nights, the nightly ranges were not significantly different when it rained for less than 50 percent of the night, and except for ♀144 in year 2, there was no difference when the canopy dripped for less than 50 percent of the night. With 2 exceptions, however, the nightly ranges were significantly smaller when it rained for more than half the night and when the forest canopy dripped for more than half the night.

No excursions were undertaken when it was raining hard or when the canopy was dripping heavily, but there were some sorties on fine nights which later turned wet, and twice an animal traveled some distance from its core area during a break in wet weather, only to return with the onset of further rain. Such activity caused the exceptions (Table 4), which with the differences in the probability levels suggest that the animals' response to wet weather was more extreme in the second than in the first year. This difference between years may have been related to the animals' poor condition late in the second year, but may also be influenced by annual differences in the duration, intensity, and timing of the rainfall and by the weather during the previous 24–48 hours; the small samples do not permit finer analysis.

Sudden heavy downpours always caused the animals to take refuge at once in the nearest available shelter no matter what the season, though they usually re-

Table 4.—Median and range of nightly home ranges under different conditions of precipitation and canopy drip. Asterisks show the level of significance when these home ranges are statistically smaller than those determined on dry nights. (*p < .05, **p < .01, ***p < .001)

		Dry		*Raining < 50% of night*		*Raining >50% of night*		*Canopy dripping <50% of night*		*Canopy dripping >50% of night*	
Opossum	*Year*	*Median m^2*	*Range m^2*	*Median m^2*	*Range m^2*	*Median m^2*	*Range m^2*	*Median m^2*	*Range m^2*	*Median m^2*	*Range m^2*
♀144	1	830	75-3360	548	85-2180	165**	50-1970	540	85- 570	105*	50- 810
	2	485	70-4460	200	75-1135			165*	75- 200		
♀293	1	400	70-1950	95	10-1820	195	10- 810	100	75- 540	70**	10- 465
	2	135	40- 220	142	40- 565	40***	30- 50	165	65- 135	40***	30- 50
♂291	1	642	150-2373	816	430-2013	257*	81-1640	816	430-2013	417	81-1697
	2	530	210-2960	430	64-1460	120**	8- 510	430	64-1460	120***	8- 510
♂329	1	715	70-2805	560	230-1820	235	120-1220	710	230-1820	304	120-1220
	2	990	135-1780	705	110-2800	125***	90- 550	785	585- 880	125***	90-1030

Table 5.—Mean and standard error of nightly home range size of each animal for each year, as measured on fine dry nights only.

Opossum	*Year*	*n*	*mean* (m^2)	*S.E.*
♀ 144	1	16	807	145
	2	16	736	264
♀ 293	1	17	586	147
	2	15	124	14
♂ 291	1	16	833	160
	2	16	926	208
♂ 329	1	17	902	185
	2	20	1019	103

turned to regular den sites before daylight. On June 6, 1972, however, very heavy hail at 1850 hrs forced the animals to take immediate shelter; the hail turned to heavy rain squalls, which continued until after dawn, and 3 of the 4 opossums remained under logs on the ground for the whole of the following day—a most unusual occurrence (see denning). Other aspects of activity influenced by wet weather are considered later.

Although 2 factor analyses must be treated with caution, they show that the animals generally moved less in wet weather. As there was little difference between the 2 years in the occurrence of dry and wet tracking nights (Table 3), the nightly ranges of each animal between years are directly comparable, but because there were variations in the animals' response to rain, comparisons between animals are not so valid. To free the comparisons of nightly ranges from this variable response, ranges on dry nights only (Table 5) were compared. In the first year there was no significant difference between the mean nightly range size of any of the animals. In the second year ♀293's mean nightly range was significantly smaller than that of the other female ($p < 0.05$) and those of the 2 males ($p < 0.002$). Female 293 had a smaller mean nightly range ($p < 0.01$) in the second than in the first year, and was the only animal whose range size differed significantly between the 2 years.

In relating the nightly range size to measurements of excursions (Figures 5a and 5b) and shifts in range use (Figure 6) the mean range on dry nights is preferred to the mean range of all nights, in order to avoid this variation.

Effect of time on home-range measurement

In addition to the mean nightly range sizes of each animal for each year, Table 2 also shows the mean size of the animals' ranges determined in each 3-night

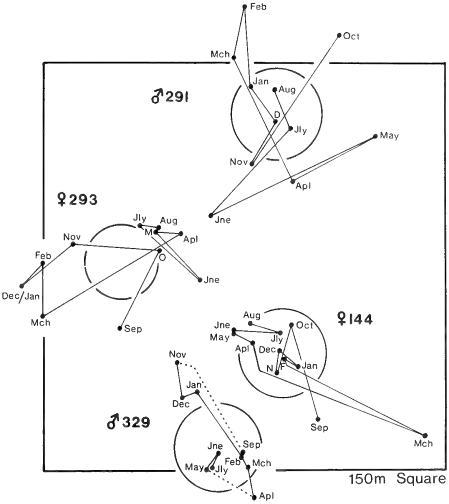

Figure 5a. Month to month shifts in the centers of activity of each animal in the first year with the mean nightly range size inscribed about the annual centers of activity.

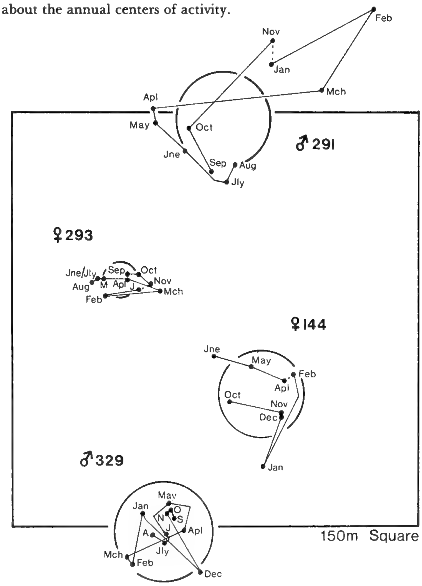

Figure 5b. Month to month shifts in the centers of activity of each animal in the second year with the mean nightly range size inscribed about the annual centers of activity.

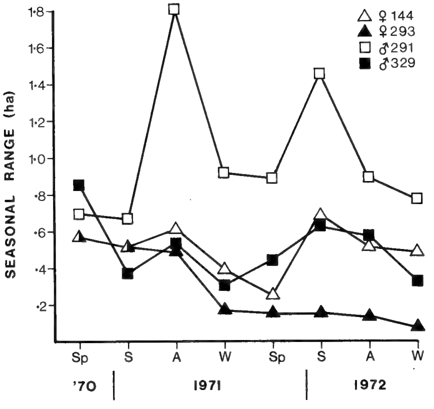

Figure 6. Seasonal home range of each animal.

tracking period, the means of the seasonal and annual ranges, and the 2-year ranges, all measured by the modified minimum-area method.

Although the limitations of tracking on only 3 successive nights each month are recognized, the increase in area occupied by the animals with increasing time is evident, being on the average 270 percent from 1 night to 3 nights, 147 percent from 3 nights to a season, and 153 percent from a season to a year. The animals' 2-year ranges were on average 116 percent greater than their annual ranges.

The increases probably result from the changing use of the home range as the opossums moved to meet their requirements. To illustrate this, shifts in monthly (3 night) centers of activity are shown joined consecutively in Figures 5a and 5b. To compare the distance of these shifts with the home-range size, a circle equal in area to the mean nightly range of each animal for each year determined on dry nights only is described about the geometric center of activity of the respective annual range.

Seasonal and annual ranges

In calculating the size of the seasonal ranges (Figure 6), all nights were included, wet or fine. The size of ♀293's range did not vary much between seasons, but was much smaller from the winter of 1971 onward, while the ranges of the other female and of ♂329 varied considerably between seasons. Male 291 showed the most pronounced changes, with distinct peaks in autumn 1971 and summer 1971-72.

The annual and cumulative 2-year ranges were measured by 3 methods: the modified minimum area, the minimum area, and the range length/range width method (Table 6). Figure 7 shows the annual ranges of each animal measured by the first method and their den sites. Comparing these areas between the first and second year, ♀144 shows little difference but ♀293's range decreased by four-fifths and ♂329 also occupied a smaller area. The range of the other male was 46 percent larger in the second year. Factors which evidently influenced these changes in the size of the seasonal and annual ranges are considered in the following sections.

Use of tree species

Most of the trees on the study area carry numerous epiphytes and lianas, some of which are preferred foods (Fitzgerald, 1978). An opossum recorded in a particular tree may not be feeding on that tree. Trees visited more frequently when flowering or fruiting were probably being eaten, and this was often confirmed by direct observation. Identification of the tree species used by opossums (Table 7) provided an index of their use of the habitat. In this analysis locations of animals in their den trees at the beginning and end of the night have been excluded and are considered later, because only a limited number of species were used for denning, and the opossums spent varying amounts of time in the den trees following the onset of activity and prior to its finish.

Elaeocarpus dentatus was the tree most often visited by all 4 animals in both years excepting only ♀144 in the first year (Table 8), and it was visited significantly more often in the second year by all except ♀293. (♀144 $\chi^2 = 7.36$, $p < .01$; ♂291 $\chi^2 = 5.14$, $p < 0.05$; ♂ 329 $\chi^2 = 4.86$, $p < 0.05$.) Mature trees of this species reaching 20 m, all with heavy loads of epiphytes and lianas, are well distributed through the study area and in both years they flowered profusely and carried heavy crops of fruits. The flesh of the unripe and ripe fruit was a popular food of the opossums during late autumn and early winter both from the trees and from the ground, and it persists until late winter. Fitzgerald (1978) found that the leaves of *E. dentatus* form only a minor part of the diet but that many flower buds and flowers are taken; this probably accounts for the opossum's sustained use of the species. These buds first appear on the trees in March (early autumn) and expand slowly until opening fully in late spring.

On May 4 and 5, 1971, ♂291 traveled up to 150 m from its den to 2 late fruiting trees (Figure 4), the fruit being the probable attraction. On both

Table 6.—Annual and cumulative 2-year home range sizes determined by 3 different methods.

Method	*Year*	*♀ 144*	*♀ 293*	*♂ 291*	*♂ 329*
Modified minimum area (ha)	1	0.92	1.41	2.21	1.54
	2	1.03	0.28	3.21	0.84
	1 + 2	2.50	1.75	4.66	2.15
Minimum area (ha)	1	2.52	2.19	2.36	2.33
	2	1.18	0.29	3.59	1.63
	1 + 2	3.01	2.24	4.75	3.06
Range length and range width (m)	1	236:195	255:142	205:172	274:157
	2	154:148	80: 58	360:177	237:119
	1 + 2	263:175	260:150	360:177	278:189

nights it spent 7 hours in or under them, but for some of this time was probably sheltering from heavy showers which occurred on both nights. These excursions contributed to ♂291's large autumn range in the first year (Figure 6). *E. dentatus* was one of the species favored by ♀144 and ♂329 for denning, and if they fed between becoming active and leaving the den their use of this species for feeding may be greater than inferred from the table.

The leaves of *Metrosideros robusta,* a tree reaching 35 m, are another major food and all 4 animals had 2–5 mature specimens within their ranges. In the first

Figure 7. Annual home ranges of each opossum and the location of their identifiable den sites.

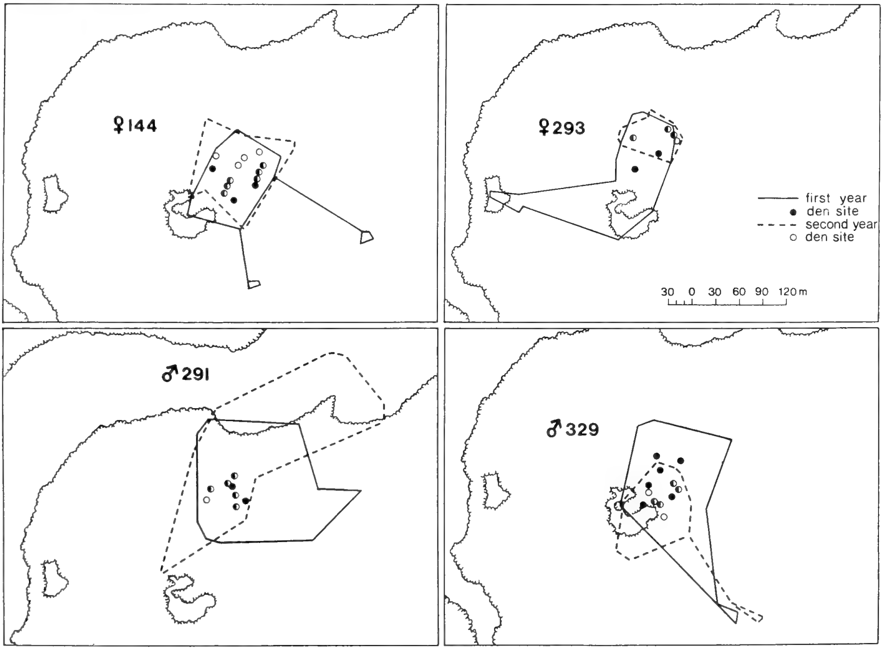

Table 7a.—Seasonal and annual percent occurrence of locations of ♀ 144 in different species of trees, shrubs, and lianas and other categories.

	First year					*Second year*				
	Sp	*S*	*A*	*W*	*Total*	*Sp*	*S*	*A*	*W*	*Total*
Beilschmiedia tawa		2.3			0.4					
Brachyglottis repanda										
Cyathea spp.		2.3			0.4	3.1	8.3			4.4
Dacrydium cupressinum								3.4		0.9
Elaeocarpus dentatus	11.8	4.7	6.0	26.8	13.8	34.4	14.6	34.5	25.0	25.7
Freycinettia banksii		2.3	2.0	2.8	1.7	3.1				0.9
Geniostoma ligustrifolium										
Hedycarya arborea	2.9	25.6		1.4	6.0	3.1	4.2			2.7
Knightia excelsa	8.8	4.7			3.4		2.1		25.0	1.8
Leptospermum scoparium										
Laurelia novae-zelandiae	8.8	4.7	2.0	11.3	7.3		2.1	6.9		2.7
Macropiper excelsum										
Melicytus ramiflorus	4.4	2.3	12.0	4.2	5.6	18.8	8.3	6.9		10.6
Metrosideros robusta	26.5	16.3	14.0	35.2	24.6		4.2	13.8		5.3
Metrosideros fulgens							2.1			0.9
Myrsine australis										
Nothofagus solandri										
Nothofagus truncata	8.8		26.0		8.2					
Pennantia corymbosa										
Podocarpus ferrugineus	2.9	2.3			1.3		2.1			0.9
Podocarpus totara										
Pseudowintera axillaris			24.0		5.2					
Rhipogonum scandens										
Rhopalostylis sapida										
Schefflera digitata							6.3	6.9		4.4
Weinmannia racemosa									25.0	0.9
Dead trees	1.5	7.0			1.7					
Unidentified (UT)	5.9	14.0	6.0	11.3	9.1	25.0	41.7	6.9		26.5
Approximate locations (A)	16.2	7.0	8.0	7.0	9.9	12.5	4.2	20.7	25.0	11.5
Unsuccessful locations (NP)	1.5	4.7			1.3					
Total (n)	68	43	50	71	232	32	48	29	4	113

year this was the species most frequented by ♀ 144 and the second most frequented species by the other 3 animals. In the second year its placing dropped to third for all animals (Table 8). In both years the 2 males visited *M. robusta* most often in summer and winter and ♀ 293 in spring and autumn. Female 144 showed no consistent pattern of use, but was recorded in this species significantly less often in the second year (χ^2 [Yates] = 20.19, $p < .001$). She had 4 large trees within her usual range but the most-used tree was blown down at the end of the first year and in falling knocked several large limbs off another tree.

M. robusta was the species most used for denning by all the animals except ♂ 329, and this may have masked seasonal variations in its use. Furthermore *M. robusta* begins life as an epiphyte, and the tree most used for its den by ♀ 293 still had large live branches of its host, *E. dentatus*, growing from it.

The leaves of *Weinmannia racemosa* are another important food of the opossums (Fitzgerald, 1978). Three small stands of young trees, and isolated mature specimens reaching 25 m are scattered unevenly over the area, but ♀ 144 had very little *W. racemosa* within her usual range and was only recorded in it once.

Table 7b.—Continued for ♀ 293.

	First year					*Second year*				
	Sp	*S*	*A*	*W*	*Total*	*Sp*	*S*	*A*	*W*	*Total*
Beilschmiedia tawa									2.6	0.5
Brachyglottis repanda										
Cyathea spp.							2.9			0.5
Dacrydium cupressinum										
Elaeocarpus dentatus	21.5	5.6	13.8	32.7	19.4	17.9	29.4	30.9	31.6	26.8
Freycinettia banksii				1.9	0.5		5.9			1.1
Geniostoma ligustrifolium										
Hedycarya arborea		22.2	5.2	9.6	7.6		11.8	10.9		5.5
Knightia excelsa	3.1		5.2		2.4	1.8		5.5		2.2
Leptospermum scoparium		5.6			0.9					
Laurelia novae-zelandiae	7.7			3.8	3.3	14.3	5.9	5.5		7.1
Macropiper excelsum										
Melicytus ramiflorus		11.1	1.7	1.9	2.6		2.9	1.8	2.6	1.6
Metrosideros robusta	20.0	11.1	13.8	13.5	15.2	14.3	8.8	18.2	2.6	12.0
Metrosideros fulgens						1.8				0.5
Myrsine australis										
Nothofagus solandri										
Nothofagus truncata	7.7				2.4					
Pennantia corymbosa			3.4		0.9					
Podocarpus ferrugineus										
Podocarpus totara		8.3			1.4					
Pseudowintera axillaris			5.2		1.4					
Rhipogonum scandens										
Rhopalostylis sapida									5.3	1.1
Schefflera digitata								1.8		0.5
Weinmannia racemosa	7.7		3.4	13.5	6.6	8.9	14.7	7.3	39.5	15.8
Dead trees										
Unidentified (UT)	12.3	22.2	17.2	5.8	13.7	12.5	11.8	9.1	5.3	9.8
Approximate locations (A)	18.5	11.1	29.3	17.3	19.9	28.6	5.9	9.1	10.5	14.8
Unsuccessful locations (NP)	1.5	2.8	1.7		1.4					
Total (n)	65	36	58	52	211	56	34	55	38	183

Male 329's range shifted southward during the first year to encompass one of the stands of young trees, while the other 2 animals had mature specimens within their established ranges. The opossums visited *W. racemosa* most often in winter and least often in autumn (Table 7). It was the second most frequented species for all animals except ♀144 in the second year (Table 8), when it was visited significantly more than in the first year (♀293 $\chi^2 = 8.55$, $p < 0.01$: ♂291 χ^2 (Yates) $= 9.56$, $p < 0.01$: ♂329 χ^2 (Yates) $= 17.69$, $p < 0.001$).

In December of the second year ♂329 was attracted for 1-2 hours on 2 successive nights to a profusely flowering *W. racemosa* 210 m from his den (Figure 4). Daylight inspection showed many of the flower racemes had parts missing, but few leaves browsed.

Although leaves form the bulk of the opossums' diet, the flowers and fruit of several species rank high in the order of preference. *Nothofagus truncata*, a species of beech reaching 30 m, flowered profusely in September 1970—the first month of the study. The 3 radiotagged animals (♂291 was not fitted with a transmitter until the end of September) all made excursions to stands of this species (Figure 4) on the

Table 7c.—Continued for ♂291.

	First year					Second year				
	Sp	*S*	*A*	*W*	*Total*	*Sp*	*S*	*A*	*W*	*Total*
Beilschmiedia tawa										
Brachyglottis repanda										
Cyathea spp.									2.0	0.6
Dacrydium cupressinum										
Elaeocarpus dentatus	5.1		21.4	13.4	11.6	6.3	4.2	47.8	14.3	19.8
Freycinettia banksii	2.6			7.3	2.9					
Geniostoma ligustrifolium						2.1	4.2		4.1	2.4
Hedycarya arborea		14.0	4.3	3.7	5.4	2.1		2.2	2.0	1.8
Knightia excelsa	7.7	2.0	7.1	1.2	4.1	4.2	8.3			2.4
Leptospermum scoparium										
Laurelia novae-zelandiae	7.7	4.0	5.7	3.7	5.0	4.2		4.3		2.4
Macropiper excelsum				1.2	0.4					
Melicytus ramiflorus	5.1	2.0	1.4	3.7	2.9		8.3	2.2		1.8
Metrosideros robusta	2.6	8.0	1.4	14.6	7.5		12.5		14.3	6.0
Metrosideros fulgens						8.3				2.4
Myrsine australis				1.2	0.4			2.2		0.6
Nothofagus solandri	35.9				5.8					
Nothofagus truncata										
Pennantia corymbosa										
Podocarpus ferrugineus	2.6	2.0		1.2	1.2	2.1				0.6
Podocarpus totara										
Pseudowintera axillaris			4.3		1.2					
Ripogonum scandens										
Rhopalostylis sapida						2.1		2.2		1.2
Schefflera digitata										
Weinmannia racemosa		2.0	4.3	2.4	2.5	10.4		4.3	20.4	10.2
Dead trees	2.6				0.4					
Unidentified (UT)	17.9	40.0	24.3	12.2	22.4	33.3	25.0	28.3	38.8	32.3
Approximate locations (A)	7.7	22.0	22.9	34.1	24.1	20.8	37.5	6.5	4.1	14.4
Unsuccessful locations (NP)	2.6	4.0	2.9		2.1	4.2				1.2
Total (n)	39	50	70	82	241	48	24	46	29	167

drier ridges bordering the study area. They moved there 1–2 hours after leaving their dens and stayed there up to 3 hours. Up to 6 other opossums were also seen in these trees during these periods, and some were seen feeding on the flowers. In the following March ♀144 again visited these trees. She moved there within 1 hour of leaving her den tree and remained there for 4–5 hours on each of 3 successive nights; and in April ♂329 revisted them for about 4 hours one night (Figure 4). *N. truncata* was carrying a heavy crop of mast at this time and the opossums were probably feeding on it. These were the only excursions involving more than one of the tagged animals.

Nothofagus solandri, another species of beech is much more sparsely distributed around the study area than is *N. truncata*. It flowered heavily in October 1970 when ♂291 traveled 100 m to a small stand of it (Figure 4), and stayed there for 4–6 hours on each of 3 successive nights, feeding on the flowers with 4 other opossums. In the second year both species of *Nothofagus* had very few flowers and none of the tagged opossums visited them during a tracking period. This absence of excursions is reflected in the smaller spring ranges of 3 of the animals in the second year (Figure 6).

A similarly marked annual difference occurred in the opossums' use of *Pseudowintera axillaris*, a small

Table 7d.—*Continued for ♂329.*

	First year					*Second year*				
	Sp	*S*	*A*	*W*	*Total*	*Sp*	*S*	*A*	*W*	*Total*
Beilschmiedia tawa		1.8		1.5	0.9	1.5				0.4
Brachyglottis repanda						1.5				0.4
Cyathea spp.			2.3		0.5		6.7		1.8	1.8
Dacrydium cupressinum		8.8	7.0	1.5	4.2					
Elaeocarpus dentatus	14.3	1.8	14.0	23.9	13.9	27.3	6.7	42.1	7.3	22.0
Freycinettia banksii										
Geniostoma ligustrifolium								1.8		0.4
Hedycarya arborea		26.3			6.9					
Knightia excelsa	16.3	3.5		1.5	5.1			3.5	1.8	1.3
Leptospermum scoparium										
Laurelia novae-zelandiae	2.0		4.7	1.5	1.9	4.5	2.2			1.8
Macropiper excelsum										
Melicytus ramiflorus	2.0				0.5	3.0			7.3	2.7
Metrosideros robusta	12.2	12.3	2.3	11.9	10.2	1.5	13.3		20.0	8.1
Metrosideros fulgens						1.5				0.4
Myrsine australis										
Nothofagus solandri										
Nothofagus truncata	16.3		7.0		5.1					
Pennantia corymbosa										
Podocarpus ferrugineus	4.1				0.9					
Podocarpus totara										
Pseudowintera axillaris			7.0		1.4					
Ripogonum scandens						1.5				0.4
Rhopalostylis sapida				1.5	0.5				1.8	0.4
Schefflera digitata							4.4		1.8	1.3
Weinmannia racemosa				13.4	4.2	15.2	17.8	3.5	32.7	17.0
Dead trees									1.8	0.4
Unidentified (UT)	20.4	19.3	41.9	26.9	26.4	25.8	40.0	45.6	23.6	33.2
Approximate locations (A)	10.2	15.8	11.6	14.9	13.4	16.7	6.7	3.5		7.2
Unsuccessful locations (NP)	2.0	10.5	2.3	1.5	4.2		2.2			0.4
Total (n)	49	57	43	67	216	66	45	57	55	223

tree common throughout the study area. In the first autumn it set a heavy crop of fruit on which all the tagged opossums were observed feeding, but in the second year the crop was very poor and none of the animals was recorded feeding in it.

Hedycarya arborea, a tree up to 15 m high, is common and widely distributed. In the first summer it carried a heavy crop of fruit and was the most frequented species that season. Opossums were regularly observed feeding on the fruit, and on January 13, 1971, ♂329 was watched for several minutes at less than 2 m. Fruits from the stems were apparently rolled in the mouth and then dropped, at the rate of 1 about every 4 seconds; most of the ripe fruit had a small portion of the flesh removed but unripe ones were unmarked. Fecal pellets found during this period contained entire ripe fruits and others just seeds. In the second year very few *H. arborea* carried fruit and the fruiting season was less well defined, but ♀293 had 2 heavily fruiting trees within her usual range; her use of these is reflected in Table 7. In the second October ♂291 was seen on 2 nights foraging for and eating germinating *H. arborea* fruit on the ground.

Table 8.—The 3 tree species most frequented by each animal each year (excluding the nightly occupancy of den trees), and the occurrence of locations in them.

		Most frequented species		
Opossum	*Year*	*1*	*2*	*3*
♀ 144	1	*Metrosideros robusta* (24.6%)	*Elaeocarpus dentatus* (13.8%)	*Nothofagus truncata* (8.2%)
	2	*Elaeocarpus dentatus* (25.7%)	*Melicytus ramiflorus* (10.6%)	*Metrosideros robusta* (5.3%)
♀ 293	1	*Elaeocarpus dentatus* (19.4%)	*Metrosideros robusta* (15.2%)	*Hedycarya arborea* (7.6%)
	2	*Elaeocarpus dentatus* (26.8%)	*Weinmannia racemosa* (15.8%)	*Metrosideros robusta* (12.0%)
♂ 291	1	*Elaeocarpus dentatus* (11.6%)	*Metrosideros robusta* (7.5%)	*Nothofagus solandri* (5.8%)
	2	*Elaeocarpus dentatus* (19.8%)	*Weinmannia racemosa* (10.2%)	*Metrosideros robusta* (6.0%)
♂ 329	1	*Elaeocarpus dentatus* (13.9%)	*Metrosideros robusta* (10.2%)	*Hedycarya arborea* (6.9%)
	2	*Elaeocarpus dentatus* (22.0%)	*Weinmannia racemosa* (17.0%)	*Metrosideros robusta* (8.1%)

A few other food species had distinct flowering and fruiting seasons, yet the opossum's visits to them were unpredictably inconsistent. For example, *Knightia excelsa* flowered in late spring in both years. In the first but not in the second spring, 3 of the animals increased their visits to them and 2 were seen eating the flowers.

The 4 opossums were recorded in a total of 26 different species of trees, shrubs, and lianas during the 2 years of the study; this total compares with the approximately 67 species present on the study area of which 7 are represented by only 1 or 2 individuals (D.J. Campbell, personal communication). Male 329 was recorded in 14 different species in each year of the study. Female 144 was recorded in 12 in the first year and 13 in the second year. The other 2 animals in each year were also recorded in 13 different species. There was no consistency in the number used each season between years or between animals. Grouping the 4 animals, the mean number of different species occupied each season in the first year was 7.5 (range 6 to 11) and in each season in the second year 6.6 (range 4 to 10).

Activity and movements of sexual significance

During the breeding season (February–May) of the first year of the study, both males made excursions associated with breeding activity (Figure 4). On the first tracking night in April ♂291 went beyond the southeast limits of his established range and was seen doggedly following another animal, presumably a female. He was in this locality for about 3 of the following 4 hours, making a single secondary excursion 150 m to the northeast. He was not actually seen during this second journey so it is not known what he was doing. The following night, within an hour of leaving his den, he again traveled beyond the southeast portion of his range, but further than the previous night. He remained there for about 3 hours during which time breeding behavior involving at least 7 other opossums was evident. Five of these animals were pacing agitatedly over an area of ground about 10 m square, and at least 2 more, both vocal, were in tangled vegetation about 5 m above the forest floor. Male 291 went up into this vegetation 3 times, but never for longer than 30 seconds, and each visit resulted in considerable commotion there. A similar social grouping later the same night involved ♂329. He traveled 115 m from his den tree of the previous day, northeastwards almost to the same place where ♂291 was found earlier. These excursions during the breeding season principally account for ♂291's large autumn range (Figure 6) in the first year. This is duplicated to a much lesser extent by ♂329, but 1 month's data are missing for him so his autumn range may have been larger.

The breeding season appeared much less active in the second compared with the first year. Although both males were seen following single opossums within their own areas, only 1 unusual movement was recorded. On May 3, ♂291 was located at 2215 hours on the main track close to the field station (Figure 4) and by 2315 hours had traveled 220 m northeast to the edge of the river bed. He had never been recorded close to the field station before and appeared to be alone at both places. In both breeding seasons each of the 2 radiotagged females was frequently seen attended by another opossum, presumably male.

Miscellaneous movements

On 6 nights in 4 of the first 7 months of the study ♀293 made long excursions to an area of mixed grasses and forbs which included a small amount of clover (*Trifolium* sp.) (Figure 4). Usually ♀293 made these excursions 4 to 5 hours after the onset of activity and remained there for about 4 hours. On the first 3 recorded visits she had her young of the year with her. She was never alone and often shared the area with up to 7 opossums all feeding frequently on the ground. The herbaceous vegetation was apparently the only attraction, and during these first 7 months she also regularly visited a similar grassed area 30 m from the field station. Her last recorded visits to these 2 areas were in March 1971. For the remaining 17 months of the study her home range was much contracted and very stable (Figures 6 and 7), presumably because it contained everything she required—*M. robusta, E. dentatus, W. racemosa,* a variety of less important species (she alone had ready access to ripe berries of *H. arborea* in the second summer), and a choice of den sites.

Male 291 behaved quite differently from ♀293. His range bordered the bed of the Orongorongo River, here about 100 m wide and usually containing 1 or 2 shallow channels about 10 m wide. The river occupies the whole bed only after prolonged rain. Between floods, vegetation becomes established, and on higher parts survives all but the worst floods (Figure 8). Male 291 was found on the river bed where the vegetation was very sparse. His visits, usually in the first half of the night, were probably to feed on low vegetation on the steep river bank, although once he was observed feeding on a solitary plant of clover on the open river bed.

In November 1971 a scabweed (*Raoulia* sp.) was in flower. This was abudant in relatively stable vegetation on the river bed. Within an hour of leaving his den tree ♂ 291 traveled 110 m to an area of scabweed where he remained for 3 hours, and was seen feeding. The next night he moved a further 110 m up the river bed (Figure 4) to another such area which he and up to 6 other opossums occupied for about 4 hours. It was too far to see what was being eaten, but later inspection showed that flowers, seed heads,

Figure 8. A general view of the Orongorongo River bed with areas of vegetation.

leaves, and roots of the scabweed had been taken, probably by opossums, though a few rabbits (*Oryctolagus cuniculus*) were also present.

In 6 of the remaining 8 months of the study ♂291 continued to make excursions up the river bed after the scab weed had finished seeding. During this period no more than 2 other opossums were ever seen on this 250 m stretch of the river bed. In February 1972 he spent 2 to 3 hours each night in the forest east of his favorite area of river bed vegetation. There was no obvious reason for his continual use of the river bed, which nonetheless explains his large summer range in the second year (Figure 6). To visit the river bed ♂291 usually had to cross one of the shallow channels, which he did by jumping between the larger stones protruding above the surface. In July 1972 the water covered all these stones, but the tracks of an opossum led to the water's edge and reappeared on the opposite bank, where ♂291 was located a few minutes later. After about 15 minutes he retraced the tracks, waded into the river, and swam to the far side, crossing 4 m of moderately fast-flowing water about 30 cm deep.

Use of the ground

The proportions of all the locations made during the active period in which the animals were on the ground are shown for each year in Table 9. The unusual night in June 1972, when 3 of the opossums were confined in ground shelter by sudden bad weather, has been omitted.

There was no seasonal trend in ground use common to all animals. The only significant difference between years was shown by ♀293, who was located less often on the ground in the second than in the first year ($\chi^2 = 7.52$, $p < .01$). The only significant difference between animals was also shown by ♀293, who was located less often on the ground than any of the others in both years. Sample sizes were too small for analysis of each animal's use of the ground in wet compared with dry weather. By pooling the data on all 4 opossums and rejecting morning and evening locations in current den trees, it was found that in the first year they spent significantly less time on the ground only when it rained for more than half the night (χ^2 (Yates) $= 9.32$, $p < 0.01$) and in the second year only when the canopy dripped for more than half the night (χ^2 (Yates) $= 4.97$, $p < 0.05$). Ground use may be influenced by other aspects of the weather, vegetation wetness, density of ground cover, food choice, animal condition and perhaps social behavior, but there were too few data for detailed analysis, and animals did not behave consistently.

Table 9.—Occurrence of each animal on the ground, during active periods only.

	Year 1		*Year 2*	
Opossum	*Total locations*	*% on ground*	*Total locations*	*% on ground*
♀144	402	15	218	21
♀293	393	9	329	4
♂291	369	18	323	21
♂329	334	16	374	19

Denning and den-site use

The location of the dens occupied daily during each weekly tracking period are shown in Figure 7. Checks between the first and second, and second and third nights' tracking, made in early morning and late afternoon, revealed no daytime shifts. The numbers of locations made are shown in Table 10 out of a maximum for each year of 48, i.e., 4 den locations for each animal each tracking week.

Dens were almost always in large trees. The percent occurrence in each tree species or on the ground is also shown in Table 10. The category "dead trees" includes only one large *Dacrydium cupressinum*, often used by ♂329 in the second year. Dens were usually in hollow trees, or trees with holes or heavy clumps of epiphytes which provided dry shelter, but the exact position of a den in a tree could not be determined. There was no consistent seasonal trend in the use of any one species for denning, nor relationship between the denning tree and locations in the same species during the previous or following night.

Ground denning occurred mainly in 1 night in June 1972, when heavy hail and later rain forced 3 of the 4 animals to take immediate shelter under logs, where they remained for the whole of the following day. Also in June 1972, ♀144 spent every day of the tracking period in the same den on the ground and most of each night on the ground too. She was in very poor condition and died within 2 months, when at least 8 years old; this exceeds the average life span of opossums (Crawley, 1970).

The number of different den sites used each year and the mean number for each season is shown in Table 10. Differences between seasonal means for each year are not significant. Some den sites were more favoured than others and used in all seasons throughout the 2 years, some were often used for a few months and then only infrequently, and others

Table 10.—Information on den sites.

	Opossum							
	♀144		*♀293*		*♂291*		*♂329*	
	Year 1	*Year 2*	*Year 1*	*Year 2*	*Year 1*	*Year 2*	*Year 1*	*Year 2*
Percent occurrence of dens in:								
Metrosideros robusta	66	58	94	95	68	38	43	10
Elaeocarpus dentatus	15	20					38	44
Laurelia novae-zelandiae	15	8	6	5	14	50	2	
Knightia excelsa	2	3			7	5	2	4
Podocarpus ferrugineus					9		5	
Dead trees								38
Ground		11				2	2	2
Unsuccessful locations	2				2	5	8	2
No.	48	36	47	42	44	42	40	48
Mean number of different den sites used each season	3.8	3.2	2.8	2.2	3.8	3.0	4.5	3.8
Number of different den sites used each year	9	10	5	4	7	6	10	6
Percent of occasions den site was changed from previous day	53	42	37	35	45	32	93	56
Percent of occasions when den was on perimeter of previous night's range	67	88	97	94	70	81	67	69
Percent of occasions when den was on perimeter of following night's range	69	92	97	90	67	74	77	72

were used only once or twice. The choice of den site was apparently not influenced by the part of the range traversed during the previous or the following night, though they did change with large shifts in range use; the new site was usually closer to the part of the range being used. On the other hand, animals sometimes spent the day outside the area being used at night, although other den sites were closer. The den was usually located right on the perimeter of the area used during the previous or following night (Table 10), but in the course of a year all den sites were eventually encompassed within the total range (Figure 7). Table 10 also shows the percent of occasions on which the den site was changed between successive days. This did not vary seasonally between animals or between years. Twice, 2 of the 4 animals spent a day in the same tree, but not necessarily in the same den, although communal denning is not uncommon (Pracy and Kean, 1969). The animals often became more vocal toward dawn, possibly when competing for a den.

The factors affecting the choice of dens each day are not clear. The weather may influence this; for example, on 3 occasions an animal was located in a den tree toward the end of the night, but moved to another tree with the onset of heavy rain just before dawn. Such movements were never detected during the day no matter when or how hard it rained. Apparently suitable dens are numerous compared with the numbers of animals present, so there should not be much competition for them. However, the existence of a social heirarchy has never been verified in the opposum and little is known of the social behavior of free-living animals. These factors may strongly influence the choice of dens and the frequency with which they are changed.

Onset and cessation of activity

It was not possible to determine when the 4 opossums actually left their dens in the evening or entered them in the morning but the onset of activity was recorded to the nearest 5 minutes on most tracking nights, and its cessation less often.

In the first year the 4 animals usually became active within 10 to 15 minutes of each other (mean 12.4 ± 2.5 min.), but in the second year this interval increased significantly (mean 23.5 ± 2.4 min. $p < 0.01$). In the first year 64 percent and in the second year 86 percent of the onset times occurred less than 1 hour before sunset and only 4 percent and 3 percent respectively, after sunset. In the second year, on 15 percent of the occasions, mostly in the winter, the start of activity was not sufficiently precise to time exactly. The animals were intermittently active when the receivers were switched on as early as 2 hours before sunset. Regular checks verified that the opossums were still in their dens, although in the second winter other opossums, hungry and in poor condition, were often seen foraging in the afternoon. Each animal usually became active within 20 minutes of the same time on different evenings of the same week, and tended to become active earlier if the previous night had been wet enough to suppress movement, but samples were too small to confirm this statistically.

The time spent in the den tree following the start of activity was determined only to the nearest hour. On 80 percent of the 256 opossum tracking nights the animals left their den trees within 2 hours of becoming active, and usually in the hour following sunset. No animal was recorded in its den tree for longer than 5 hours following the onset of activity—such delays usually being associated with continuous rain. Considerable variations in the time of departure of different individuals on any one night could have been masked by the hourly sampling interval.

It was even more difficult to time the finish of activity than its onset, since it was always uncertain which movement was the last or whether more movements would occur after the receivers were switched off. During November-April there was a distinct cessation of activity about an hour before sunrise, unless the animals had been forced to retire earlier by rain; activity then often ceased 2-3 hours before sunrise. In late autumn, winter, and early spring, particularly in the second year, intermittent activity was often detected 2-3 hours after sunrise. On 36 percent of the 256 tracking nights listening at dawn failed to time the finish of activity.

As with the onset of activity, the 4 animals ceased to be active within a relatively short time of each other, averaging 20 minutes in the first year. The hourly records again precluded detailed analysis of the times spent in the den tree prior to the end of activity in the morning. On 76 percent of the 256 tracking nights the animals were in the trees chosen for denning within 3 hours before sunrise. Return to the den tree earlier than this was usually associated with heavy rain; this sometimes happened up to 10-12 hours before sunrise. These observations on departure from and return to the den site are similar to those obtained by Winter (1963), who timed the movements of an opossum at one den in Otago, New Zealand.

Given the limits of the hourly recording, the times that the animals spent away from the den sites on dry and on wet nights, or when the canopy was dripping, are compared in Table 11. These results agree with those in Table 4, illustrating that in wet weather the opossums did not move so far at night and also that they spent less time moving. Both ♀293 and ♂291 spent significantly less time away from the den in wet weather in the second than in the first year.

Discussion

Definitions of "home range" and the use of the term vary considerably in the literature, but none has been found applicable to animals which move in 3 dimensions in a forest habitat. The opossums' vertical range probably had a marked effect upon, and was more important than, their horizontal range. The duration of the period over which measurements are made is also usually ignored, yet it may have a profound influence on the eventual size of the ranges determined (Table 2). These factors make it particularly difficult to compare the home range sizes determined by radiotracking with those measured by other workers in different habitats using trapping techniques, for example Winter (1963) and Jolly (1973) in mixed forest, scrub, and pasture habitat in New Zealand, and Dunnet (1956, 1964) in open eucalypt woodland in Australia. The cumulative 2-year ranges determined by the minimum area method (Table 6) were all greater than the mean trap-revealed ranges determined by the same method for each sex by Crawley (1973) over 32 months in 1966-68 on the same study area. However, a detailed com-

Table 11.—Mean percentage of the active period spent away from the den site each year under different conditions of precipitation and canopy drip.

	Completely dry		*Raining <50% of night*		*Raining >50% of night*		*Canopy dripping <50% of night*		*Canopy dripping >50% of night*	
Opossum	*Year 1*	*Year 2*	*Year 1*	*Year 2*	*Year 1*	*Year 2*	*Year 1*	*Year 2*	*Year 1*	*Year 2*
♀144	80.2	72.9	72.4	66.2	56.1***	14.3	72.0	56.4*	54.5***	14.3
♀293	66.5	68.4	65.3	65.4	50.5**	27.3***	60.0	60.0	47.3**	28.3***
♂291	82.8	77.3	85.0	76.3	85.0	37.9***	84.0	70.9	84.5	43.5***
♂329	82.4	84.4	86.4	78.5	70.4*	56.1***	87.5	78.2	69.0*	59.8***

Asterisks show the level of significance when these proportions are significantly smaller than those determined on dry nights in the same year (* $p < .05$, ** $p < .01$, *** $p < .001$). The sample for ♀ 144 in the second year was too small to test statistically.

parsion of the ranges of the 4 study animals with those determined over the same period by live-trapping will be made in a later paper.

Dunnet (1964) found that male opossums had mutually exclusive ranges, but that the ranges of females overlapped. No evidence to support this was found in this study. On the contrary, animals appeared to move about and make excursions without opposition from neighbors, and although generally solitary they were often seen feeding in twos and threes and occasionally in larger numbers on seasonally and locally abundant food sources. This does not discount, however, the existence of a social hierarchy, and it was occasionally evident that some animals were dominant over others when several were feeding together.

The excursions and shifts in home range use measured in this study indicated that although these opossums were generally sedentary, they were not rigidly confined to 1 area but responded positively to various opportunities as they occurred. They moved over a surprisingly small area each night (on average less than 1000 m^2) yet their movements, particularly the excursions, were closely related to variations in food availability and distribution, and to the reproductive activity of males. That they moved so little is strongly indicative of how concentrated their resources were.

It has been observed that opossums often concentrate their feeding on only 1 or 2 individuals of a species and leave neighbouring ones of the same species untouched (Elder, 1965; Meads, 1976). The data on tree use was examined for evidence of this, and although certain specimens of *M. robusta* and *E. dentatus* were more favored than others by individual opossums for periods up to 3–4 months, they were also being used for denning. Without knowing what the animals were doing between becoming active and leaving their den trees interpretation of this aspect of tree use is not possible. Nevertheless, the use of the various tree species by the animals reflected their preferences for certain foods, particularly fruits and flowers. Fitzgerald (1978) has found in a concurrent study of food preferences on the same area, using the technique of fecal analysis, that the leaves of *M. robusta* and *W. racemosa* are major foods. *M. robusta* was one of the most frequented species by all animals in both years (Table 8) and *W. racemosa* in the second year. The apparent importance of *E. dentatus* to all animals in this study was probably due to the popularity of its fruits and flowers, both difficult to identify and quantify in the feces. Two important foods of the opossum are the leaves and fruit of *Ripogonum scandens* and the leaves of *Metrosideros fulgens*; both are very common, woody lianas, the former being particularly rampant in the forest canopy. They are barely mentioned in this study, however, because it was impossible to determine whether an animal located in a tree was using either of these species.

Mason (1958), also in the Orongorongo Valley, examined the stomach contents of 6 opossums every fortnight from July 1946 to May 1947 to determine the foods being eaten. Apart from the evident popularity of the leaves of *M. robusta* and *W. racemosa* and the fruit of *Hedycarya arborea*, there is little further agreement between her results and the opossums' use of the tree species in this study. This probably results from the much larger and more diverse area sampled by Mason, differences in the abundance of seasonal foods, and the continuing modification of the forest composition (Kean, 1971) to which the animals must adjust.

The flowers and fruit of several trees and shrubs were more abundant in the first than in the second year of this study. The popularity of these as food in the first year is shown in Table 8, where one or other of these species was the third most frequented by all animals. In the second year, lacking such foods, the 4 opossums were recorded more often in *E. dentatus* (statistically significant except for ♀293) and *W. racemosa* (all significantly), and were recorded in several other species for the first time. This change in food availability and diet resulted in fewer excursions in the second year and almost certainly caused the decrease in condition of 3 of the animals in the final autumn and winter—a trend in common with the rest of the population. These factors probably accounted for the imprecise start and finish of nightly activity toward the end of the study and perhaps for the animals' more extreme response to wet weather, but relationships with several environmental factors are not clear and many more were not measured. Clearly, detailed work on the feeding activity of opossums, its occurrence and duration both in and away from den trees, and a careful study of the effects of weather on all aspects of opossum activity could well lead to a better understanding of how the animals use this forest habitat, of their reactions to changes in its quality, and of the changes which they are imposing on it.

Summary

Two male and 2 female opossums fitted with transmitters were located hourly on 3 successive nights each month for 2 years. Mean nightly range sizes, measured by an adjusted minimum area method, varied between animals, but were usually less than 1000 m^2 and were significantly smaller when it rained for more than half the night. Animals traveled outside their core areas, up to 200 m from their current den sites, to feed on seasonally occurring foods, mainly fruits and flowers. Males traveled similar distances to mate. There was no evidence of territorialism. The 4 animals had annual home range sizes of 0.28 ha to 3.21 ha. Excluding locations in current den trees the most frequented tree species were *Elaeocarpus dentatus* and *Metrosideros robusta* or *Weinmannia racemosa*. In the first year one or other of the species carrying a heavy crop of flowers or fruit was the third most frequented, but in the second year such foods were scarce and the species seldom visited. The proportion of the time spent on the ground differed between animals (6 percent–20 percent) over the 2 years of the study, but for unknown reasons. Each animal had a number of different den sites (6–13) located in a total of 6 different tree species, the most popular being *Metrosideros robusta*. Dens were often changed daily and most were on the perimeter of the nightly range. The 4 opossums usually became active within the hour before sunset, left the den tree during the hour following sunset, and returned to the den tree and ceased activity in the 3 hours before dawn. These times were influenced by the weather and possibly the animal's condition, with less time spent away from den trees on wet nights, particularly in the second year.

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Introduction

In the early part of the nineteenth century, when European settlement began in New Zealand, almost all of the country below 1000 m (about 60–70 percent of the total area) was forested. The ecological balance was radically disturbed by the clearing of forest for agriculture and by the introduction of many species of plants and animals. Today only about 20 percent of the land remains as indigenous forest, mostly on mountain lands, in heavy rainfall areas, and on the central North Island volcanic plateau.

The Australian brush-tailed opossum, one of the introduced animals, is a nocturnal arboreal herbivore which occupies a wide range of habitats in Australia, including dry sclerophyll forests, open woodland, and broadleaf evergreen forest. It was brought into New Zealand for its valuable fur [in the year ending June 1974, 1.5 million skins brought about $4 million (New Zealand Statistics Department)]. Opossums in 2 main color phases, black and gray, were introduced from both Tasmania and mainland Australia. Though first introduced in 1840, the main period of introduction was in the 1890s, when New Zealand-bred stock was also released by Acclimatization Societies. Spread was rapid because the opossums adapted successfully to the new conditions and too few were taken for their fur to check the increasing population. Also, until 1946, the opossums were partially protected. From about 1930, however, damage to both indigenous and exotic pine forest became increasingly obvious (Zotov, 1949; Pracy and Kean, 1963), and by 1947 all restrictions against killing opossums were removed. In 1951 a bounty system was introduced (but discontinued in 1960) and today the opossum is classified as a noxious animal. Its dispersal into the few remaining unoccupied parts of the country continues, and methods of controlling populations at economically or ecologically acceptable densities have not succeeded. Control methods include aerial distribution of bait treated with 1080 (sodium monofluoroacetate), laying of cyanide and phosphorized jam, trapping, and shooting. The indifferent results of all these methods suggest that information on the biology and ecology of the animal may be inadequate.

This lack of information about opossums was one of the reasons for the intensive research program being undertaken by Ecology Division, D.S.I.R., in the Orongorongo Valley, 18 km east of Wellington at the southern tip of New Zealand's North Island. Most of the detailed opossum studies are carried out in 4.4 ha of flat to gently sloping old fan material, about 100 m a.s.l. The evergreen mixed, broadleaf podocarp forest carries about 7.5 opossums per ha. The rainfall is 2443 mm/year, distributed fairly evenly throughout the year, and temperatures average 15.5°C in summer and 6.7°C in winter.

A live-trapping study of the opossums, begun in 1966, determined population density and fluctuation, breeding success, and trap-revealed home range (Crawley, 1973). An additional estimate of home range together with information on den sites and tree use was obtained by using radio transmitters fitted to 4 animals for 2 years (Ward, 1978). A study of the evidence of opossum browsing on one of the main food trees (*Metrosideros robusta*), begun in 1969, shows that these large emergent trees are being killed (Meads, 1976). Research into the food of the opossum was also started in 1969 (Dunnet, et al. 1973). The analysis of feces to determine the foods eaten, the live-trapping study, and the observations on *Metrosideros robusta* are continuing.

This paper summarizes results of 4 years of fecal analyses, with information on the vegetation and phenology of some of the tree species. The field study showed that very few species were being eaten in an area of great species diversity, and that others were eaten only seasonally. Consequently, laboratory trials with captive animals were undertaken in an attempt to find the reasons for their preferences.

Preliminary feeding trials have yielded much information and indicated where further research is required. Chemical analysis of some species has been carried out, and a simple technique has been used to assess the presence of alkaloids, triterpenes, saponins, and leucoanthocyanins in the leaves of 6 tree species. The presence of any of these chemicals may influence both palatability and toxicity.

Much more work is needed on the nutritional requirements of the opossum and on the reasons for preferential selection of foods. The morphology and physiology of the digestive system may also indicate type and degree of breakdown of the components of the food, while gut microbiology will also influence nutrient availability.

If these studies can elucidate the preferential selection of particular foods in particular areas it may be possible to control opossum densities to acceptable levels in the different forest types and thus minimize the economic loss and the accelerated changes in species composition of the forest.

Methods

Field studies

(a) FECAL ANALYSIS

Because the leaf cuticles from different plant species vary markedly in resistance to digestion, influencing the proportions of each species' cuticle observed microscopically in the feces, an index of digestion (Dunnet et al., 1973) for the 13 species eaten most commonly was used to correct the observed frequencies of occurrence of fragments of specific cuticle in the feces. A reference collection of plant cuticles was made from over one hundred species present in or near the study area.

Fecal pellets for analysis were collected monthly from 20 or more animals routinely live-trapped in the study area. Marked animals were caught during the evening in box traps with fecal collecting trays placed under the wire mesh floor of the trap. One pellet from each animal was collected the following morning. For analyzing the feces, a method was evolved based on the maceration techniques used by other workers, e.g., Baumgartner and Martin (1939), Dusi (1949), Croker (1959), Stewart (1965), and Williams (1969). Because individual variation is great (Dunnet et al. 1973), all the pellets collected from the opossums each month were pooled to obtain a record of foods eaten by the population of opossums rather than by individual animals. Identification of 540 abaxial fragments of leaf cuticle was made, and frequency of occurrence results were corrected to proportion by weight. A further scanning of the slides gave information on foods other than leaves, e.g., fruit, flowers, or bark, by the simple frequency of occurrence of fragments.

(b) VEGETATION SURVEY

Conventional methods of determing the biomass of vegetation are too destructive in places where both animals and forest must not be seriously disturbed. Consequently, a vegetation survey was undertaken on the area where opossums were trapped for fecal collection.

The study area of 4.4 ha had live traps for opossums set at marked 30 m intervals on a square grid. To compare the food eaten by opossums with its availability, the vegetation was surveyed in the summer of 1972–1973 on 64 circular plots, each 100 m^2, centered on the grid intercept pegs. All plants except ground ferns and mosses were identified, their heights recorded if over 0.3 m and diameter at breast height (dbh) measured if greater than 8 cm. The proportion of the ground covered by seedlings, ground ferns, mosses, and other miscellaneous items was assessed. Five set points were used to determine strata and canopy composition from point analyses. The epiphyte-liana load on the trees was estimated, and the presence or absence in each of 8 plot segments of two liana species (*Metrosideros fulgens* and *Ripogonum scandens*) was determined. The composition and abundance of the various species gave a measure of the availability of potential opossum foods.

(c) PLANT PHENOLOGY

From January 1971 until December 1974, monthly records were made of the phenology of some of the major tree species in the area. Three events were recognized: new growth, flowering, and fruiting (seeding). New growth was divided into (a) none, (b) vegetative bud stage, (c) partially expanded, and (d) fully expanded leaves. Flowering had 5 categories: (a) none, (b) buds, (c) buds with some flowers, (d) flowers all open, (e) most flowers fallen. Fruiting and seeding had 4 categories: (a) none, (b) set, immature fruit, (c) ripe fruit, (d) dehisced seed.

Laboratory studies

(a) FEEDING TRIALS

Three different types of feeding trials with captive opossums were carried out over a period of about 18 months. Animals, generally caught from suburban properties, were kept in an animal house where 10–12 had free run of a 6.0 m by 2.5 m room. They were fed pelleted food, apples, green vegetation, and bread and had access to water at all times. Healthy adult males and females were transferred to individual stainless steel feeding cages 76 by 60 by 60 cm, with mesh floors and collecting trays for feces and urine. Removable food hoppers and water containers were attached to the front door and a wooden sleeping box to the side of the cage.

In initial trials, 4 opossums were fed single species diets for 21 days with water *ad lib*. The animals, the food eaten and the feces produced were weighed daily.

Leaves of three species, *Pseudopanax arboreum* (formerly *Neopanax arboreum*), *Weinmannia racemosa*, and *Melicytus ramiflorus*, were fed separately. Subsequently, 4 animals that had been used in the earlier feeding trials were fed a different diet of white bread and soaked dried peas.

For a more rigorous trial, 6 male and 6 female opossums were fed a standard diet of pelleted herbivore food for 8 weeks. The food and feces were again weighed, water intake and urine output measured, and the animals weighed daily. The first 4 weeks were considered a settling in period for the individually caged animals. During the second 4 weeks an aliquot of feces from each animal was freeze-dried daily and an aliquot of urine from each animal was frozen each day; these, together with a freeze-dried sample of pelleted food, were subsequently analyzed for hemicellulose, cellulose, lignin, nitrogen, energy, ash, urinary nitrogen, and urinary energy by the Analytical Group, Applied Biochemistry Division, D.S.I.R. Methods for determining precise levels of the various structural carbohydrate fractions in herbage are open to error (Bailey, 1973) and allow only general comparisons to be made.

(b) CHEMICAL TESTS

Leaves of *Metrosideros robusta* and *M. fulgens* were collected at dusk each month for a year, immediately deep frozen and later analyzed for ash, nitrogen, lipids, energy, water soluble starches, pectin, hemicellulose, cellulose, and lignin.

Tests were also made for some secondary compounds in the leaves of 6 plant species. Collections were made monthly for 12 months from *Metrosideros robusta*, *M. fulgens*, *Weinmannia racemosa*, *Ripogonum scandens*, *Melicytus ramiflorus*, and *Hedycarya arborea*. Leaves were dried at a temperature below 60°C for approximately 36 hours and were finely broken up before simple tests for triterpenes, saponins, leucoanthocyanins, or alkaloids were carried out (Cambie et al., 1961).

Results

Field studies

(a) FECAL ANALYSIS

The main species eaten (*Weinmannia racemosa* and *Metrosideros robusta*) comprised about 60 percent of

Table 1.—Monthly occurrence of leaves in opossum diet.

	Species with Index												
	Weinmannia racemosa 0.639	*Metrosideros robusta* 0.778	*Metrosideros fulgens* 1.024	*Melicytus ramiflorus* 0.175	*Ripogonum scandens* 0.623	*Geniostoma ligustrifolium* 0.085	*Pseudopanax arboreum* 1.000	*Elaeocarpus dentatus* 0.516	*Beilschmiedia tawa* 0.912	*Laurelia novaezelandiae* 0.871	*Myrsine salicina* 1.034	*Schefflera digitata* 0.081	*Leptospermum ericoides* 2.301
Month	*Mean monthly percentage occurrence by weight of leaves*												
May	34.3	18.6	2.2	16.5	23.0	1.1	1.9	0.7	0.3	0	1.2	0	0.2
June	29.2	25.2	2.2	10.1	19.2	3.9	5.7	1.1	0.3	0.1	1.0	1.7	0.3
July	28.5	36.3	1.2	16.2	10.0	3.2	2.4	0.6	1.1	0.1	0.1	0.2	0
August	33.2	22.5	6.0	8.8	7.5	7.3	9.2	0.4	1.9	0	3.4	0	0
September	24.0	28.8	7.2	16.0	5.6	7.1	8.2	1.7	0.2	0.7	0.2	0	0
October	15.2	27.0	28.4	5.5	5.1	6.6	6.8	4.3	0	0.3	0.5	0.3	0
November	19.6	19.2	29.4	5.0	1.6	2.6	7.6	7.0	4.3	2.5	0.2	0.3	0.5
December	35.9	22.4	21.3	2.3	0.8	3.8	2.7	4.2	3.0	3.0	0.3	0.3	0.3
January	48.0	34.4	2.7	3.7	0.9	4.6	1.6	0	0.8	1.5	0.3	1.0	0
February	35.8	51.8	0.6	1.1	0.8	5.2	2.0	0.3	0.9	0.9	0	0	0.4
March	42.8	44.6	0.8	0.4	1.5	6.8	2.5	0	0.2	0.3	0	0	0
April	45.8	20.4	3.1	11.5	7.2	6.0	3.6	0	0	0.6	1.4	0.3	0

the diet over the 4 year period (Table 1, 2), decreasing in spring when *Metrosideros fulgens* was eaten in quantity and in winter when *Ripogonum scandens* was eaten, in all 4 years. The other species appear to be eaten sporadically at any season. Some species may have become more important in the diet over the 4 years, e.g. *Melicytus ramiflorus* and *Geniostoma ligustrifolium,* others less, e.g., *Pseudopanax arboreum* and, perhaps *Beilschmiedia tawa,*

The 13 species can be divided roughly into 3 groups, characterized by the way they contribute to the diet: those contributing substantially and regularly, *Weinmannia racemosa* and *Metrosideros robusta;* those contributing seasonally large amounts or moderate amounts regularly, *Metrosideros fulgens, Ripogonum scandens, Melicytus ramiflorus, Geniostoma ligustrifolium,* and *Pseudopanax arboreum*; and those species regularly or sporadically contributing small amounts, *Elaeocarpus dentatus, Beilschmiedia tawa, Laurelia novaezelandiae, Myrsine salicina, Schefflera digitata,* and *Leptospermum ericoides.*

The mean monthly frequencies of occurrence of fragments of foods other than leaves (Table 3) do not necessarily represent the proportions eaten because of probable differences in digestibility. Bark will survive largely intact while flowers leave few identifiable fragments. The figures, however, are useful for general comparison from month to month.

Abaxial leaf fragments comprised about 66 percent of the total identified. Portions of flowers were present in all months, many of the fragments in winter and spring from the buds of *Elaeocarpus dentatus.* Remnants of fruit and seeds were present in the feces in 10 of the 12 months. Petiole fragments formed a consistent, though generally small, part of the diet in every month. Bark was also eaten in all months, but more in late summer and autumn than in other seasons. Fragments of fern flesh from developing fronds, and fern scale, and cuticle from older fronds were also regularly present. Invertebrate fragments occurred in small quantities in most months of the year.

(b) VEGETATION SURVEY

From their percentage occurrence at all heights (Table 4), the species can be divided into groups. Tree ferns (*Cyathea* spp. and *Dicksonia* sp.) were most frequent (19.7 percent) with *Hedycarya arborea* (13.4 percent), *Elaeocarpus dentatus* (10.2 percent) and *Melicytus ramiflorus* (9.4 percent). The second group comprises

Table 2.—Annual occurrence of leaves in opossum diet.

	Species												
	Weinmannia racemosa	*Metrosideros robusta*	*Metrosideros fulgens*	*Melicytus ramiflorus*	*Ripogonum scandens*	*Geniostoma ligustrifolium*	*Pseudopanax arboreum*	*Elaeocarpus dentatus*	*Beilschmiedia tawa*	*Laurelia novaezelandiae*	*Myrsine salicina*	*Schefflera digitata*	*Leptospermum ericoides*
Year	*Percentage occurrence by weight of leaves, mean ± S.D.*												
1	32.5 ±16.35	29.9 ±15.52	8.2 ±11.60	5.3 ±4.84	12.9 ±15.11	2.6 ±3.00	3.8 ±3.12	0.8 ±1.09	1.5 ±2.46	0.3 ±0.41	1.4 ±2.94	0.4 ±0.94	0.2 ±0.32
2	36.9 ±18.04	33.9 ±17.40	5.4 ±7.33	5.9 ±7.07	3.3 ±4.38	3.9 ±3.77	5.5 ±4.03	2.2 ±3.71	1.5 ±2.68	0.4 ±0.66	0.8 ±1.14	0.2 ±0.43	0.2 ±0.55
3	33.3 ±16.70	26.6 ±11.55	10.7 ±13.97	6.6 ±6.93	7.9 ±8.46	4.9 ±3.10	6.1 ±5.96	1.1 ±1.62	0.9 ±1.09	1.0 ±1.41	0.0 —	0.7 ±1.48	0.0 —
4	28.0 ±8.77	26.8 ±19.93	10.7 ±12.62	14.6 ±15.10	3.5 ±5.31	8.0 ±5.21	2.5 ±2.76	2.5 ±5.88	0.5 ±0.74	1.6 ±2.07	0.8 ±0.93	0.1 ±0.32	0.1 ±0.31
All years	32.7 ±15.23	29.3 ±16.14	8.7 ±11.48	8.1 ±9.82	6.9 ±9.85	4.9 ±4.26	4.5 ±4.27	1.6 ±3.57	1.1 ±1.91	0.8 ±1.38	0.7 ±1.67	0.3 ±0.92	0.1 ±0.35

Table 3.—Monthly occurrence of types of food in opossum diet.

	Type of food fragment									
	Abaxial leaf	*Flower*	*Fruit*	*Seed*	*Petiole*	*Bark*	*Fern flesh*	*Fern cuticle or scale*	*Invertebrate*	*Unknown*
Month	*Mean monthly percentage by frequency of occurrence*									
May	61.9	16.0	1.0	0.7	0.7	10.4	0.5	0.6	2.2	6.1
June	62.2	21.4	0	3.5	3.4	5.0	0	0.8	0.6	3.2
July	59.8	22.3	0	2.9	3.3	4.6	1.7	1.1	0.9	3.4
August	70.2	16.7	1.2	2.1	3.0	0.7	1.7	1.6	0.2	2.4
September	70.0	16.2	0.8	0.3	3.4	1.8	2.2	1.1	0	4.2
October	67.6	15.5	1.5	0.3	3.6	0.8	2.3	0.9	1.5	6.0
November	61.5	15.8	1.5	0	4.5	3.3	2.7	3.4	1.7	5.5
December	72.8	6.2	2.1	0.5	4.8	2.1	1.6	4.9	1.3	3.7
January	68.6	8.2	2.6	0	1.9	8.4	2.1	4.2	1.8	2.2
February	61.4	5.5	4.7	1.7	2.3	12.0	3.8	2.7	1.7	4.1
March	67.0	3.8	5.7	3.9	3.2	11.7	1.3	0.2	0.5	2.3
April	63.3	7.5	4.4	2.2	1.9	10.4	4.1	0.5	1.0	4.6

Table 4.—Abundance and stratification of species from point analysis.

	Height in meters								
Species	*3–4*	*5–9*	*10–14*	*15–19*	*20–24*	*25–29*	*>30*	*Total*	*% Total*
Astelia solandri	1	—	—	—	—	—	—	1	0.2
Beilschmiedia tawa	—	4	1	1	—	—	—	6	0.9
Carpodetus serratus	—	2	—	—	—	—	—	2	0.3
Collospermum hastatum	1	—	—	—	—	—	—	1	0.2
Coprosma areolata	1	2	—	—	—	—	—	3	0.5
C. australis	3	3	—	—	—	—	—	6	0.9
C. lucida	—	1	—	—	—	—	—	1	0.2
C. robusta	—	2	—	—	—	—	—	2	0.3
Corynocarpus laevigatus	—	—	1	—	—	—	—	1	0.2
Cyathea cunninghamii	1	3	—	—	—	—	—	4	0.6
C. dealbata	31	41	—	—	—	—	—	72	11.1
C. medullaris	2	7	4	—	—	—	—	13	2.0
C. smithii	12	20	—	—	—	—	—	32	4.9
Dacrydium cupressinum	—	—	—	—	4	5	3	12	1.8
Dicksonia squarrosa	2	5	—	—	—	—	—	7	1.1
Elaeocarpus dentatus	—	7	18	34	7	—	—	66	10.2
Freycinettia baueriana	2	1	2	—	—	—	—	5	0.8
Geniostoma liqustrifolium	9	2	—	—	—	—	—	11	1.9
Griselinia lucida	—	2	2	—	—	—	—	4	0.6
Hedycarya arborea	6	64	14	3	—	—	—	87	13.4
Knightia excelsa	—	—	1	7	1	—	—	9	1.4
Laurelia novaezelandiae	3	8	3	15	5	0	—	34	5.2
Macropiper excelsum	3	5	—	—	—	—	—	8	1.2
Melicytus ramiflorus	1	39	16	5	—	—	—	61	9.4
Metrosideros diffusa	—	4	3	—	—	—	—	7	1.1
M. fulgens	5	12	3	—	—	—	—	20	3.1
M. robusta	—	—	—	1	7	14	3	25	3.8
Myrsine australis	—	1	—	—	—	—	—	1	0.2
Nothofagus truncata	—	1	—	2	—	—	—	3	0.5
Oleari rani	1	6	—	—	—	—	—	7	1.1
Pennantia corymbosa	1	1	—	—	—	—	—	2	0.3
Pittosporum eugenioides	—	1	—	—	—	—	—	1	0.2
Podocarpus ferrigineus	1	—	—	1	2	—	3	7	1.1
P. spicatus	—	—	—	—	1	—	4	5	0.8
Pseudowintera axillaris	10	24	—	—	—	—	—	34	5.2
Rhopolostylis sapida	4	6	—	—	—	—	—	10	1.5
Ripogonum scandens	1	21	4	1	—	—	—	27	4.2
Schefflera digitata	1	24	1	—	—	—	—	26	4.0
Weinmannia racemosa	—	6	10	11	—	—	—	27	4.2

those species which each represent about 3-5 percent of the vegetation, *Laurelia novaezelandiae, Pseudowintera axillaris, Metrosideros robusta, M. fulgens, Weinmannia racemosa, Ripogonum scandens*, and *Schefflera digitata*. All other species, the third group, each contributed less than 2 percent.

Ripogonum scandens, a strongly ramifying liana was present in 76 percent of the 512 segments of the 64 quadrats, while *Metrosideros fulgens,* a much more compact liana, was present in 24 percent.

The open, litter-covered nature of the forest floor was indicated by the ground-cover assessment in the 512 segments: leaf litter 64 percent; ground ferns 17 percent; seedlings 9 percent; monocotyledons 7 percent; *Metrosideros* species, mosses, and gravel each 1 percent.

(c) PLANT PHENOLOGY

Monthly records of the phenology of a number of plant species, made during 3 of the 4 years of the food study, showed marked interspecific differences in the duration and abundance of new growth, flowering, and fruiting, as well as intraspecific differences between years. The phenology of *Elaeocarpus dentatus* and *Hedycarya arborea*, whose fruit and flowers contribute to the diet of the opossum, is outlined in Table 5. Flowerbuds of *Elaeocarpus dentatus* first appeared in the axils of the leaves in February, though they did not flower until November. Some of the large succulent drupes, formed in mid to late summer, remained on the tree and were available to opossums until late winter. The differences in the duration of flowering, fruiting, and new growth over the 3 years were minor, but the percentage of trees with fruit varied from about 80 percent in 1971 to 66 percent in 1972 and just over 30 percent in 1973. Leaves of this species were eaten occasionally, perhaps accidentally, with the buds and fruit.

Hedycarya arborea had green, ripening, or ripe fruit present on some of the trees at all times. Flower buds appeared in winter and developed slowly until flowers opened in late spring or early summer. Fruit set in the summer of one year ripened in the spring or summer of the following year. Fewer drupes were present in 1972 than in the other two years and like *Elaeocarpus dentatus* the period of the new growth was confined to spring and early summer.

Laboratory trials

(a) FEEDING TRIALS

Table 6 gives the duration of each trial, the number of opossums, the mean daily intake and output, together with the mean body weights at the commencement of each trial and the percent of weight change incurred by the completion of the trial. Kilocalories used per kg of body weight per day were also calculated. The response of the animals differed in each trial (Tables 7 and 8). Table 7 gives the mean values of the constituents in the food and feces from the feeding trials, while Table 8 gives the percentage of these constituents that the animals extracted. The percentage of nitrogen extracted was very different in the 3 diets. Lack of precision in structural carbohydrate determination is probably responsible for the anomalous result (Table 8) where lignin appears to have been digested.

(b) CHEMICAL TESTS ON TWO *Metrosideros* SPECIES

The main leaf constituents of *M. robusta* and *M. fulgens* are summarized in Table 9. Percentages of structural and soluble carbohydrates in *M. robusta* are generally slightly higher than those of *M. fulgens* while nitrogen and ash have higher values in *M. fulgens*. The energy values (cal/g) are not appreciably different and probably are accounted for by the higher lipid content in *M. fulgens*. The highest value for lipid in this species occurs in November (10.88) (Table 9), which is when most *M. fulgens* is eaten (Table 1).

(c) CHEMICAL CHARACTERISTICS OF THE LEAVES

Metrosideros robusta. This species gave negative tests for all 12 months for triterpenes, as did the other 5 species. Saponins were present only in February and leucoanthocyanins in all months except June, July, and August. The test for alkaloids was negative in all months.

Metrosideros fulgens. Leucoanthocyanins were present in all months, and saponins irregularly. Tests for alkaloids were negative.

Weinmannia racemosa. Saponins and alkaloids were absent and leucoanthocyanins present in all months.

Ripogonum scandens. This liana had a strong stable reaction for saponins in all months. From May to November (autumn and winter) alkaloids were present, and from October to April (spring and summer) leucoanthocyanins were present.

Melicytus ramiflorus. Tests gave strong positive results for alkaloids in all months, but no leucoanthocyanins. Saponins were present in August, September, and November.

Hedycarya arborea. Saponins were present in all months, leucoanthocyanins were present in 9. The alkaloid tests for 8 of the 9 months when tests were successfully carried out were positive. A black precipitate of unknown origin interfered with the results from May, June, and July.

Discussion

Food habits

Accurate determination of the diet of herbivores from analysis of fecal pellets is difficult (Hercus, 1960, Storr, 1961, Stewart, 1967, Free et al., 1970, and Dunnet et al., 1973). The two main problems are the identification of species and variations in the proportions of different species recovered from the feces. In the Orongorongo Valley, opossums ate few species, and these had relatively thick cuticled leaves with distinctive patterns. Estimating how much epidermal cuticle of the leaves has been digested is not simple

Table 5.—Phenology of two tree species.

Event	*Stage*	*Percentage occurrence*																		
		1971												*1972*						
		J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*J*	*F*	*M*	*A*	*M*	*J*	*J*
Fruit	dehisce																			
	ripe			24	57	62	24	14									19	14	14	10
	unripe	29	76	57	24									52	67	72	43	29	5	
Flower	flower fall		14											19						
	open	52	10										33	5						
	partly open	33										33	48							
	bud				19	24	38	67	71	81	81	52				5	10	14	29	33
New growth	expanded													43	14					
	expanding													10						
	unexpanded																			
		Elaeocarpus dentatus N = 21																		
Fruit	dehisce																			
	ripe	72	28	14	14						3		3	3						15
	unripe	3	16	14	11	11	8	8	6	6	3	3	39	46	56	56	56	54	51	36
Flower	flower fall												11							
	open											14	20							
	partly open							3			3	44								
	bud						3	64	86	83	81	39						3	5	8
New growth	expanded											42								
	expanding										36	50								
	unexpanded							50	78	92	58	3								3
		Hedycarya arborea N = 37(+)																		

(Dunnet et al., 1973), but an index of digestion for the 13 main species eaten by the opossums in the Orongorongo Valley was used to correct the observed frequency of occurence of cuticle fragments in the feces. Correction factors range widely, from 0.081 for *Schefflera digitata* with a large, soft leaf, to 2.301 for *Leptospermum ericoides*, a small-leaved sclerophyllous species; this emphasizes the necessity of applying the correction to obtain absolute values of the relative amounts of each species eaten. Correction factors have some limitations, but the results obtained using them will be very much more realistic than those from the observed frequency of occurrence.

Kirk (1920), Zotov (1949), Kean and Pracy (1953), Mason (1958), Gilmore (1966, 1967), and Dunnet et al. (1973) have studied the food of opossums in forests or the effects of opossums on indigenous forests in New Zealand, and Gilmore (1965) and Harvie (1973) their diet on pastoral land. Analysis of feces was used by Dunnet et al. (1973) and in part by Gilmore (1967). Kirk (1920), Mason (1958), Gilmore (1965, 1966), and Harvie (1973) analyzed the contents of stomachs; while Zotov (1949) and Kean and Pracy (1953) relied on visual evidence of browsed vegetation. Despite the different techniques used, some results were common to all the studies. First, the average number of leaf species eaten per night was 3. Second, there was strong selection for leaves of a few of the many species present; though some species were never eaten, others if present, were always eaten, but there was no constant order of preference. Third, flowers, fruit, and the leaves of some plants commonly considered poisonous contributed regularly to all the diets.

Effects on the vegetation

Unfortunately, much of the work on the diet or food preferences of opossums, and in fact of most herbivores, has failed to include a detailed account of the vegetation and of the availability of the different foods

					1973											
A	*S*	*O*	*N*	*D*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
								5	19	14	10	5				
				24	33	29	29	19	5	10	5	5				48
																76
			24	14											72	10
			14												11	
38	38	14				5	5	48	57	57	62	67	76	81		
				43	67											38
			10	14											24	19
		10	10												29	
13	3	3	8	27	14	17	11	8	6		3	3				6
36	32	30	22	12	23	3	6	6	6	8	6	6	6	6	8	14
				5	8										25	
			27	16											36	
			11	3									11	53		
18	21	32	8							36	42	42	67	20		
			22	73											6	81
		3	32	8										36	94	3
3	8	68									8	47	28	25		

eaten. Mason (1958), studying foods of opossums in the Orongorongo Valley from stomach analysis, listed the plants adjacent to the traps in which the animals were caught and compared this with the species in the stomachs. Gilmore (1967), studying the food of the opossum in one area of the South Island, listed the species present, with an assessment of abundance of the 5 main species for 1 area, but only a brief general description of the vegetation in 3 other areas. In studies of ungulates, McAllister (1972) sampled the vegetation in the territories of impala (*Aepyceros m. melampus*) by estimating leaf cover of each of 12 species eaten and converting these to proportions by dry weight. Stewart and Stewart (1970) studied the food of 8 animal species in Southern Kenya. Grasses were given an abundance symbol while other species were listed. None of these techniques gives sufficiently ditailed information on what was available for the animal to eat, and consequently it is not possible to assess the impact of the animals' feeding either on the total vegetation or on any species. This may not always have been intended. However, with a background of economic loss from the damage sustained to both indigenous and exotic forests in New Zealand from opossum browse, together with the secondary effects of erosion and river control, the emphasis of this food study was not only on the animal but also on its impact on the vegetation.

Table 4 summarizes the vegetation survey. Figure 1, combining Tables 1 and 4, compares the composition of the vegetation with the diet of the opossums. The 2 species which form about 60 percent of the leaf diet of the animals, *Weinmannia racemosa* and *Metrosideros robusta*, although in the top 10 for availability at 4.2 and 3.8 percent respectively, are becoming much less abundant in the area. *M. robusta*, studied intensely for 6 years, is being drastically affected by the opossums (Meads, 1976). Eleven of 50 large (< 30 m tall) emergent *M. robusta* trees have died during the 6 years, and more are severely defoliated.

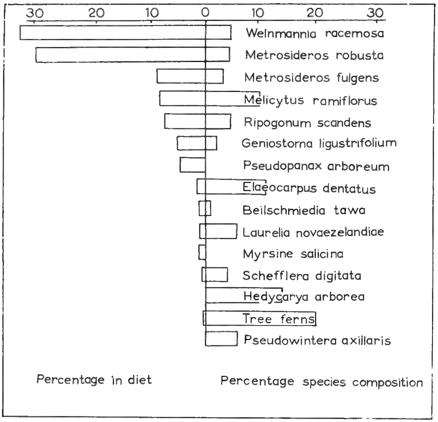

Figure 1. Comparison of percentage occurrence of leaves of species eaten by oppossums with percentage of species available.

Their apparent inability to produce new growth in response to browse, as do some species, must hasten their death. *M. robusta* trees from which opossums are excluded by wide metal bands on the trunks, regain vitality in a few years. Though detailed information on *W. racemosa* is not available, dead or dying specimens are common in and near the study area. If *W. racemosa* and *M. robusta* continue to supply such a large proportion of the opossum's food, the effects already noted on both species must accelerate.

Metrosideros fulgens, eaten mainly in the spring, appears to be sufficient to withstand browsing at the present level; as does *Ripogonum scandens.* The flowers of *M. fulgens* and the fruit of *R. scandens* are also eaten by the opossums; both occur in most months of the year. *Melicytus ramiflorus* is abundant (9.4 percent) and is probably not endangered; it also has a remarkable ability to produce new growth at almost any time of the year, as well as in response to browse.

Some *Beilschmiedia tawa* trees have died in the last few years, probably from continued heavy browsing by opossums, and very few large trees of this species remain. *Myrsine salicina* is represented in the study area by about 4 specimens, all heavily browsed and nearly dead; there is little evidence of regeneration, even though seed sources are present at higher altitudes. *Pseudopanax arboreum* is represented in the study area and adjacent forest by a few spindly, browsed saplings.

These 3 species, *B. tawa, M. salicina,* and *P. arboreum,* are strongly selected by opossums, whose continued browsing on them and on *M. robusta* and *W. racemosa* will probably change the species composition of the area rapidly. In the late 1940s the most preferred species in the same area included *Fuchsia excorticata* and *Alectryon excelsus* (Mason, 1958), both now absent except for some seedlings of both and a few heavily browsed trees of *A. excelsus.* This could well be the fate of the 5 earlier listed species. It is not known whether the gaps left in the forest will be filled with so-called "unpalatable" species; whether these species will then become more acceptable and, in turn, be eaten by the opossum; or whether the opossum population will decline because of food shortages. The

Table 6.—Summary of results from five opossum feeding trials.

Diet	*Number of opossums*	*Length of trial (days)*	*Food g D. W.*	*Feces g D. W.*	*Water ml*	*Urine ml*	*Kcal/kg/ day*	*Body weight kg*	*% Weight change*
Commercial herbivore pellets	12	28	84.0	35.9	296	184	80.56	2.73	+ 4.3
Peas and bread	4	21	Peas 60.1 Bread 29.4	7.6	*	*	112.20	3.02	+28.1
Pseudopanax arboreum leaves	4	21	16.3	7.0	*	*	14.48	2.83	−18.1
Weinmannia racemosa leaves	2	17	27.5	13.2	*	*	*	2.72	−18.0
Melicytus ramiflorus leaves	2	18	15.7	7.3	*	*	*	2.22	−18.0

Table 7.—Mean values of constituents from three feeding trials.

Constituent	*Commercial herbivore pellets*		*Peas and Bread*			*Pseudopanax arboreum Leaves*	
	Food	*Feces*	*Peas*	*Bread*	*Feces*	*Food*	*Feces*
Energy (cal/g)	4479.6	4453.4	4502.6	4337.9	4815.2	5367.7	6525.4
Ash %	8.9	1.3	31.8	2.3	10.6	6.2	5.1
Nitrogen %	3.6	2.8	4.2	2.0	5.1	1.3	2.3
Lignin %	4.3	7.2	trace	trace	*	10.3	23.7
Cellulose %	10.0	16.8	trace	trace	*	7.2	10.9
Hemicellulose %	25.7	18.8	trace	trace	*	2.9	2.4
Pectin %	*	*	2.6	< 1.0	*	7.9	0.8
Water soluble starch %	*	*	22.5	31.2	*	17.4	1.4
Lipid %	*	*	4.4	1.0	*	*	*

* data not available

Table 8.—Dietary constituents extracted by opossums.

Diet	*Energy % (cal)*	*Ash %*	*Nitrogen %*	*Lignin %*	*Cellulose %*	*Hemi-cellulose %*	*Pectin %*	*Water soluble starches %*
Commercial herbivore pellets	87.4	93.8	67.2	17.6	28.5	68.7	*	*
Peas and bread	90.8	95.8	87.6	*	*	*	*	*
Pseudopanax arboreum leaves	47.8	64.5	23.4	1.3	35.1	64.5	95.4	96.6

* data not available

Table 9.—Leaf constituents of two *Metrosideros* species.

	Metrosideros robusta			*Metrosideros fulgens*		
Constituents	*Mean*	*Range*	*S.D.*	*Mean*	*Range*	*S.D.*
Energy cal/g	4976	4804–5260	112.2	5064	4936–5360	117.9
Ash %	4.59	4.3–5.0	0.23	5.1	4.2–5.9	0.34
Nitrogen %	0.9	0.8–1.1	0.08	1.1	0.9–1.2	0.10
Lignin %	13.5	12.3–15.7	0.94	11.4	9.7–12.4	0.85
Cellulose %	16.2	13.4–17.8	1.28	14.2	11.7–15.6	1.38
Hemicellulose %	8.4	7.0–9.6	0.77	8.8	7.0–11.0	1.49
Pectin %	5.3	4.7–6.0	0.43	4.4	3.4–6.9	0.86
Water soluble starch %	8.8	7.2–9.8	0.98	8.7	7.4–10.6	0.94
Lipid %	8.0	6.9–8.9	0.52	9.0	8.1–10.9	0.84

continued study of the vegetation and the opossum, its diet and nutrition, should answer some of these questions. It would be easier to predict the outcome if it were known why the opossums feed so selectively on a few plant species.

Use of supplementary foods

Defoliated and browsed trees are the most obvious signs of opossums in the forest. It is also this preference for a leaf diet together with marked selection of certain species that creates both short and long-term changes in the vegetation. But opossums also eat other types of food; buds, flowers, and fruit, for instance, which may be important to the animals. The sheer bulk of leaves required to provide adequate nutrition, or the inadequate nutritional constituents in leaves, may necessitate the ingestion of some supplementary food. The amounts of buds, flowers, and fruit on the trees fluctuated between years, but it is not known how this affected the opossums. Some fruits are available over long periods; *Elaeocarpus dentatus* fruit is eaten green or ripe from January until August and *Ripogonum scandens* fruit may ripen at almost any time of year. Other species have a much more confined fruiting period, e.g., *Pennantia corymbosa* from January until March. *Hedycarya arborea* fruit, though present on the trees for at least 12 months, is eaten only when ripe, usually for 6–8 weeks in the summer.

Buds and flowers also contribute to the diet. *Metrosideros robusta* and *M. fulgens* flowers are eaten, *M. robusta* flowering only in December and January, *M. fulgens* sporadically in all months. *Hedycarya arborea* and *Knightia excelsa* buds are produced in late autumn, but neither flower until late spring. Both buds and flowers are eaten. *Elaeocarpus dentatus* provides buds, flowers, or fruit in all months of the year. This lack of synchrony in flowering and fruiting between species provides some supplementary foods, together with leaf petioles, bark, and ferns, throughout the entire year, but the amounts taken and their nutritional significance remain to be determined.

Laboratory studies

When 4 years' field study of opossums showed not only that their food preferences were pronounced but also that some were seasonal, laboratory work was begun to try to explain the preferences. Little information existed about the food requirements of opossums or how these were satisfied by their choice of food. The reasons for an animal's selection of food are notoriously complex and no consensus has yet been reached (Arnold, 1964; Moss and Parkinson, 1972; Janzen, 1978).

The first experiments in this study were designed to find out how much opossums ate and what fraction was digested. From these trials, the lack of knowledge of gut physiology and microbiology essential to understand nutrition and digestion also became evident. The opossum has a simple stomach, with a small intestine about 280 cm in length, caecum 50–60 cm long, and the large intestine about 190 cm long. Gilmore (1966) gives the relative lengths of the different parts of the intestine as small intestine 50 percent, caecum 11 percent, and large intestine 39 percent. These compare with relative proportions in the ox (a ruminant) and the rabbit (coprophagous) of 81:2:17 and 61:11:28, respectively. The opossum's proportions suggest that cellulose breakdown and digestion occur in the caecum as in most monogastric herbivores.

Table 6 summarizes the input-output results of the feeding trials. The 3 different types of food, commercial herbivore pellets, peas and bread, and single species of leaf, give very different results, the magnitude of which emphasizes the danger of extrapolating from only 1 type of trial. If weight response is an appropriate criterion, however, it can be generalized from the 5 diets fed (a) that single species diets are nutritionally inadequate and (b) that peas and bread provide a diet more abundant in available dietary nutrients than the herbivore pellets.

The mean values of the constituents in the food and the feces for 3 of the 5 diets (Table 7) show major differences. Structural carbohydrates, as might be expected, were negligible in the peas and bread diet and absent in the feces. Cellulose and hemicellulose were higher in the herbivore pellets than in the *P. arboreum* leaves, while nitrogen and water-soluble starches were higher in the peas and bread. *P. arboreum* had the highest lipid content and caloric value. When these facts are considered with Table 6, it can be seen how the opossums responded to each particular diet and what percentage of the constituents they extracted (Table 8). Energy, ash, and nitrogen values are highest in the peas and bread diet and lowest in the *P. arboreum* diet. Proportion of cellulose extracted was slightly higher in *P. arboreum*, but for all other constituents *P. arboreum* had the lowest values, particularly for nitrogen. The form of many of the constituents may influence their availability; for example, low protein intake in hares can adversely affect the uptake of other nutrients as well as influencing its own availability (Holter et al., 1974), thus aggravating the original shortage of protein.

In the tests on 2 species of *Metrosideros* (Table 9), the high lipid value in November may indicate why *M. fulgens* is eaten in spring. Also, knowing how opossums digest the constituents of *Pseudopanax* *arboreum,* it is interesting to compare the nutritional constituents of the *Metrosideros* species with those of *P. arboreum.* Structural carbohydrates are much higher in the *Metrosideros* species and water-soluble starch much lower. Speculating, it would appear that in order to extract an equivalent amount of water-soluble starch from *Metrosideros* species, an animal would need to eat more and pass it through the gut faster than with *P. arboreum.* More rapid rate of passage would reduce cellulose and hemicellulose breakdown in the caecum, which in turn would require even greater amounts eaten and more rapid rates of passage. There must be some more acceptable explanation than this. Supplementary foods with high and available nutritional components may be necessary when the main leaf species eaten are nutritionally deficient.

Influence of toxic (secondary) compounds in the diet

Whether an animal eats a food simply because it likes the flavor, rather than because of its nutritional content, inconsistencies of preference in different areas still have to be explained. The presence and balancing of toxic compounds in the diet may explain some of these inconsistencies. Janzen (1978) has proposed that toxicity be measured by the difference between the energy gained by ingesting a toxic food and the energy expended in countering its toxins. If this proposition is correct, and if, on balance, the diet of leaves is nutritionally inadequate for opossums, then supplementary foods may be important, particularly if these are flowers or fruit with a high nutritive value.

The chemical characteristics of the 6 tree species tested suggests that secondary compounds may indeed contribute to selectivity. The species eaten most frequently, *Weinmannia racemosa, Metrosideros robusta,* and *M. fulgens,* contained much less of the toxic compounds for which tests were made than the other 3 species. Of the latter, 2 eaten much less often than *W. racemosa* and *M. robusta (Ripogonum scandens* and *Melicytus ramiflorus*) and *Hedycarya arborea,* seldom eaten, all gave strong positive reactions to 3 of the 4 tests: the alkaloid reaction for *M. ramiflorus* was particularly strong and the saponin reaction for *R. scandens* were also strong. The toxicity of these species may make them very "uneconomical" foods. Further information is required on the nutritional value, the levels of secondary compounds and the responses of opossums to the various foods eaten to determine which aspects of the food are important. Opossums are easy to keep in captivity, and results from laboratory studies of wild-caught animals should be relatively reliable. This adaptability has assisted the opossum to become established in a new and very different environment from that in which it evolved in Australia.

Summary

The diet of a population of opossums in 4.4 ha of lowland evergreen forest in the Orongorongo Valley, east of Wellington, New Zealand, was investigated over 4 years. A survey and routine phenological record of vegetation assisted interpretation of monthly fecal analyses. An index of digestion was used to correct the observed frequencies of leaf cuticles in feces, and fragments of other foods were recorded by frequency of occurrence.

Approximately 60 percent of the leaf diet was taken from 2 moderately abundant species of tree, *Metrosideros robusta* and *Weinmannia racemosa,* which were eaten in all months. The trees are being defoliated and killed by the animals. Two abundant lianas, *Metrosideros fulgens* and *Ripogonum scandens,* together contributed about 15 percent, but were eaten seasonally. About another 10 tree species were eaten regularly in smaller amounts. Many tree and epiphyte species were seldom or never browsed by the opossums.

Reasons for this selection of species were sought by feeding trials with captive animals, and chemical analysis of food and feces. In duplicate 8-week trials, 12 adult opossums (6 male, 6 female) were fed commercially pelleted herbivore food, and body weights and all intake and output were recorded daily. Other trials involved leaves of single tree species and a diet of peas and bread. Opossums on high-quality pelleted food, or on peas and bread, maintained or gained body weight, those on single-species diets lost weight.

Analyses of the constituents of the leaves of 2 *Metrosideros* species eaten and simple tests for triterpenes, saponins, leucoanthocyanins, and alkaloids in leaves of 6 species were carried out monthly for a year. The lipid content of *Metrosideros fulgens* was considerably higher at the season when it was eaten than at other times of the year.

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Appendix—Taxonomic order of plant species mentioned in the text (after H. H. Allan, 1961, and L. B. Moore and E. Edgar, 1970).

Filicales *Family*	*Latin Name*
Dicksoniaceae	*Dicksonia squarrosa* (Forst.f.) Swartz
Cyathaceae	*Cyathea dealbata* (Forst.f.) Swartz
	C. medullaris (Forst.f.) Swartz
	C. cunninghamii Hook.f.
	C. smithii Hook.f.
Spermatopsida	1. *Gymnospermae*
Podocarpaceae	*Podocarpus spicatus* R. Br. ex Mirbel
	P. ferrugineus G. Benn. ex D. Don
	Dacrydium cupressinum Lamb.
	2. *Angiospermae*
	1. *Dicotyledones*
Winteraceae	*Pseudowintera axillaris* (J.R. et G. Forst.) Dandy
Lauraceae	*Beilschmiedia tawa* (A. Cunn.) Benth. et Hook.f., ex Kirk
Monomiaceae	*Hedycarya arborea* J.R. et G. Forst.
	Laurelia novaezelandiae A. Cunn.
Piperaceae	*Macropiper excelsum* (Forst.f.) Miq.
Violaceae	*Melicytus ramiflorus* J.R. et G. Forst.
Onagraceae	*Fuchsia excorticata* (J.R. et G. Forst.) Linn.f.
Proteaceae	*Knightia excelsa* R. Br.
Pittosporaceae	*Pittosporum eugenioides* A. Cunn.
Myrtaceae	*Leptospermum ericoides* A. Rich.
	Metrosideros robusta A. Cunn.
	M. fulgens Sol. ex Gaertn.
Elaeocarpaceae	*Elaeocarpus dentatus* (J.R. et G. Forst.) Vahl
Cunoniaceae	*Weinmannia racemosa* Linn.f.
Escalloniaceae	*Carpodetus serratus* G.R. et G. Forst.
Fagaceae	*Nothofagus truncata* (Col.) Ckn
Corynocarpaceae	*Corynocarpus laevigatus* J.R. et G. Forst.
Icacinaceae	*Pennantia corymbosa* J.R. et G. Forst.
Sapindaceae	*Alectryon excelsus* Gaertn.
Araliaceae	*Schefflera digitata* J.R. et G. Forst.
	Neopanax arboreum (Murr) Allan comb. nov.
Cornaceae	*Griselinia lucida* Forst. f.
Myrsinaceae	*Myrsine salicina* Hew. ex Hook.f.
	M. australis (A. Rich.) Allan
Loganiaceae	*Geniostoma ligustrifolium* A. Cunn.
Rubiaceae	*Coprosma areolata* Cheesem.
	C. australis (A. Rich.) Robinson
	C. robusta Raoul
	C. lucida J.R. et G. Forst.
Compositae	*Olearia rani* (A. Cunn.) Druce
	2. *Monocotyledones*
Liliaceae	*Astelia solandri* A. Cunn.
	Collospermum hastatum (Col.) Skottsb.
Simlaceae	*Ripogonum scandens* J.R. et G. Forst.
Pandanaceae	*Freycinetia banksii* A. Cunn.

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Population Strategies of Four Species of Australian "Possums"

Introduction

The eastern ranges of mainland Australia, extending from Cape York in the north to Victoria in the south, contain the last extensive areas of forest which have remained largely unmodified by European man and his introductions.

A prominent feature of most of these forests is the dominance of species of the genus *Eucalyptus* (F. Myrtaceae). It has been suggested that the remarkable diversity within the Eucalypts represents an active radiation of the genus during the last 2 million years (Gill, 1975). The future of eastern Australian forests is uncertain because of the recent intensification and extension of forest management practices in all eastern states. These practices include the large-scale clearing of indigenous forests and woodlands for subsequent planting with introduced conifers, mainly *Pinus* spp., and the granting of licenses to woodchip large areas of native Eucalypt forests. The scope of the pressure being exerted on native forests is well documented by the Routleys (1974). It is in these tree communities of the east that the great majority of Australia's arboreal marsupials are found.

The three opossum families represented in Australia (Phalangeridae, Petauridae, Burramyidae) contain 13 genera comprising 23 species (Ride, 1970). Of these, 19 species in 11 genera are found in the tree communities associated with the Great Dividing Range, but, despite this concentration the population characteristics of only 4 have been examined in any depth. These are the greater glider, *Schoinobates volans* (Kerr), the ringtail possum, *Pseudocheirus peregrinus* (Boddaert), the brush-tailed possum, *Trichosurus vulpecula* (Kerr), and the mountain possum, *Trichosurus caninus* (Ogilby).

EDITOR'S NOTE: The term "possums" is employed in Australia to distinguish members of the Phalangeridae from the American opossums (Didelphidae and Caenolestidae). In 1770 Captain Cook gave the name "opossums" to the genus *Pseudocheirus* because of a superficial resemblance to American opossums; "possums" is a contraction and is used in the United States as well for *Didelphis*. The word "opossums" here refers to "possums" of the Australian family Phalangeridae.

The data on several of these have been presented by Tyndale-Biscoe (1973), but recent work (How, 1972; Crawley, 1973; Griffith, 1973) has added considerably to our understanding of the biology of these opossums. I want, here, to put this work in perspective and examine the relationship between the population strategies of these 4 species and the type of community in which they occur.

The Species

The 4 opossum species being considered belong to 2 families within the Order Diprotodonta and Superfamily Phalangeroidea (Kirsch, 1968).

The greater glider, *S. volans*, and the ringtail opossum, *P. peregrinus*, belong to the Family Petauridae, which also contains one of the 2 other genera of marsupial gliders, *Petaurus*. The congenerics, *T. vulpecula* and *T. caninus* belong to the Family Phalangeridae, which is taxonomically closely related to the Family Petauridae (Kirsch, 1968).

The 4 species are entirely nocturnal, but vary in the degree to which they are arboreal (Eisenberg, 1978). *Schoinobates volans* is entirely arboreal, while *T. caninus* frequently feeds on the ground. Both *T. vulpecula* and *T. caninus* are readily captured in baited traps placed on logs or on the ground although they are principally arboreal feeders. *Pseudocheirus peregrinus* is seldom seen on the ground and feeds entirely arboreally. All species have prehensile tails except *S. volans*, whose tail is used primarily for balance and may aid in giving direction during glides. All species use hollows in either trees, stumps, or logs, but *P. peregrinus* can build an independent nest or drey of twigs and leaves. The availability of hollows is, therefore, not a limiting factor in the distribution of *P. peregrinus* as it may be with the other species.

There is considerable intraspecific variation in pelage (Troughton, 1954) and body size (Eisenberg, 1978) over the range of all 4 species. In the southeast of Australia, *S. volans* has a head-body length of 35-40 cm and an adult body weight of 1200-1500 gms, while *P. peregrinus* weighs 700-1000 gms and has a length of between 17-20 cm. The congeners *T. vulpecula* and *T. caninus* are of similar size (35-45 cm), but *T. caninus* is slightly heavier weighing 2500-4000 gm compared to 2000-3500 gm for *T. vulpecula*.

Distribution and Abundance

Schoinobates volans is common in the tall sclerophyll communities of eastern Australia between eastern Victoria and northern Queensland. The density of gliders in these communities appears to be relatively constant at about 1 glider to 1.2 ha (Tyndale-Biscoe and Smith, 1969a; Griffith, 1973).

Pseudocheirus peregrinus is perhaps the most abundant of all the arboreal opossums, and densities of 1 opossum to 0.10 ha have been recorded in favorable habitats (How, unpublished). This species occurs from Cape York to southeastern South Australia, in southwestern Western Australia and Tasmania. Several subspecies are recognized throughout its range, and populations occur in most tree and tall-shrub communities of these regions. During the years 1923 to 1955 the subspecies *P.p. convolutor* was heavily exploited for the fur trade in Tasmania and over 7.5 million skins were taken (Guiler, 1957).

Trichosurus vulpecula, the most widespread of all opossums, also occurs in most tree communities. In northern and northwestern Australia, however, only *T. arnhemensis* is found (Ride, 1970), while in the wet sclerophyll forests and rain forests of the southeast, *T. vulpecula* is replaced by *T. caninus* (Owen, 1964; Calaby, 1966; How, 1972). Introduced in New Zealand in the last century, *T. vulpecula* is now widespread throughout that country and a sizable fur trade has been established around its pelt. The density of *T. vulpecula* in Australia is highly variable, being low in the mallee scrubs of the western plains and as high as 1 opossum to 0.72 ha in gardens and homesteads (Dunnet, 1956). In woodland and dry sclerophyll forests of southestern Australia the density is between 2.2 ha and 2.7 ha per individual (Dunnet, 1964; How, 1972). Exceptionally high densities of 0.124 ha per individual (Kean and Pracy, 1953) and 0.206 ha per individual (Batchelor et al., 1967) have been recorded in certain areas of New Zealand. The abundance of this species in Tasmania can be gauged by the fact that over a million pelts of both melanic and gray color phases were taken between 1923 and 1955 (Guiler, 1957).

Trichosurus caninus is confined to the forests of southeastern Australia from just north of Brisbane to Wilsons Promontory, the southernmost tip of the mainland. It occurs only in the wet sclerophyll and rain forests of this region, but is relatively abundant in these areas. How (1972) found that the density of this species in the wet sclerophyll forest of northeastern N.S.W. was 1 opossum to 3.3 ha.

Diet

As well as being arboreal, all 4 species of opossums feed primarily on foliage.

Schoinobates volans feeds entirely on ***Eucalyptus*** spp. leaves (Marples, 1973). Although the preferred species may vary depending on the locality (Smith, 1969; Griffith, 1973), it is principally the dominant eucalypts of the association that are consumed.

Pseudocheirus peregrinus is primarily a foliaceous feeder but occasionally feeds on the fruits of some species. Thomson and Owen (1964) examined the stomach contents of 76 animals and found that they feed on 1 or 2 species of tree or shrub each night regardless of the community in which they occurred. Mature foliage was preferred among the eucalypts eaten, but in tall shrubs and smaller trees, such as *Kunzea*, *Melaleuca*, and *Leptospermum*, the young leaves, shoots, and buds were preferred.

Trichosurus vulpecula has highly adaptable dietary preferences. Owen and Thomson (1965) found that in natural communities in Australia mature eucalypt foliage was the predominant component of stomach contents, but a few indigenous shrubs were also present. On examining 40 stomachs they found 25 percent contained more than 1 food species but only 20 percent contained understory species. By contrast, this species in New Zealand shows a remarkably wide acceptance of plant species (Mason, 1958; Fitzgerald, 1978), including both grasses and clover (Gilmore, 1965a; 1965b). Harvie (1973) analyzed the stomach contents of 550 opossums shot on farmland in New Zealand to find that 30 percent of their diet was pasture species, and she concluded that at high opossum densities this could result in considerable economic loss to farmers.

Trichosurus caninus utilizes a wide variety of plant species in natural communities. Owen and Thomson (1965) examined 51 stomachs of this species and recorded a variety of herb layer species, fungi, and occasionally lichens, together with the leaves of shrubs and trees. In contrast to *T. vulpecula*, 92 percent of *T. caninus* stomachs contained more than 1 food species and 88 percent contained understory species.

The fact that the mature foliage of *Eucalyptus* is preferred by all species may support Thomson and Owen's (1964) belief that this is correlated with the high concentrations of cyanogenetic glucosides present in the young foliage of certain members of this genus (Finnemore et al., 1935).

Reproductive Biology

The reproductive strategies employed by populations of these species of possum vary considerably (Table 1).

Schoinobates volans is polyoestrous, with breeding confined to a short period in the late autumn when a single young is born (Smith, 1969). Smith's evidence suggested that maturity in females was not reached until they were 2 years old. Tyndale-Biscoe and Smith (1969a) noted that sexual maturity was probably attained in the second breeding season after birth and that between 60-75 percent of the adult females bred.

Pseudocheirus peregrinus was polyoestrous and nearly always polyovular (Hughes et al., 1965). The breeding season was from April to November and 1-3 young were born in a single litter. Thomson and Owen (1964), however, cite circumstantial evidence which suggested that 2 litters may be born each year, and How (unpublished) recorded a population in which 50 percent of the females bred for a second time, after successfully weaning the young of the first litter. Maturity occurred at about 12 months in females and over 90 percent of the females bred during the season (Thomson and Owen, 1964).

There is considerable literature dealing with the reproductive biology of *T. vulpecula*. This species is polyoestrous and monovular (Pilton and Sharman, 1962). In most populations, breeding seasons occurred in the autumn and the spring (Dunnet, 1964; Smith

Table 1.—The reproductive parameters of four species of arboreal possums.

	S. volans	*P. peregrinus*	*T. vulpecula*	*T. caninus*
Oestrous	Polyoestrous [1]	Polyoestrous [3]	Polyoestrous [5]	Polyoestrous [7]
Ovulation	Monovular [1]	Polyovular [3]	Monovular [5]	Monovular [7]
Female maturity (months)	24 [1]	12 [4]	9–12 [5]	24–36 [8]
Adult females breeding (%)	60–75 [2]	90 [4]	90 [6]	80 [8]
Breeding season	Apr-June [1]	Apr-Nov [3]	Mar-May & Sept-Nov [6]	Mar-May [8]

[1] Smith (1969)
[2] Tyndale-Biscoe and Smith (1969a)
[3] Hughes et al. (1965)
[4] Thomson and Owen (1964)
[5] Pilton and Sharman (1962)
[6] Dunnet (1964)
[7] Smith and How (1973)
[8] How (1972)

Table 2.—The fertility and subadult development in four species of arboreal possums.

	S. volans	*P. peregrinus*	*T. vulpecula*	*T. caninus*
Annual fertility	0.62–0.67 [1,2]	1.8 [3]	0.9–1.4 [5,6]	0.73 [6]
Weaning (months)	7–12 [1,2]	6–7 [3]	6–7 [5,6]	8–9 [6]
Age at dispersal (months)	—	8–12 [3,4]	8–18 [5,6]	18–36 [6]
Mortality (%)	20 male [1] specific	68 [3,4]	Male 83 [6] Female 50	65 [6]

[1] Tyndale-Biscoe and Smith (1969a)
[2] Griffith (1973)
[3] Thomson and Owen (1964)
[4] Marsh (1967)
[5] Dunnet (1964)
[6] How (1972)

et al., 1969; Gilmore, 1969). In certain New Zealand and Australian populations, however, there was only a single autumn season of births (Smith et al., 1969; Kean, 1971). Females mature at about 12 months, but some may begin oestrous cycling and breed by 9 months (Pilton and Sharman, 1962). The only exception to this pattern of maturity in *T. vulpecula* was found in a New Zealand population in which females first bred in their third year (Crawley, 1973). Over 90 percent of females breed at least once during the year (Dunnet, 1964; How, 1972).

Trichosurus caninus is also polyoestrous and monovular (Smith and How, 1973). Females mature during the second breeding season after birth, but only 50 percent produce young when 2 years old. There is also a slight decline in breeding amongst animals older than 4 years, with the result that only 80 percent of the females in the adult population produce young (How, 1972).

Fertility and Subadult Development

About 68 percent of *S. volans* females bred in any 1 year (Tyndale-Biscoe and Smith, 1969a) and since this species was monovular and a monoseasonal breeder, the annual fertility was 0.68. Griffith (1973) found that only 5 of the 8 (62 percent) females observed in his study area were lactating or had pouch young when they were shot in mid October (Table 2). The other 3 females were in a nonbreeding condition, but there was no indication whether this resulted from a failure to breed or from having lost a pouch young earlier in the season. The young are probably weaned after 7 months (Tyndale-Biscoe and Smith, 1969a), but some females were still lactating and had young associated a year after the beginning of the breeding season (Griffith, 1973). As *S. volans* populations have only been studied by permanent removal, no data are available on the time of dispersal of the subadults. The implied mortality is relatively low, however, in the first year, with a definite male-specific mortality occurring during this time (Tyndale-Biscoe and Smith, 1969a).

The mean size of *P. peregrinus* litters is 2, and since 90 percent of females breed each year, the annual fertility is approximately 1.80. This fertility figure could be considerably increased in populations where there are females who bred twice annually. Young were generally weaned at 6-7 months (Thomson and Owen, 1964). Mortality was high during the first year of life with estimates varying from 68 percent (Thomson and Owen, 1964) to between 45-75 percent (Marsh, 1967). Although it was difficult to differentiate between the dispersal, which occurred late in the first year, and mortality, Marsh believed most mortality occurred after the young became independent.

Trichosurus vulpecula usually has 2 breeding seasons a year with about 90 percent of females breeding in autumn and 50 percent breeding in spring (Dunnet, 1964), resulting in an annual fertility of 1.4. In those populations where a second season was absent annual fertility may be as low as 0.9. Lactation in *T. vulpecula* lasts 6-7 months, when the young become independent and begin to disperse (Dunnet, 1964; How, 1972). Dispersal and mortality were, again, hard to differentiate, but there appeared to be a male-specific mortality acting on the newly independent young (Dunnet, 1964; How, 1972). About 83 percent of the males born disappear from the population before the age of 1 year while only 50 percent of the females disappear.

Annual fertility in stable *T. caninus* populations is low (0.73) since all 1-year-old and half the 2-year-old females do not breed. The young are weaned at 8-9 months, but lactation may continue for up to 11 months. As dispersal of young occurred after 18 months of age, the mortality of 65 percent during the

Table 3.—The adult population structure in four species of arboreal possums.

	S. volans	*P. peregrinus*	*T. vulpecula*	*T. caninus*
Dispersion pattern	Solitary [1]	Pairs/groups [3]	Solitary [5]	Pairs [6]
Sex ratio	0.38 [1]	0.48 [3]	0.38 [6]	0.50 [6]
Annual survival (%)	c 20 [2]	—	20 [6]	15 [6]
Longevity (years)	10 [2]	4-5 [3]	6-13 [7,8]	10 [6]
Range (ha)	—	0.37 [4]	0.81–7.45 [6,8] (male) 0.46–4.67 [6,8] (female)	7.67 (male) [6] 4.85 (female)

[1] Tyndale-Biscoe and Smith (1969a)
[2] Griffith (1973)
[3] Thomson and Owen (1964)
[4] Tyndale-Biscoe (1973)
[5] Kean (1967)
[6] How (1972)
[7] MacLean (1967)
[8] Crawley (1973)

first year represented real mortality and was not confused with dispersal. This high mortality of dependent young was explained by 2 factors. First, all 2-year-old primiparous females lost the young from their pouches during early lactation. Second, there was high mortality (85 percent) among the young of adult females when the young of a previous season was still resident in its maternal area. No sex-specific mortality was recorded in the young of this species, but females usually dispersed a year earlier than males (How, 1972).

Adult Population Structure

Tyndale-Biscoe and Smith (1969a) suggested that there was a tendency for *S. volans* to space out in the forest and that this factor operated more strongly intrasexually (Table 3). The male-specific mortality that operated in the juveniles of this species altered the adult sex ratio to 0.38. The sampling methods used to examine populations of this species make the survival of adults difficult to calculate, but Griffith (1973), extrapolating from the amount of cementum deposited on the lower incisors, estimated the annual adult mortality at about 20 percent with a longevity in excess of 10 years. Tyndale-Biscoe and Smith (1969a) concluded that some animals must survive for 15 years if the population was to remain stable. No specific assessment of the range area utilized by *S. volans* has been made. Observations during spotlighting showed individuals occurred over areas of 0.44 ha, 0.33 ha, and 0.16 ha (Griffith, 1973); however, these correlate poorly with a density of 1.2-2.4 ha reported by Tyndale-Biscoe and Smith (1969a) and probably are a gross underestimate of real range areas.

Pseudocheirus peregrinus is gregarious, with up to 3 adults located in any 1 nest and as many as 5 nests being utilized by each individual. The adult sex-ratio was near parity (0.48) and there was a low mortality among adults until the end of their fourth year, when it increased rapidly. Individuals live about 4 years (Thomson and Owen,1964). The area utilized by *P. peregrinus* in different habitat types is highly variable and not well documented, but Tyndale-Biscoe's (1973) review of the ecology of the phalangers put the average home range size for this species at 0.37 ha.

Studies of the behaviour of *T. vulpecula* (Kean, 1967; Winter, personal communication) have shown that the social structure of this species is based on the individual rather than on pairs or groups. In some populations males may establish territories (Dunnet, 1964), but the work of Winter suggests that dispersion was regulated by antagonistic encounters, which established an individual distance and den ownership, and that olfactory and vocal communications reduced the number and intensity of these interactions. Most populations of this species have an adult sex-ratio of around 0.38 (Dunnet, 1964; How, 1972); however, Crawley (1973) reported sexual parity in his Orongorongo population in New Zealand. Adult survival is high and life expectancy is about 6-7 years. In a 3-year study of a stable woodland population, adult mortality was around 20 percent per year (How, 1972). Individuals as old as 5 years 10 months in Australia (MacLean, 1967) and over 13 years in New Zealand (Crawley, 1970) have been recorded in natural populations. In all cases the ranges occupied by males were significantly larger than those of females, although the absolute size of these ranges varied with habitat and locality. How (1972), Dunnet (1964), and Crawley (1973) found range areas for males of 7.41 ha, 3.01 ha, and 0.81 ha, respectively, while those of females were 5.67 ha, 1.08 ha, and 0.46 ha.

There is strong evidence to suggest that adult *T. caninus* are paired (How, 1972). The adult sex ratio was parity, and there was a well-defined intersexual overlap in central-range areas. Further, on several occasions adult males and females showing this range overlap were trapped simultaneously in the same trap. Mortality among the adults over the 4 years of study was about 15 percent per annum, while some individuals were still present in the population at an age in excess of 10 years. The trap-indicated ranges for this species were 7.67 ha for males and 4.85 ha for females.

Discussion

In eastern Australia there is a range of climatic conditions and communities as one progresses eastward from the center of the continent. These vary from the deserts of the central region, where climatic conditions are unpredictable, through to the more stable forested regions of the eastern divide, where the climate is more equable. There is a correlation, within a range of climatic conditions such as these, between the degree of climatic stability and the type of selection operating on the species. Populations which occur in uncertain climatic regions are likely to have been selected for productivity (*r*-selected) while those in predictable climatic regions tend to be selected for maximum efficiency in utilizing resources and the production of young (*K*-selected). Between these two extremes there is a selection continuum (Pianka, 1970).

Brereton (1971) showed that within the Australian parrots there was a variety of social systems and population regulatory mechanisms which were well adapted to the type of community in which they occurred. They range from the gregarious social system and density-independent population regulation of the budgerigar (*Melopsittacus undulatus*), a species of the arid and semiarid central regions, to the less gregarious and density-dependent mechanisms of the rosellas (*Platycercus* spp.) in the forested regions of the east. This study is, therefore, in broad agreement with the concept of an *r*-*K* selected continuum. Similarly, Richardson (1975) has shown that many of the biological parameters of the eastern gray kangaroo, *Macropus giganteus,* reflect stronger K-selection pressures than do the same parameters of the red kangaroo. *Megaleia rufa*, a closely related species.

All 4 species of opossum discussed here are arboreal herbivores, which means that they occur in more equable climatic regions, and consequently population strategies toward the *K*-selected end of the spectrum would be expected. Although this proves to be the case, there are strategies used by these species which can be even more closely correlated with the degree of predictability of the community in which each occurs.

Schoinobates volans occurs only in the tall eucalypt forests of the east of the continent and feeds entirely on mature *Eucalyptus* leaves. It has presumably evolved in these predictable habitats, as there are no records of this species from similar forest types of the southwest of the continent. There is a single, short breeding season each year during which only two-thirds of the adult females breed. Lactation may continue for up to 12 months, while maturity amongst females occurs during their late second or early third years. Tyndale-Biscoe and Smith (1969a) have postulated that there is a causal relationship between the number of breeding females approximating the number of adult males, and suggested that this species is monogamous. This species is severely affected by habitat modification and destruction, with less than 30 percent of displaced gliders surviving the first week. Also, there was no immigration of displaced gliders into an adjacent unfelled forest, which had had its density artificially depleted, indicating that gliders die in situ rather than emigrate and die through failure to become established (Tyndale-Biscoe and Smith, 1969b).

Compared to similar parameters for opossums in less predictable communities, the parameters employed by *S. volans* populations are more those of the *K*-selected end of the continuum (Pianka, 1970). The conclusion that this species may be regulated by factors operating on the birth rate and influencing the sex-specific mortality of juveniles (Tyndale-Biscoe and Smith, 1969a) has received support from the work of Griffith (1973). In a shot sample, taken to evaluate ageing methods, Griffith found that adult sex ratio was parity and that 92 percent of females in this sample bred. Thus, in some populations of this species, lowered fertility and sex-specific mortality do not operate, and consequently population size may be regulated through these factors.

Trichosurus caninus is confined to stable communities: the wet sclerophyll and rainforests of southeastern mainland Australia. In these forests the species has a short autumnal breeding season with the young being suckled for over 8 months. The rate of growth and development of young in this species has been shown to be considerably slower than its congener *T. vulpecula* (How, unpublished). Females may become mature and produce young in their third year, but only at 3 years of age are all females parous. There is a high mortality among the dependent young of this species, and some females 4 years of age or older may fail to reproduce during the year.

How (1972) showed that in nearly 90 percent of the cases where a young failed to survive to independence from an adult female or when a female did not produce young during the season, then the young of the previous year was still located in its maternal home range. This high probability of repreductive failure or dependent young mortality when the previous young is still resident indicates that an intrinsic mechanism, induced by this behavioural association, probably operates to regulate population size in *T. caninus*. The nature of this intrinsic mechanism is currently being investigated.

This species shows the *K*-selected parameters of slower development, delayed reproduction, and later dispersal when compared to its congener *T. vulpecula*.

Pseudocheirus peregrinus occurs throughout most of Australia's wooded regions but is most abundant in subclimax communities (Thomson and Owen, 1964). Studies of this species indicate that females breed throughout an extended season from autumn to late spring. Although it is usual for only a single litter of about 2 young to be born during the season, there are certain populations occurring in subclimax communities which produce 2 litters a year. Mortality among the dependent young is low, but during the dispersal stage (6 to 12 months) it is high, so that only 32 percent survive to maturity at 12 months.

Populations of this species have, then, a relatively high fertility, but also a high mortality among independent young. Regulation appears to be by density-dependent factors which operate through the ability of the young to survive the period of dispersal and establishment in the population. These strategies are well suited to more opportunistic species which can adjust to changes in the environment or colonize new areas.

Trichosurus vulpecula is the most widespread of the species considered, and its populations have been the subject of the most research (Tyndale-Biscoe, 1955; Dunnet, 1956, 1964; Gilmore, 1969; How, 1972; Crawley, 1973). This species occurs in tree communities over most of Australia but is not sympatric with *T. caninus* or *T. arnhemensis*. There are usually 2 breeding seasons for *T. vulpecula*, a major one in the autumn and a secondary spring season, and it is not uncommon for females to produce young in both. Mortality of dependent young is low, but as with *P. peregrinus*, it is high among the independent dispersing young and only 25 percent reach the age of 1 year. In all Australian and most New Zealand populations a male-specific mortality operates during the dispersal phase. Females mature late in their first or early in their second year and by 2 years all females are parous (Smith et al., 1969).

It is apparent from these data that *T. vulpecula* has a high fertility and high survival among dependent young and thus maximizes the potential recruitment for the population. The realized recruitment is determined by density-dependent factors operating through the survival of independent young. This is the strategy of a species well adapted to utilizing several types of communities and colonizing new regions rapidly. This is illustrated in *T. vulpecula* by its wide distribution in Australia, from the equable rain-forest regions to the less predictable woodlands, and by its rapid spread throughout most of New Zealand after its introduction (Pracy, 1962).

There are, however, populations of *T. vulpecula* which show considerable variation in the general parameters. In some Australian populations the spring breeding season is absent (Smith et al., 1969) or much reduced (How, 1972). These 2 populations occurred in the dry sclerophyll forests of northeastern N.S.W., a region characterized by summer rainfall and cold, dry winters. Under such conditions there may have been selection against spring young which would be newly weaned and dispersing during their first winter. The delayed onset of maturity and extended period of lactation in the females of a New Zealand population (Kean, 1959; Crawley, 1973) may be an adaption by this population for the strategy of long-term stability in relation to the food resource (Kean, 1971). These variations illustrate that there can be considerable interpopulation differences in *T. vulpecula*.

From studies of Australian opossums, it appears that many of the population parameters of species restricted to the stable tall sclerophyll and rain-forest communities reflect stronger K selection pressures than similar parameters in closely related species, less restricted in their distribution.

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Ecology of the Koala, *Phascolarctos cinereus* (Goldfuss) Marsupialia: Phascolarctidae, in Australia

Introduction

The koala is an arboreal, folivorous marsupial native to eastern Australia. At the beginning of European colonization of Australia in 1778, its range is believed to have extended from about latitude 20° S in Queensland to latitude 38° S in southern Victoria and southeastern South Australia, with populations occurring both east and west of the Great Dividing Range.

Northern (Oldfield, 1923) and southern (Troughton, 1935) races of the central "type" have been described which differ principally in size and in the color, length, and thickness of the pelage. Koalas are not closely related to other Australian arboreal marsupials and Thomas (1888), Iredale and Troughton (1934), and Kirsch (1968) placed them in a monotypic family, Phascolarctidae. Anatomical (Sonntag, 1922; Pearson, 1949; Hughes, 1965) and blood sera (Kirsch, 1968) studies suggest that koalas are most closely related to wombats, *Vombatus* and *Lasiorhinus* spp., and Kirsch put both koalas and wombats in a Superfamily Vombatoidea.

Koalas are relatively large arboreal mammals, male specimens of the Victorian race sometimes weighing in excess of 13 k. They are atypical in mammalian form, however, the tail being a short stub and they resemble sloths of the New World in that they appear to be adapted to a life of "tree-clinging" rather than one of "tree-climbing."

The geographic range of koalas is broadly occupied by the formation known in Australia as "sclerophyll forest." This formation is dominated by hardwood trees of the genus *Eucalyptus* L'Herit. (Myrtaceae), and koalas are typically exclusive browsers of eucalyptus foliage. Over 600 spp. of eucalyptus have been described, although many have a limited range, and few of the species recorded for Victoria, for example, are also represented in northern New South Wales or Queensland. In sclerophyll forest, eucalyptus trees normally occur in mixed stands composed of 2 or more codominant species. Species diversity is, therefore, often low, although Pryor (Burdon and Chilvers, 1974) showed that as many as 12 different species associations may be represented within a single square mile of forest.

It was noted in the earliest days of European settlement that koalas were very selective browsers, captive animals often rejecting some types of foliage offered, and populations in the wild appearing to be associated with the occurrence of certain species, notably *E. viminalis* Labill. This item of knowledge has become an article of folklore.

This paper reports life historical data and aspects of the ecology of the koala, based principally on data gathered in a field study of a marked population of koalas in Flinders Chase, Kangaroo Island, South Australia (Eberhard, 1972). Koalas are not native to Kangaroo Island, the present population originating from the introduction of Victorian-caught animals in 1923. It is believed, however, wherever possible generalizations are attempted, that the environment of these animals resembles those characteristic of many parts of the koalas' natural range, and, wherever possible, generalizations are attempted.

Life History

Life History data for the koala is summarized in Table 1.

In eastern Australia, the mating season for koalas is variously said to extend from September to January in New South Wales and from November to February in Victoria. On Flinders Chase, females gave birth during a season extending from late December to early April, with a peak in February. One young is produced as a rule, although twins have been recorded.

In the absence of previous observations on marked animals, it has remained uncertain as to whether koalas in the wild breed in successive years. Females on Flinders Chase commonly did so, and of 4 marked mature females which remained under observation over 4 successive years, 2 carried young each year and 2 carried young in 3 of the 4 years. In these same years the proportion of females carrying pouch young varied between 0.63 (n = 19) and 0.82 (n = 11) of all sexually mature females caught over periods encompassing the end of the breeding season.

Asdell (1946) reported that koalas are monoestrous, but Briese (1970) examined vaginal smears taken from captive female koalas and found in 3 out of 11 animals successive peaks of cornified epithelial cells at 27 to 30-day intervals, suggesting an oestrous cycle of that period (of the remaining 8 koalas, 4 showed no cyclic events and 4 showed cell fluctuations of 26 to 29-day intervals, but successive oestruses could not be positively established).

Table 1.—Koala life history data.

Oestrus	Cyclical, every 27-30 days during an annual breeding season
Gestation	35 days
Modal litter size	1
Birth weight	from 0.36 g
Duration of pouch life	7 months
Age at start of weaning	6 months
Age at completion of weaning	12 months, or earlier
Minimum period between successive births of surviving young	9-12 months
Sexual maturity	end of 2nd year, or later (females). Males unknown.
Physical maturity	During or after fourth year (females), fifth year (males)
Maximum weight (Victorian Race)	10 k+ (females); 13 k+ (males)
Maximum longevity	10-20 years

The gestation period is reported by Troughton (1941) and Pollock (personal communication) to be about 35 days. Troughton also quoted a birthweight of 5.5 gr (0.36g).

Fleay (1937) reported that the young of a koala held in the Melbourne Zoo was completely independent of the pouch at 5 months, while Toughton (1941) quoted a total pouch life of 8 months. Fleay, however, did not indicate how accurately the date of birth was determined and Minchin (1937) reported a koala still using the pouch when at least 6 months of age. On Flinders Chase the earliest that females were seen carrying young on their bellies was late July, while some females were not seen with young until as late as November. With a birth season from late December to early April, these data suggest a total pouch life of about 7 months.

It is at about the end of pouch life that the coprophagic phase of weaning takes place, reported by Minchin (1937) and Fleay (1937), in which over a period of up to 6 weeks, the young feeds regularly from the female's cloaca on material passed from higher up in the digestive tract.

It was apparent on Flinders Chase that young were often carried and suckled up to a time when the parent female bred again. Weaning in koalas, therefore, has a remarkable beginning and may extend over a period of up to 6 months.

Records of the development of marked animals of known age on Flinders Chase indicated that full physical maturity may not be reached until some time after the fourth year of growth for females or fifth year for males. Sexual maturity may be reached by females at the end of their second year, but not all females of this age are likely to breed. Whether a female koala produces a young for the first time in the second or third breeding season after the season of its birth may depend on whether the female was born early or late in the season.

Koalas are popularly supposed to live in captivity for up to 20 years (Faulkner, 1922; Troughton, 1941). On Flinders Chase it was apparent that maximum longevity in the wild might easily exceed 10 years.

Behavior and Population Dynamics

The Field study

A field study of koalas was carried out on Flinders Chase largely between January 1967 and June 1969. Koalas are not native to Kangaroo Island, although fossil material of Pleistocene age has been recorded (Pledge, personal communication). The present population originated with the introduction of Victorian animals in 1923.

A total of 10 species of eucalyptus trees occur within the boundaries of Flinders Chase, but the koalas are associated with the limited occurrences of *E. viminalis* in flats of the Rocky River. The koalas have colonized all the available stands of *E. viminalis*, and though individuals have been found wandering many miles from the Rocky River, extensive searches (Philpott, 1965; Eberhard, 1972) have failed to find evidence of colonies in tree associations which do not include *E. viminalis*. The species which are widespread and abundant on Flinders Chase are *E. cladocalyx, E. fasciculosa, E. obliqua, E. baxteri, E. diversifolia, E. rugosa, E. remota,* and *E. cosmophylla*. Koalas do browse the foliage of all these species but the evidence of the distribution suggests that none of them are in themselves a sufficient food for koalas.

In the course of the study, several small study areas were periodically visited and exhaustively searched each day for 7 or more consecutive days at a time. New animals encountered were always caught and marked, and the locations of all koalas were recorded on maps showing the position of all trees. The principal study area covered an area of 11.3 ha and contained 258 trees of which 106 were *E. viminalis*. Of a total 1024 sightings of koalas in this area, 872 were of animals in *E. viminalis* trees. Over the 2½ years of the study, in this and other areas, 140 different koalas were caught a total of 249 times, and 2136 observations of marked animals were made.

Home range

Home range behavior of koalas is illustrated in Tables 2 and 3 in which all observations of 19 animals are arrayed in each case as the number of trees for which a particular frequency of sighting was made. The data refer to adult koalas which persisted in the study area for a period of at least 6 months. It is very apparent from the tables that these animals showed considerable faithfulness to particular trees—1 female being observed in the 1 tree 82 times out of a total of 106 sightings.

Home range is a term which may be defined in a way appropriate to the animal and the available data. In this case, the number of trees in which multiple sightings were made is considered to be an appropriate measure. Data on home range size, and frequency of occurrence in both the home range and the most commonly used tree, are given in Table 4, for the 4 animals which were present within the study area at a frequency greater than 0.85. For these animals the data measure nearly complete home ranges.

The trees comprising each of the above home ranges were not necessarily adjacent. Indeed, the areas containing them occupied between 1 and 2.5 ha and there were trees within these home range areas rarely, if ever, used by koalas.

If it is assumed that the behavior of animals when outside the boundaries of the study area was likely to resemble their behavior within, then the data on all animals, adjusted in the case of home range size by the frequency of occurrence within the study area, can be used to summarize home range behavior of koalas on Flinders Chase. If this is done, a very similar result to that of Table 4 is obtained, based, however, on 919 observations of 19 adult animals. In fact, these total data suggest that the average animal had a home range of 14-15 trees within which it occurred 83 percent of the time, although 35 percent of the time was spent in the most commonly used home range tree.

To a degree, the tendency of koalas to strongly favor 1 particular tree appears maladaptive, since on Flinders Chase it commonly resulted in quite severe

Table 2.—Home range behavior of koalas: sightings arrayed as the number of trees for which a particular frequency of sighting was made. Data for eleven females

Frequency of sightings	*Number of trees*										
	(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*	*(9)*	*(10)*	*(11)*
82						1					
15				1							
14		1									
13	1						1				
12							1				
11								1			
10											
9								1			
8	1	1	1		1						
7		1	1		1				1		
6	2		1			2					
5	2	3	2					3	1		
4	2	1				1			1		1
3	4	3	4			1		1	1	2	1
2	5	4	2	3	2	1	4	3	2	1	
1	22	3	8	1		3	2	6	10	3	4
Total sightings	95	68	55	22	19	106	35	50	33	11	11
Frequency of occurrence in study areas	0.92	0.86	0.78	0.74	0.63	0.52	0.50	0.49	0.38	0.30	0.17

Table 3.—Home range behavior of koalas: sightings arrayed as the number of trees for which a particular frequency of sighting was made. Data for eight males

Frequency of sightings	*Number of trees*							
	(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*	*(8)*
35					1			
30		1						
22	1							
21			1					
18			1					
16			1					
9						1		
8						1		
7		1	2					1
6			2	1		1		
5			2		1	1		
4		2			2		1	
3	1	2			2	1	1	1
2	1	6	3	9	3	5	2	2
1	8	19	2	8	2	5	9	6
Total sightings	35	82	120	32	62	46	20	20
Frequency of occurrence in study areas	0.98	0.86	0.62	0.56	0.50	0.40	0.29	0.28

Table 4.—Home range behavior of koalas: home range size and frequency of occurrence in most commonly-used tree

Animal	*(1)*	*(2)*	*(3)*	*(4)*	*Mean*
Total sightings	95	68	35	82	78
Total trees	39	17	11	31	24.5
Home range*	17	14	3	12	11.5
Frequency of occurrence in home range	0.77	0.96	0.77	0.77	0.82
Frequency of occurrence in most commonly used tree	0.14	0.21	0.63	0.37	0.34

* Number of trees in which multiple sightings were made.

defoliation of such trees. Large specimens of the Victorian race of koalas may consume nightly in captivity up to 500 g of food, representing in some types of foliage about 500 leaves. Such animals in the wild, occupying a single tree 35 percent of the time, might annually harvest some 60–70 k or 60–70,000 leaves. Large, vigorous trees should be able to withstand such browsing from a single koala since eucalyptus trees can replace the crown within 3 months, although the average life of leaves is probably closer to 12 months (Jacobs, 1955). However, koalas commonly feed repeatedly in 1 area of the crown and thus may defoliate a particular branch, leading to the death of its outermost parts. In this way in time even large trees may become stag-headed and depend on continual renewal of a secondary crown resulting from the development of ordinarily suppressed buds concealed in the outer tissues of trunk and branches.

The data on home ranges given in this part are based on observation made of koalas during the day. Koalas, of course, are nocturnal animals, and it may be suggested that these data are not representative of actual movements and behavior. Nighttime observation of koalas, however, showed that for the most part animals found in the 1 tree on consecutive days had remained there overnight and that those that had moved had most probably made only 1 change. In fact, of 65 records of koala overnight movement, 47 involved 0 or only 1 change, while only 3 involved more than 2 movements between trees.

Territorial behavior

The home ranges of adult, resident koalas were largely separate, and although the ranges of some males did *spatially* overlap with those of females and include trees used in common, of 425 sightings made of adult residents in the principal study area, only 62 sightings involved trespass into a tree commonly used by another.

Koalas are, therefore, solitary rather than gregarious animals, and few pairs or larger groups are seen in single trees. Data given in Tables 5 and 6 show the frequency of various group sizes and the composition of the interacting pairs which these groups represent.

It proved difficult to test whether the home ranges of koalas were territories according to Noble's definition of territory as "any *defended* area" (Burt, 1943), although it was clear that they were territories in an ecological sense (Jewell, 1966; Kaufmann, 1971).

Table 5.—Frequency of group size in koalas.

	Group Size			
	Single koalas	*Pairs*	*Group of Three*	*Total*
Number of groups	828	108	7	943
% of total	88	11	1	100

Table 6.—Composition of inter-acting animals, as pairs.

Class	*Number*	*% of total*
Young with parental female	68	53
Young with other adult	20	16
Resident adults	7	5
Other	34	26
Total	129	100

There was, however, some indirect evidence that koala home ranges were defended areas. Thus, although actual physical conflict was rarely observed, several natural and contrived "trespasses" into occupied trees resulted in savage attacks by resident animals.

Furthermore, it seemed clear that the *E. viminalis* trees were a resource in short supply, and some considerable pressure was needed to prevent other animals from establishing themselves. Thus, in the principal study area, although the average number of koalas seen on any one day was 10, equivalent to a density of 1 koala per 11 *E. viminalis* trees, the average size of the population utilizing these trees was 19. This average daily "surplus" of 9 animals was necessarily feeding on species other than *E. viminalis*, and since feeding trials and other observations clearly showed that *E. viminalis* was the most palatable species, it was difficult to understand why these animals sought an inferior food (also available within the study area) if social intolerance was not a governing factor.

Koalas are capable of a variety of vocalizations, the males particularly uttering during the breeding season very loud calls. Males also exude a powerful scent from a large sternal gland and it seems likely that scents and calls establish a sphere-of-influence, or territory, within which are contained the home range trees.

Parental behavior

Young koalas are weaned at the age of 12 months, or earlier. Thereafter they persist in the parental home range and may commonly be observed together with the parent female. Few persist, however, through the third year of growth and some disappear within 6 months of final weaning. Sightings of marked animals indicated that these young on leaving the parental home range followed a nomadic existence, wandering extensively on the outskirts of the *E. viminalis* distribution.

The origin of the dispersal of young animals was not clear. A few observations did suggest, however, that an important factor may have been aggression by parent females. Thus, in the one observed case where a parent female itself died or emigrated, the young, a female, persisted in the home range until the conclusion of the study, at which stage it was between 36 and 42 months of age, had bred, and otherwise appeared to have the status of an adult resident.

Population dynamics

A high survival rate among koalas with home ranges established in *E. vimimalis* groves, the dispersal of young from parental home ranges, and the limitation to density imposed by social intolerance appeared to be the important factors governing the dynamics of the koala populations.

This is illustrated in Table 7, in which the known composition of the population making use of trees in the principal study area is analyzed in terms of adult residents, young produced in the area, and "nomads." "Residents" were defined as adult animals which had persisted in the study area population for a period of at least 6 months. This definition was based on data shown in Table 8, which refer to the maximum persistence in the study area population of "immigrants," following the initial marking of all animals in June-December 1966. In view of the discontinuity between the 43 koalas that remained for from 1 to 5 months and the 3 which persisted for from 13 to 19 months, residents were defined as above.

Table 8.—Persistence of "immigrants" to marked populations of koalas

Persistence (months)	1	2–5	13	19
No. Koalas	34	9	1	2

Not all nomads were young animals, but of the 43 nomads referred to, only 8 were clearly fully grown animals, while 10 were less than 2 years in age. Since the number of nomad animals in the population did not appear to increase, despite the continuing dispersal of young from parental home ranges, it was clear that this class of the population was subject to heavy mortality.

Table 7.—Composition of a marked population of koalas

	Resident adults	*Nomads*	*1965 Pouch young*	*1966 Pouch young*	*1967 Pouch young*	*1968 Pouch young*	*Total*
July 1967	8	2	0	4			14
Oct. 1967	8	5		4			17
Dec. 1967	8	7		2			17
Jan. 1968	7	8		4	3		22
Mar. 1968	8	7		4	3		22
May 1968	10	5		3	3		21
July 1968	11	4		4	3		22
Jan. 1969	10	1		2	1	5	19
Jun. 1969	9	3		1	0	5	18

Koalas and Eucalyptus Trees

Feeding behavior

Koalas can show wonderful dexterity in reaching leaves carried on shoots at the extremities of branches, and in many trees there are few places, if any, that are inaccessible to them. Feeding usually begins within a half hour after nightfall and though animals may be active at any time, they are mostly so in the late evening and early morning. Koalas typically begin to browse by grasping a shoot and pulling it toward them. They seize the leaf by the petiole and detach it with a quick jerk. Koalas consume stem material and eat buds and flowers. They are said to occasionally ingest a little earth and Bolliger (1962) has reported on the finding of gravel in the cecum of a koala, its presence presumably the result of this habit. Koalas may strip bark from young shoots and even eat tough, woody fruits, but the bulk and principal item of diet is leaf.

Selective browsing by koalas

The earliest European accounts of the koala (Waterhouse, 1846; Troughton 1941) remarked on the selectivity shown by browsing koalas. Of course, many herbivorous animals are known to be very selective feeders, but the koala's unusual habit of remaining unconcealed during the day in the trees on which it feeds, has meant that its discrimination in choosing species of eucalyptus is readily apparent. This, together with the common failure of koalas to thrive in captivity and the apparent impossibility of weaning them to more conventional diets, has made the koala's specialization in respect to its food an article of folklore.

A number of naturalists, e.g., Sutton (1934), Lewis (1934), Pratt (1937), Fleay (1937), have reported their observations on the species of eucalypts preferred by koalas. But these observations have been necessarily couched in vague terms and are often inconsistent, one with another. Perhaps the only reliable conclusions that can be drawn from these reports are that:

1. On present information, only a few species of eucalypts are unequivocally able to satisfy the koalas' nutritional requirements. These include, notably, *E. viminalis* in Victoria and *E. tereticornis* and *E. punctata* in Queensland and northern New South Wales.

2. Koalas do not thrive in captivity, and this is usually considered a dietary problem. Periodic, heavy mortality is a common experience. In captivity koalas show striking preferences but nonetheless attempt a wide range of species. However, since it is practice to always provide such proven staples as *E. viminalis, E. tereticornis* or *E. punctata,* and to feed other species as additions to the staple, there is a plentiful lack of data on the ability of koalas to survive on other species.

On Flinders Chase 10 species of eucalyptus were available to koalas, 8 of which were widespread and abundant. However, although koalas were observed to feed on nearly all of these species, and in some cases might browse for days or even weeks at a time on apparently any locally available trees, it was clear from the distribution of the resident populations (which coincided exactly with the distribution of *E. viminalis*), and the behavior of individual animals, that the koalas strongly favored *E. viminalis* and were dependent on that species for survival in the long term.

Feeding trials on confined animals confirmed the favored nature of *E. viminalis* foliage and showed that at least 2 of the remaining species would be rejected as food by hungry animals.

Eucalyptus foliage as food

Eucalyptus browse seems an unpromising food, because except for the very young leaves it is tough and fibrous. Spencer (1968) reported the following unremarkable proximate composition for dried *Eucalyptus microtheca* leaf: protein 6.4 percent, fat 2.4 percent, fiber 13.6 percent, ash 8.2 percent, and nitrogen-free extract 69.4 percent. Proximate composition, of course, may be a poor indicator of palatibility or nutritive value, particularly with plants that harbor toxins.

A notable characteristic of eucalypts is the presence in the leaves of considerable quantities of essential oil. Baker and Smith (1920) surveyed many hundreds of species for commercial potential and reported yields ranging from 0 to over 3 percent for leaf-cut and processed as for commercial distillation. Perhaps partly because of the availability of this information, but also because the various components of the oils are generally toxic substances (Haagen-Smit, 1948), the possible significance of these oils for the koalas has frequently attracted comment.

Pratt (1937) advanced a two-fold theory which explained the various preferences and dietary requirements of koalas on the basis of the lethal toxicity of large doses of oil and thermoregulatory needs coupled with the physiological effects of sublethal doses. The evidence for this theory is unconvincing, however. Pratt's assertion that koalas in Queensland prefer a high-cineole oil is supported in part by references to species on which the koalas browse "very rarely and sparingly," and the argument overlooks the incidence of such oils among the Queensland species generally. Furthermore, the advantage on a hot Queensland day of a hypothermia induced by cineole-intoxication is more than likely to be offset by the accompanying disposition to cardiac and respiratory failure (MacPherson, 1925; Cleland, 1946).

It is not evident that koalas seek species with low yields of essential oil, since preferred species such as *E. viminalis* are moderate to high yielding, and species such as *E. cladocalyx* and *E. fasciculosa*, which are rejected by koalas on Flinders Chase, have very low yields. Nor is there an evident relationship between composition of oil and the allegedly preferred species, although conclusions based on Baker and Smith's data (Baker and Smith, 1920), such as those made by Fleay (1937), may be in error since more recent studies have demonstrated considerable variation in yields and compositions associated with "physiological forms" (Penfold and Willis, 1961), individual trees (Southwell, 1973), leaf age (McKern et al., 1951) and seasons (Berry et al., 1937).

Even so, the presence in eucalyptus leaf of quantities of terpenes, phenols, and other hostile compounds may not be without significance to koalas feeding on them. Cleland (1946) measured the toxicity of cineole, an important component of many eucalyptus oils, for a number of animals and reported a minimum lethal dose of 1.2g cineole per kilo of body weight for *Trichosurus vulpecula*, a marsupial which feeds to a degree on eucalyptus foliage. Eberhard et al. (1975) calculated that koalas feeding on the high-yielding species *Eucalyptus radiata* ssp. *radiata* would daily ingest about this amount of cineole. They also reported data from a test in which koalas feeding on *E. punctata* ssp. *punctata* (a favored food tree of koalas in New South Wales) were ingesting daily up to 10 ml of a terpene-rich oil, only about 15 percent of which was excreted in a steam volatile form in the feces.

The amount and composition of the oil may have considerable significance for gut flora. Nagy et al. (1964) found the essential oils of big sagebrush to have broad antibacterial properties and to inhibit the growth of cultured micro-organisms from the rumen of mule deer, *Odocoileus hemionus*. Their studies suggested that for this animal an exclusive diet of big sagebrush would result in a definite depression of rumen microbial activity.

Ecology of Koalas in Australia

Recent reduction of range

The range of koalas in Australia has been greatly reduced from that at the time of the beginning of European colonization. The clearing of forests has probably been the most important single factor, although changing patterns of wild-fire and epidemic disease may have also played a part. The killing of koalas for the fur trade, which persisted until the close of the 1927 open season in Queensland, may also have resulted in the extermination of local populations since at times it was undoubtedly carried out on a large scale. Troughton (1941) reported that in the year 1924 a total of 2 million koala skins were exported from Australia.

Availability of nutritious food

Trees of the genus *Eucalyptus* are widely distributed in Australia and omnipresent within the natural range of koalas. In the wild, koalas have been reported feeding on the closely related *Angophora* and *Tristania* spp., but typically they are exclusive browsers of eucalyptus foliage.

Not all species, however, are equivalent food-resources. Some species at least are completely rejected by captive koalas and the available data suggest that there may be relatively few species which provide both palatable and nutritious food for koalas.

It seems likely, therefore, that the distribution of potentially palatable and nutritious species of eucalypts may be a very significant factor limiting both the geographic range of koalas and the pattern of dispersion of local populations within the range.

Importance of social behavior in limiting density

On Flinders Chase it was concluded that within the limits of the distribution of the resident population, density was limited by the social intolerance of koalas, and it was considered that this was likely to be generally characteristic of populations in which the available food species formed a thickly growing monoculture.

It was also apparent, however, that the limit set to density was not nicely adjusted to the carrying capacity of the habitat, since in 1 study area at least it was evident that many trees were severely defoliated and that the death of trees was exceeding natural increase of the food stock through regeneration. It was not considered that the koalas alone were responsible for this situation since the general failure of many trees in this area to respond to the growing season suggested that they were over-mature or stressed in some other way. This observation however, is not subversive to the conclusion that the limit set to density by social behavior may not be appropriate to the carrying capacity of the habitat.

This is not a singular instance. Koalas have apparently multiplied in a number of island sanctuaries to which they have been introduced to the extent where they have destroyed most of their trees and then undergone a catastrophic decline in numbers (McNally, 1957). Kershaw (1934) and Pearse (personal communication) have reported natural populations of koalas on mainland Australia defoliating trees and declining in numbers. The scarcity of these reports, however, suggests that the phenomenon is relatively uncommon.

Not all koala populations are likely to occur in favored habitats where suitable food trees form a vigorous and thickly growing monoculture. In cases where trees of the important food species form a sparse population, i.e., are subordinate species in a tree association or form a savannah-woodland, it is likely that social behavior does not limit density, the size of the population being determined in the long term by the distribution and density of the food trees. Social behavior does not limit density since: (a) animals wander too widely to effectively maintain territories or (b) so heavily browse trees that the amount of foliage itself is the "limiting factor" (Watson and Moss, 1970).

Other components of the environment

(1) PREDATORS

Koalas are robust animals with few potential nonhuman predators. On the ground, all animals would be vulnerable to predation by the Australian dingo, *Canis familiaris,* and young animals may also be vulnerable to occasional predation by wedge-tailed eagles, *Aquila audax,* or powerful owls, *Ninox strenua.* It is clear from recorded myths (Massola, 1968; McKeown, 1938; Reed, 1965; and Ryan, 1964) and early observations quoted by Iredale and Whitley (1934) and Waterhouse (1846) that Australian aborigines hunted and killed koalas for food.

(2) PARASITES AND PATHOGENS

Koalas in general are nonverminous animals, though they may carry the intestinal cestode parasite *Prototaenia obesa,* and were the host carrying the parasite responsible for the nomen nudum *Taenia geophiloides* (Mackerras, 1958).

Stead (1934) and Troughton (1941) reported that at times between 1885 and 1903, epidemics involving some form of opthalmic disease and periostitis of the skull swept away millions of koalas in eastern Australia. Pratt (1937), Bolliger and Backhouse (1960), Backhouse and Bolliger (1960; 1961), and Finckh and Bolliger (1962; 1963) have listed a number of morbid conditions to which koalas admitted to sanctuaries have been found prone. Remarkable among these are relatively high incidences of cryptococcosis and cystic ovarian lesions.

(3) WEATHER

Throughout their range koalas are subject to climatic conditions varying from subtropical to Mediterranean. They do not make a "nest" or seek out limb hollows, sleeping simply curled up in a convenient fork exposed to weather.

Koalas can thermoregulate efficiently (Robinson, 1954) and also have a very thrifty water economy, rivaling such celebrated desert animals as camels and kangaroo rats, *Dipodomys deserti* (Eberhard, 1972). They differ from camels, however, in that they cannot seek drinking water at a distance (and do not in any case naturally drink), and differ from fossorial rodents in that they have no refuge comparable to a burrow. It is, therefore, possible that in the more inland parts of their range, where high temperatures coupled with low humidities are common, weather may periodically impose stresses on their water economy which they could not withstand.

(4) FIRE AND OTHER HAZARDS

Fire is a periodic phenomenon in mainland Australia and Philpott (1965) thought that fire might be important in keeping koala densities below the maximum long-term carrying capacity of the habitat. Fires may undoubtedly kill koalas but it is unlikely that their effects are other than "local" or "temporary."

Eucalypts are generally resistant to damage by fire and rapidly develop a secondary crown through the development of dormant buds concealed in the outer tissues of trunk and branches (Jacobs, 1936). Eucalypt regeneration is promoted by fire, which favors the development of sclerophyll forest formations at the expense of rain forests.

Fire, drought, or other causes of stress to trees may influence leaf chemistry. Finnemore et al. (1935) reported that 1 of 2 samples of *E. viminalis* foliage tested for hydrocyanic acid gave a positive result. Pratt (1937) thought that the presence of a cyanogenetic [sic] glucoside in *Eucalyptus* foliage constituted a hazard for koalas.

Co-evolution of Koalas and Eucalypts

Fossil material with phascolarctine affinities has been described from Miocene, Oligocene, and Pliocene Tertiary deposits (Stirton, 1957; Stirton et al., 1961 and 1967; Bartholomai, 1968; Turnbull and Lundelius, 1970). *Eucalyptus* fossils are known from the early Tertiary (Burbidge, 1960) although there is evidence that up until mid Tertiary times Australia generally supported a mesophytic forest type of southern beech (*Nothofagus*), conifers (*Podocarpus*), and broad-leaved trees (Cracraft, 1973). During the Pleistocene *Phascolarctos stirtoni* (Bartholomai, 1968) inhabited southeastern Queensland while pleistocene remains of *Phascolarctos cinereus* are known from South Australia (Pledge, personal communication) and Western Australia (Glanert, 1910; Bartholomai, 1968).

We do not know what may have been the habits of *Phascolarctos stirtoni, Pseudokoala erlita, Perikoala palankarinnica, Litokoala kutjamarpensis* and other Tertiary or Recent phascolarctine types. It is clear, however, that the evolution of *Phascolarctos cinereus* at least has involved adaptation to exploiting the potential food resource of *Eucalyptus* foliage. Two adaptations, one of behavior and the other of physiology, appear to be fundamental to the interpretation of present-day distribution and abundance of koalas in Australia. *Territorial behaviour* by koalas may limit the density of koalas in favorable environments. *Specialization in feeding capability,* restricting koalas to a limited range of species, may limit the distribution of local populations of koalas. Speculation concerning the evolution of these attributes is fraught with hazards, but the questions are fundamental and some provisional observations at least should be attempted.

Specialization in feeding capability

Two species of Australian mammals, *Trichosurus vulpecula* and *Pseudocheirus peregrinus,* are arboreal herbivores which feed to a degree on eucalyptus foliage, although they prefer other foods and have an unspecialized feeding capability. *Trichosurus* is nowadays very abundant in many areas where improved pastures and orchards have been created, and *Pseudocheirus* may be common where shrub genera such as *Melaleuca, Leptosperum,* and *Kunzea* occur (Thomson and Owen, 1964). However, it is very evident to any naturalist who has wandered through Australian sclerophyll forests that these partial browsers of eucalyptus foliage leave vast resources untapped.

Two herbivores, *Phascolarctos cinereus* and *Schoinobates volans,* have evolved a greater capacity to exploit this large potential food resource. Little has so far been said concerning *Schoinobates,* for the reason that very little is known of its feeding habits, although like *Phascolarctos* it is said to browse exclusively on eucalyptus foliage and is reputed to be very selective (Fleay, 1947). This critical selectivity by these animals implies that eucalyptus foliage does not represent a single potential niche to a mammalian folivore, but a number of niches, in which the successful efficient exploitation of one might preclude the exploitation of others. In some cases the important distinction between species or species groups may concern leaf chemistry. It seems inherently unlikely, however, that the chemistry of any species or group would be so hostile as to preclude the necessary physiological adaptation. The answer why some species or types, rather than others, have come to be exploited by evolving koalas or gliders may have as much to do with the ecology of the trees, as with the chemistry of their foliage.

In this respect it may be significant that in the sclerophyll forest formation of southeastern Australia, *E. viminalis,* for example, is an abundant wide-ranging species (Ladiges and Ashton, 1974), which in the recent past may have had an even more extensive distribution (Pryor, 1955).

One proposition, therefore, with the merit of simplicity, is that koalas in southeastern Australia have adapted to exploiting *E. viminalis* and chemically allied types, rather than some other species complex, for the reason that in recent times this tree has been the most common and wide-ranging species in habitats otherwise suitable for koalas.

Territorial behavior

Significent characteristics of the koalas' food resource are that it is discontinuously distributed in large units which are long-lived and self-renewing. Further, renewal is to a large measure dependent on favorable weather, the age and genetic potential for growth of the tree, and other factors largely independent of the koalas' feeding. It is clear that, provided a koala does not press too heavily on a suitable tree, it should reap a lifetime's harvest. In these circumstances, sedentary behavior by an animal which has found a suitable tree and is necessarily ill-equipped for extensive ground movement, would appear to be an excellent strategy.

It is one thing, of course, to be "sedentary," another to be "territorial." In this respect it may be an important observation that as far as is known, koalas have for long enjoyed environments free of potential predators, dangerously severe weather extremes, or other factors which might commonly prevent them from multiplying to a level where individuals have to compete for a food resource in short supply whatever the total abundance of that resource may be. In these circumstances, the potential adaptive values of territorial behavior, which would preempt for individuals access to such a resource, is readily apparent.

Summary

The koala, *Phascolarctos cinereus* (Goldfuss, 1817) is an arboreal, folivorous marsupial native to the sclerophyll forest formation of eastern Australia. It is an exclusive browser of foliage from trees of the genus *Eucalyptus* L'Herit. (Myrtaceae), which dominate these forests.

Life history data are reported. Koalas are monovular and polyoestrous during a restricted annual breeding season. At birth young weigh < 1.0 g and pouch life continues for about 7 months. Growth continues for at least 5 years although females may reach sexual maturity in their second year. Longevity is in excess of 10 years.

A population study is discussed. Koalas in the wild are territorial, although there may be some spatial overlap between male and female territories and young sometimes coexist during their second or even third year with parent females. Territorial behavior limits density, but in some circumstances koala populations defoliate and kill forest trees.

Information on food preferences and needs is reviewed. In captivity, koalas are known to reject or feed poorly on many species of eucalypts, while only a few, e.g., *E. viminalis*, *E. punctata*, and *E. tereticornis*, seem to be invariably palatable and nutritious. In the field this selectivity is reflected in the distribution of populations which may be restricted to the local occurrences of such favored species. The essential oil varies considerably between *Eucalyptus* species in yield and composition, but it is evident that koalas must detoxify and excrete relatively large quantities of these oils. The possible significance of essential oils in the diet of koalas is reviewed.

The evolutionary significance of territoriality to koalas and aspects of the co-evolution of koalas and eucalypts are discussed briefly.

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Habitat Selection and Use by Two-toed and Three-toed Sloths[1]

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Introduction

Habitat selection by sloths and other arboreal folivores involves a complex interaction among many factors, such as the physiological state of the animal and of the plants it uses as food; the recent past history of movement and feeding by the folivore; the more remote social history of the individual and perhaps its ancestors; plant species diversity and composition in the portion of the forest where the animal lives; and seasonal changes in the composition and availability of the various plants which the animal uses.

In this paper, we will not be able to characterize all of the interactions of all the factors which influence sloths in their choice of habitat. Perhaps it is enough to indicate that we do not yet fully understand why each sloth was found where it was on a particular day.

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[1] Dedicated to the memory of Griff Ewer.

This paper describes and characterizes the kinds of habitat which radiomarked two-toed (*Choloepus hoffmanni*) and three-toed sloths (*Bradypus variegatus*) (Wetzel and Kock, 1973) selected on Barro Colorado Island, Panama Canal Zone (BCI). After characterizing the habitat which the sloths used and some taxonomic and nontaxonomic attributes of trees and lianas which influenced their choices, we present data on microclimate at the sloth's surface and compare it with data of a similar kind from the surrounding forest canopy. We show that the animals attempt to regulate their body temperature by moving about in the canopy of the forest to places which increase or decrease the light intensity at their surface. We show the importance of the need to behaviorally thermoregulate and to seek protection from predation in influencing the sloths to choose trees with certain nontaxonomic attributes. We then summarize the results of experiments in which we measured the rates at which three-toed sloths digest leaves of various kinds and developmental ages, and the rate at which food passed through free-living sloths. We show that a sloth could starve to death with a full stomach if it made the wrong choice in a kind of leaf it ingested. We describe the influence of social inheritance of home range space and tree species preferences by young three-toed sloths on the ability of three-toed sloths to compete with other arboreal folivores, and speculate on the importance of the ability of sloths to use many species of trees in limiting the radiation of primates and other mammals into the neotropical arboreal folivore niche.

Habitat selection by sloths is evidenced by choices which individual radiomarked animals made among the large number of trees of many species and diverse growth forms which grew on each sloth's home range space. Sloths of the 2 species live in microsympatry in the highly complex tropical monsoon forest on BCI and elsewhere, and indeed share the use of some tree species and individual trees (Montgomery and Sunquist, 1975).

The plant species diversity in this environment is high (cf. Leigh and Smythe, 1978; Milton, 1978; Thorington, 1975) as is the diversity of plant growth forms. Furthermore, the dispersion patterns of tropical tree and liana species result in few individuals of a species being near each other (A. Hladik, 1978) or even on the relatively small home range space of a sloth; many species of trees on a sloth's home range space are probably represented by only one individual. There is thus a potentially very large number of habitat choices which a sloth can make from among the tree species, tree types, and the lianas which are supported by the trees on the sloth's home range space.

The habitat choice which a sloth had made was indicated to us by the tree in which the animal was found at a particular time. The tree, with the plants which that tree supported, was the unit in which we measured habitat selection by sloths.

Sloths of the 2 species probably used the trees in which they were radiolocated during daytime for different purposes. Two-toed sloths used the trees for support and concealment while they slept and rested; they were active almost entirely at night (Sunquist and Montgomery, 1973.) Three-toed sloths were active both during the day and at night.

A three-toed sloth moved into a tree and stayed there for at least 24 hours. On the average, they changed from tree to tree on about 60 percent of dates during the study. Two-toed sloths, by contrast, spent little time at single locations during their nocturnal activities, and moved comparatively long distances each night. Most of the two-toed sloths changed to a different tree between successive days in 90 percent of applicable measures.

The tree in which a sloth was found provided not only shelter and a means of support for the animal's body while it rested, but a substrate for movement and pathways into adjacent trees. The tree might have provided food in the form of leaves, or leaves from the lianas which the tree supported may have been eaten by sloths of both species. In addition, two-toed sloths may have eaten fruit from the tree or the lianas. We were seldom able to observe three-toed sloths while they fed; two-toed sloths presumably feed at night when they are active, and we never observed them feeding. In total, we saw three-toed sloths feed on leaves from 25 tree species and 1 species of liana (Montgomery and Sunquist, 1975).

The tree might also have provided access to sunlight and shade, and thus a means for regulating body temperature. The foliage and stems of the tree and the lianas in it might have offered concealment from predators.

The habitat in which sloths live is complex, not only because of the high species diversity and dispersion of plant speices, but also in terms of horizontal and vertical structural components. The complexity of this structure provides numerous pathways by which sloths can move about in their arboreal environment (see also Grand, 1978). Sloths normally come to the ground only to defecate, and they defecate at about weekly intervals (Montgomery and Sunquist, 1975; Waage and Montgomery, 1976). To descend from the forest canopy to ground level requires only a few minutes each week. At other times, the sloth lives and moves about in the canopy and subcanopy of the forest, many meters above the ground.

The movements of sloths which allow them to choose among the trees on their home range spaces and select suitable habitat take place through and on the arboreal structure of the trees themselves. The crowns of the trees are interlaced with lianas, and the end branches of adjacent trees may interlace. There are many pathways for lateral movement in the arboreal environment, and sloths take advantage of these pathways when moving between trees. It is not only unnecessary for the sloths to come to the ground to make a habitat choice, but to do so would cost additional energy and would perhaps increase the risk of predation.

Methods

We outline here the methods which were used to capture, radiomark, and radiolocate sloths, and give a brief description of the study area. Methods used only in some portion of the study are described in the appropriate section of the paper.

Our information about where sloths were, and thus about the portions of the habitat which each sloth selected, came from radiolocating sloths marked with radio transmitters fitted as collars around each animal's neck (Montgomery et al., 1973). To capture a sloth, we climbed the tree where it was seen or radiolocated, and used extendable aluminum poles, a noose, and a saw to capture the animal (Montgomery and Sunquist, 1975; Waage and Montgomery, 1976). The sloth was taken to the laboratory, where it was weighed, measured, and fitted with a radio collar, if necessary. Female sloths were examined to determine whether they were lactating, and whether an embryo could be felt by palpating the abdomen.

Totals of 52 three-toed and 12 two-toed sloths were captured, in addition to those which were used in only one portion of the study, such as determining rates of digestion. Of the 64 sloths, 31 three-toed and 11 two-toed were radiomarked and tracked. The bulk of the radiolocations were of 9 adult three-toed sloths and 6 adult two-toed sloths, each of which was radiotracked for a period of 3 or more months. However, radiolocation data for all 42 marked animals was used to compute frequencies with which tree species were used, indices of preference for nontaxonomic tree characteristics, and other measures of habitat preference.

We radiolocated each sloth whenever possible, but not more often than once per day. Throughout the paper, the term "radiolocation" refers to finding a sloth in a tree on a particular date. Accuracy of each radiolocation was sufficient to show not only the individual tree which the sloth had selected, but also the animal's height above the ground and the part of the tree it was using (Montgomery et al., 1973). We rarely saw the sloths, even when we knew where they were, because they lived high in the canopy of the forest and the dense vegetation blocked our view.

Most radiolocations of sloths were of animals which lived within 500 m of the laboratory clearing on the northeast side of BCI. The forest where our study sloths lived (Bennett, 1963) was of young to medium age, with poorly defined strata. The lower stratum reached 12 m, and a discontinuous upper stratum reached 24–35 m. Parts of the area were recently disturbed and tree-falls opened gaps in the canopy (Leigh and Smythe, 1978), resulting in a mixing of forest age and structure. Perhaps as many as 800 plant species (Croat, in press) including trees and the many kinds of lianas which grew in them (see following), were available to the radio-marked sloths as potential food and as substrate for their movements and activities.

Results and Discussion

Selection of trees for taxonomic and nontaxonomic attributes

Four general categories of tree attributes are of potential importance in providing characters by which a sloth can choose a tree. These are (1) the tree species, (2) the growth form of the tree, including age-related aspects such as size and seasonal changes, (3) the other species of plants, primarily lianas, which grow in and through the crown of the tree itself, and (4) the spacing and local distribution of trees of each species.

DIVERSITY AND INTERSPERSION OF TREES. In any small area of forest on BCI, a sloth had available a very large number of tree species from which to choose. These trees showed a range of nontaxonomic attributes as well, and trees with various attributes were likewise interspersed.

We chose 2 areas of the forest to provide data for evaluating the relationships among species diversity, interspersion of trees of various size and other nontaxonomic attributes, and the amounts of use which radiomarked sloths made of the individual trees. We considered that trees with stems 15 cm or less in diameter at breast height (dbh) were probably not important to sloths, and did not include these smaller trees in our sample.

We identified each tree as to species, then measured the height of the top of the crown, the height of the bottom of the crown, and the width of the crown with an optical rangefinder. Robin Foster helped with identification of trees. We estimated the cross-sectional area of each tree crown by multiplying the crown depth by its width. We estimated the percentage of each tree crown which would be exposed to direct sunlight if viewed from directly above. We ranked the mass of lianas in each tree crown on a scale of 1 = none to 4 = many. According to our ranking, a tree that had many lianas usually had several liana species growing in and through its crown and contained in its crown approximately as many liana leaves as tree leaves, or more.

These measures were made on trees which grew on 2 areas which were included in the home range spaces of 12 radiomarked sloths. The Lutz area was 0.34 ha, and the Allee area 0.43 ha. On the total 0.77 ha there were 298 trees of 15 cm or greater dbh. These 298 trees included 91 species, and perhaps as many species of liana grew in their crowns (see following). Sloths were radiolocated in 76 (25.5 percent) of the trees; 40 of the 91 tree species were used by the sloths. Twelve different three-toed sloths were radiolocated there a total of 58 times. These totals include radiolocations of independent young as well as of adult sloths.

TREE SPECIES DIVERSITY. Species diversity among the trees in areas of BCI used by radiomarked sloths was high, providing each animal with a wide choice in selecting species from among the trees which grew on its relatively small home range space. Home ranges of sloths were usually less than 2 ha in total area (Montgomery and Sunquist, 1975); we radiolocated some individual three-toed sloths in 50 or more trees of 30 or more species.

The great species diversity among the trees on the 2 sample areas (Table 1) was typical of that in other areas of BCI used by the radiomarked sloths (Thorington, 1975; Milton, 1978). A total of 91 tree species grew on the 0.77 ha total area, and each of the 2 smaller sample areas included about 60 tree species. Most tree species on each of the 2 areas were represented by only 1 individual, and 80 percent or more of the tree species were represented by 3 or fewer trees.

A very few tree species were represented by more than 5 percent of the total trees on the areas. In the Lutz area, 17 of 151 trees were *Alseis blackiania,* an understory tree which was used infrequently by sloths of either species (Montgomery and Sunquist, 1975). In the Allee area, 14 of 147 trees were *Anacardium*

Table 1.—Species diversity among 298 trees of 91 species that grew on 2 areas of BCI, and the differential use that radiomarked sloths made of tree species that occurred at various frequencies. The Lutz area included 0.34 ha, and 151 trees of 61 species grew there. The Allee area included 0.43 ha, on which there were 147 trees of 57 species. Trees with stems smaller than 15 cm were not identified. Nine three-toed sloths were radiolocated on the areas a total of 629 times, while 3 two-toed sloths were radiolocated there 58 times.

	Number of Trees										
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10–22*	
LUTZ AREA											
Percent of 61 tree species	51	18	16	3	2	5	2	0	0	3	
Percent of 422 three-toed sloth radiolocations	40	7	40	0	2	6	0	0	0	6	$\chi^2 = 201$; 5 df; $p < 0.01$
Percent of 38 two-toed sloth radiolocations	21	3	32	0	3	39	0	0	0	3	$\chi^2 = 67$; 5 df; $p < 0.01$
ALLEE AREA											
Percent of 57 tree species	52	19	9	9	2	2	0	0	0	7	
Percent of 207 three-toed sloth radiolocations	42	15	3	1	0	14	0	0	0	24	$\chi^2 = 159$; 5 df; $p < 0.01$
Percent of 20 two-toed sloth radiolocations	50	39	0	5	0	0	0	0	0	6	$\chi^2 = 4$; 5 df; n.s.

excelsum, while 15 were *Astrocaryum standleyanum,* an understory palm covered with long, sharp spines. Three-toed sloths rested in *Astrocaryum* trees at times, perhaps to gain protection from predators which would be deterred by the spines. Less than 1 percent of all radiolocations of three-toed sloths were in *Astrocaryum* trees, however. By contrast, *Anacardium excelsum* trees were used in 30 percent of all two-toed sloth radiolocations, and about 5 percent of all radiolocations of three-toed sloths; trees of that species were important habitat features for both species of sloth (Montgomery and Sunquist, 1975).

Sloths of both species probably avoided using tree species when individuals of those species were rare in the forest. On both sample areas, three-toed sloths were radiolocated less often than expected in tree species represented by only 1 or 2 individuals (Table 1). Likewise, two-toed sloths on the Lutz area were radiolocated in tree species represented by only 1 or 2 individuals less often than would be expected from the frequency with which trees of those species were found on the areas. Two-toed sloths radiolocated on the Allee area, however, used tree species no differently than would be expected on the basis of the frequency of occurrence of trees of those species.

Sloths differentially chose tree species which grew on the study area at moderate to high densities. On the Lutz area, both two-toed and three-toed sloths used a higher proportion of species that were represented by 3-6 individuals (9-18 trees per ha), apparently avoiding tree species that were represented by only 1 individual. On the Allee area, where use of tree species by two-toed sloths was no different than that predicted by the frequency of occurrence of individuals of the various species, three-toed sloths used trees of species which were moderately well represented on the area, or which were of relatively high density there (14 per ha and 23-51 trees per ha). There too, trees of species which were poorly represented in the forest were generally not used in proportion to their relative abundance.

There should be an advantage in avoiding use of species whose individuals are widely separated, because the energy cost of moving among rare trees would be higher. At this level of analysis, sloths tended to choose tree species in such a way as to reduce the energy cost of moving among them. An additional advantage in avoiding the use of rare trees was suggested by Freeland and Janzen (1974). They suggested that one factor in the ability of ruminant-like animals to detoxify secondary plant compounds is the recent experience which the animal's gut flora has had with the toxins. Thus, an animal should avoid continually ingesting novel foods if it is to maintain a healthy gut flora, or should severely limit the intake of new kinds of leaf. There is not necessarily a relationship, however, between the sloth's use of the more common trees and a tendency to avoid use of novel ones. Most sloths tended to use many species of tree within relatively short periods of time. For example, 1 adult female three-toed sloth used a total of 10 tree species during a 33-day period, and 8 of the species were visited only once (Montgomery and Sunquist, 1975). Approximately 40 percent of all tree species used by an individual three-toed sloth were used only once.

If the three-toed sloths fed from all or most of the trees which they used, then their movement and feeding pattern would seem to have contradicted the prediction of Freeland and Janzen (1974) that an herbivorous mammal with a gut adapted for ruminant or ruminant-like digestion would tend to avoid intake of novel foods.

SELECTION FOR TREE SPECIES. Sloths of both species used many tree species on BCI. In total, three-toed sloths were radiolocated in 98 tree species, and two-toed sloths in 52 tree species (Montgomery and Sunquist, 1975). Most individual three-toed sloths were found in 20 or more tree species, and most two-toed sloths in more than 15 tree species.

Three-toed sloths, when considered as a species rather than as individuals, were generalists with respect to the large number of tree species they used. They were radiolocated in 23 of the 61 tree species which we identified on the Lutz sample area, and in 20 of the 57 tree species on the Allee sample area. For the 2 areas combined, three-toed sloths were radiolocated in 40 of the total 91 tree species.

The three-toed sloths that included portions of the sample areas in their home range spaces showed statistical selection for a total of 12 tree species, and selection against 9 species (Table 2). Statistical selection was indicated when the overall frequency of use of the tree species differed significantly ($p. < 0.01$) from that expected on the basis of the frequency of occurrence of trees of the species (cf. Nichols and Warner, 1972). *Anacardium excelsum* trees were selected for on the Allee sample area, but selected against on the Lutz area. Most tree species which were selected for were represented on a sample area by only 1 or 2 trees. Those trees did not necessarily receive a large part of the total use of trees on the sample areas by three-toed sloths, but were used out of proportion to their occurrence. This disproportionate use usually resulted from radiolocations of only 1 sloth in the tree(s).

A total of 7 tree species were statistically selected for by the three-toed sloths which lived on the Allee area (Table 2). The only *Dipteryx panamensis* tree on the Allee area was the modal tree of sloth number

Table 2.—Selection of tree species by sloths from among the 147 trees of 57 species which grew on the 0.43 ha Allee sample area, and from among the 151 trees of 61 species which grew on the 0.34 ha Lutz sample area. Three-toed sloths were radiolocated on the Allee area 207 times, and on the Lutz area 422 times. Two-toed sloths were radiolocated on the Allee area 20 times, and on the Lutz area 38 times. The statistical significance of differences between the frequency with which trees of a species were found on a sample area and the frequency with which radiomarked sloths were located in trees of that species was tested with the χ^2 statistic. Levels of significance are: ** = $p < 0.01$; *** = $p < 0.001$.

Sample area	*Tree species*	*Percent of trees on area*	*Percent of radiolocations*	*Number of Sloths*	*Ratio of radiolocations to percent of trees*	*Level of significance*
ALLEE AREA						
Three-toed Sloths						
	**Dipteryx panamensis*	0.7†	30.0	1	44.0	***
	Inga goldmannii	0.7	5.3	1	7.8	***
	Hyeronima laxiflora	1.4	9.2	1	6.7	***
	Pterocarpus hayesii	1.4	4.8	2	3.5	***
	Trichilia cipo	0.7	2.4	1	3.5	**
	**Gustavia superba*	4.1	14.0	2	3.4	***
	**Anacardium excelsum*	9.5	17.9	6	1.9	***
	Astrocaryum standleyanum	10.2	3.4	3	0.3	***
	**Poulsenia armata*	6.8	0.5	1	0.1	***
LUTZ AREA						
Three-toed Sloths						
	**Ficus trigonata*	0.7†	19.9	1	30.1	***
	**Inga goldmannii*	0.7†	13.5	1	20.5	***
	Lacmellea panamensis	1.2	29.6	3	14.9	***
	Zuelania guidonia	1.3	5.4	1	4.1	***
	Chrysophyllum panamensis	2.0	6.4	2	3.2	***
	Hura crepitans	0.7	1.9	1	2.9	**
	Sterculia apetala	0.7	1.9	1	2.9	**
	Alseis blackiania	11.3	5.7	3	0.5	***
	Luhea seemannii	4.0	1.2	5	0.3	**
	**Anacardium excelsum*	4.0	0.7	4	0.2	**
	Hirtella triandra	2.6	0.5	1	0.2	**
	Astrocaryum standleyanum	4.6	0.5	1	0.1	***
	Virola nobelis	8.6	0.7	2	0.1	***
	Heisteria concinna	2.0	0.0	0	0.0	**
	Beilschmedia pendula	2.0	0.0	0	0.0	**
	Jacaranda copaia	2.0	0.0	0	0.0	**
ALLEE AREA						
Two-toed Sloths						
	Diptery panamensis	0.7	30.0	1	44.1	***
	Sapium caudatum	0.7	15.0	1	22.1	***
	Terminalia amazonica	1.4	20.0	1	14.7	***
	Spondias nigrescens	1.3	15.0	1	11.0	***
LUTZ AREA						
Two-toed Sloths						
	Trattinickia aspera	0.7	13.2	1	19.9	***
	Chrysophyllum panamensis	2.0	18.4	2	9.3	***
	**Anacardium excelsum*	4.0	34.2	3	8.6	***
	Licania platypus	2.0	10.5	2	5.3	**

† Modal trees of individual three-toed sloths.

*Modal tree species of individual sloths.

231 (Montgomery and Sunquist, 1975), and all of the radiolocations in that tree were of that 1 sloth and her young. On the Lutz area, where a total of 7 of the 61 tree species were statistically selected for, the only *Ficus trigonata* was the modal tree of sloth number 208, and no other sloth was radiolocated in that tree. Likewise, the only *Inga goldmannii* on the Lutz area was the modal tree of sloth number 225, and no other three-toed sloth was radiolocated there.

Two-toed sloths showed statistical selection for even fewer of the tree species on the sample areas and, because there were so few radiolocations of two-toed sloths, we were unable to demonstrate that any species were selected against by them. Four tree species were selected for by two-toed sloths on each of the 2 sample areas (Table 2). *Anacardium excelsum* trees were not selected by the two-toed sloth which used the Allee area, whereas trees of that species were used by all 3 two-toed sloths which lived on the Lutz area and the species was statistically selected for there.

In general, the apparent statistical selection of tree species by three-toed sloths as a species resulted from the selection of a few of the trees by individual sloths. With the possible exceptions of *Anacardium excelsum* and *Lacmellea panamensis* (Table 2), there were no apparent general preferences for tree species by most three-toed sloths.

An individual sloth used most of the trees and most of the tree species only once. Eight or fewer individual trees and 4 or fewer tree species accounted for 50 percent or more of the radiolocations of each of 6 two-toed sloths; likewise, 8 or fewer trees and 8 or fewer tree species were used by each of 9 three-toed sloths. Each sloth tended to use trees that were different from trees used by other sloths sharing its home range space (Montgomery and Sunquist, 1975). The tree in which a sloth was radiolocated most often was termed that sloth's modal tree; no 2 sloths had the same modal tree.

Three-toed sloths as a species appeared to be generalists with respect to the tree species they used, but, as individuals, each specialized on a few species. The tree species on which individuals specialized differed from sloth to sloth. Three-toed sloths tended to use a different set of tree species from other sloths in the same portion of the forest, or to use tree species at very different relative frequencies (Table 3). The tree species in which each sloth was radiolocated most often was called that sloth's modal tree species (Montgomery and Sunquist, 1975). Two of the 9 adult three-toed sloths had the same modal tree species (Table 3), but their home range spaces did not overlap. Modal tree species of any three-toed sloths living in the same portion of the forest were the same only in cases when juvenile sloths inherited a portion of their mother's home range space (see following). In most cases, the modal tree species of a three-toed sloth was not used at all by other sloths, or was rarely used.

Radiomarked two-toed sloths, by contrast, tended to have the same modal tree species, although they did not share modal trees (Montgomery and Sunquist, 1975). Four of the 6 adult two-toed sloths used *Anacardium excelsum* as their modal tree species.

Table 3.—The lack of consistency is shown among three-toed sloths in their use of tree species on BCI. The modal species for each sloth was the tree species used most often by it. Modal tree species for each of 9 three-toed sloths are listed, and the rank which that species had in the use of all tree species for the 9 sloths is shown. Dashes indicate that a sloth was never radiolocated in a tree of the species.

	Three-toed sloth number								
Modal tree species	*#2*	*#5*	*#6*	*#8*	*#19*	*#21*	*#25*	*#27*	*#31*
Gustavia superba	1	—	—	—	—	—	—	—	—
Anacardium excelsum	5.5	1*	—	21.5	13.5	1*	13.5	9	6
Tetragastris panamensis	—	4	1	21.5	11	9	—	—	18.5
Ficus trigonata	—	—	—	1	2.5	—	10.5	20.5	—
Ficus obtusifolia	—	—	—	—	1	—	—	—	—
Inga goldmannii	5.5	17.5	16.5	—	13.5	17.5	1	—	—
Poulsenia armata	3	11.5	6	21.5	7	4	—	1	12.5
Dipteryx panamensis	7.5	7	—	21.5	—	—	10.5	20.5	1

* The two sloths with *Anacardium excelsum* as a modal species did not share home range space.

DIVERSITY AND INTERSPERSION OF LIANA SPECIES. Even to an observer at ground level, lianas appear to be an important component of the canopy of tropical moist forest. About 50 percent of the 298 trees on our sample areas had lianas in their crowns, and sloths of both species selected trees in large part on the basis of presence or absence of lianas in the tree crown (see following). A. Hladik (1974;1978) measured the relative amounts of leaf from trees on a sample area in Gabon, and from the lianas which those trees supported. She found that liana species formed more than one-third of the total (33 liana species, 57 tree species), and liana leaf biomass was about 60 percent that of tree-leaf biomass. Montgomery, et al. (in preparation) speculate that, because lianas tend to survive tree-falls and trees do not, individual lianas are among the oldest plants in a particular portion of forest, and may dominate other plant growth forms at some stages of succession of tropical forests. In this section, we show that three-toed sloths probably did not select particular trees in order to gain access to particular liana species which grew in the tree crown.

To explore the possibility that modal trees and individuals of the sloth's modal tree species might have been chosen to gain access to 1 or more species of liana which grew in most tree crowns, we identified all lianas which grew in all modal trees and all individuals of three-toed sloth's modal tree species. We did not do such an analysis for two-toed sloths because of the small numbers of individuals which were radiomarked, and the few radiolocations of those individuals.

We examined all modal trees and all trees of modal species from the ground, and climbed those with lianas growing in their crown. We collected a sample of each liana species, and pressed and dried typical specimens. When it was necessary to verify the plant's identification, we sent the specimen to Dr. Tom Croat of the Missouri Botanical Garden. Lianas were usually identified on the basis of sterile characters (cf. Croat, 1978).

The number of liana species per modal tree ranged from 0 to 7; the average was slightly more than 2 liana species per modal tree (28 liana species in 13 trees). Three of the 13 modal trees lacked lianas in their crowns, while samples of 7 liana species were collected from the crown of one modal tree. The 10 modal trees with lianas in their crowns included individuals of 28 liana species.

Most of the liana species (23 of 28) were found in the crown of only 1 of the modal trees. Individuals of 2 liana species, *Tontalea richardii* and *Doliocarpus olivaceus,* were found in 3 of the trees. Individuals of 3 liana species, *Petraea aspera, Coccoloba parimensis,* and *Hippocratea volubilis,* were each found in 2 trees.

There were 39 trees of modal species for all 13 three-toed sloths combined. Of these trees 11 (18 percent) had no lianas in their crowns. The remaining 28 trees contained a total of 55 liana species, distributed so that each of 28 of the liana species was found in only 1 of the 28 trees (Table 4). Thus, half of the liana species were found in only 1 tree each. About 10 percent of the liana species were found in 5 or more trees. No liana species was collected from more than 30 percent of the trees which contained lianas, and most liana species occurred in 10 percent of the trees or less.

There were trees of 13 species included in the 28 trees of modal species from which we collected lianas. On this basis, the 55 liana species collected represent an average of more than 4 liana species per tree species.

Ten of the trees from which we collected lianas were *Anacardium excelsum*, an important tree species for both kinds of sloth. The identities of the lianas collected from *Anacardium* give some insight into the diversity and interspersion of lianas that can occur in 1 species of tropical tree. The 10 trees contained an average of 5.5 liana species per tree. There were 32 different liana species in the trees (Table 5). Most (59 percent) of the liana species were found in only 1 of the trees, and no species was found in more than 40 percent of the trees.

On the basis of the lack of consistency with which lianas of any species were found in most trees used, either by a single three-toed sloth or by three-toed sloths in general, we conclude that habitat selection by three-toed sloths on the basis of presence or absence of a particular liana species was unlikely.

Table 4.—Species diversity of the lianas found in the crowns of 39 trees used by three-toed sloths as their modal species. A total of 55 liana species were collected from 28 of the trees (11 had no lianas in their crowns).

Number of tree crowns with the liana species	*Liana species*	
	Number	*Percent of 55*
1	28	51
2	8	14
3	8	14
4	5	9
5	1	2
6, 7, 8	5	9

Table 5.—Species diversity among the 32 liana species found in the crowns of 10 *Anacardium excelsum* trees which had been used by three-toed sloths.

Number of Anacardium *crowns with the liana species*	*Liana species*	
	Number	*Percent of 32*
1	19	59
2	5	16
3	6	19
4	2	6
5 or more	0	0

SELECTION FOR NONTAXONOMIC TREE ATTRIBUTES. The species of tree, and perhaps the species of liana which grew in the tree crown, were probably important in influencing an individual sloth to choose one tree over another, and some nontaxonomic attributes of trees also influenced those choices. We used radiolocation and tree-measurement data from the 2 sample areas, supported by radiolocation and tree-measurement data from sloths living on other parts of BCI and the trees in which they were radiolocated, to determine the relative importance of these nontaxonomic attributes in influencing habitat selection by the sloths.

For sloths which used the sample areas, the number of times sloths were radiolocated in each tree and the nontaxonomic attributes which we measured for each tree were used to compute a Kendall nonparametric rank correlation matrix (Nie et al., 1970). The matrix was computed on tree use by two-toed sloths, tree use by three-toed sloths, exposure of the tree crown to direct sunlight, amounts of lianas in the crown, cross-sectional area of the crown, and maximum height of the tree.

There was considerable similarity in the influence which the nontaxonomic attributes had on the choice of trees by two-toed and three-toed sloths, and use of some trees was shared by individuals of the 2 sloth species. Even though there were only about one-tenth the number of radiolocations made of two-toed sloths on the sample areas (58 locations of two-toed and 629 locations of three-toed sloths), 12 of the 68 trees used by three-toed sloths were also used by two-toed sloths. Use of trees by radiomarked individuals of the 2 species was positively correlated; the Kendall rank correlation (Table 6) between tree use by individuals of the 2 sloth species (Tau = 0.16) was significant ($p<0.01$).

Exposure of the tree crown to direct sunlight, the mass of lianas in the tree crown, and the size of the crown were attributes of trees which may have influenced habitat choices by the sloths. Except for lianas and tree height, these attributes were intercorrelated with respect to rank of occurrence among the 298 trees. As would be expected, attributes of trees which usually change with tree size were intercorrelated (Table 6).

Nontaxonomic attributes of trees which influenced the use of trees by three-toed sloths differed from those which influenced two-toed sloths (Table 7). Three-toed sloths tended to choose trees more for the degree to which the tree crown was exposed to sunlight, while two-toed sloths tended to choose trees with masses of lianas in their crowns. The size and height of the tree crown apparently did not signifi-

Table 6.—Correlations among amounts of use sloths made of trees on sample areas, and some nontaxonomic attributes of the trees. Partial Kendall nonparametric rank correlation coefficients (Tau) are shown for all significant correlations ($p < 0.01$); the nonsignificant correlation is indicated by n.s. Attributes of all 298 trees with 15 cm dbh or greater on 0.77 ha were measured and characterized. Radiomarked sloths were radiolocated in 76 of the trees (25.5 percent); three-toed sloths were radiolocated on the sample areas 629 times (9 sloths), while two-toed sloths were radiolocated there 58 times (3 sloths).

	Use by two-toed sloths	*Use by three-toed sloths*	*Exposure of tree crown to sun*	*Lianas in tree crown*	*Cross-sectional area of crown*	*Height of tree crown*
Use by two-toed sloths	X	0.16	0.26	0.30	0.23	0.19
Use by three-toed sloths		X	0.31	0.22	0.26	0.19
Exposure of tree crown to sun			X	0.21	0.40	0.47
Lianas in tree crown				X	0.18	n.s.
Cross-sectional area of crown					X	0.52
Height of tree crown						X

Table 7.—The relative importance of some nontaxonomic attributes of trees selected for use by two-toed and three-toed sloths. A stepwise multiple regression on Kendall nonparametric rank correlation coefficients (Tau), among use sloths made of trees on sample areas and attributes of all trees on the areas, is shown. Nonsignificant ($p > 0.01$) contributors to the multiple regression are indicated by n.s.

	Two-toed sloth		*Three-toed sloth*	
Tree attribute	*Beta*	*F*	*Beta*	*F*
Exposure of tree crown to sun	0.15	5.3	0.23	12.4
Lianas in tree crown	0.24	18.8	0.15	5.1
Cross-sectional area of tree crown	0.10	n.s.	0.13	4.8
Height of tree crown	0.04	n.s.	0.01	n.s.

cantly influence choice of trees by two-toed sloths. Three-toed sloths may have attempted to maximize 3 attributes. These were, in order of importance, exposure to sunlight, lianas, and size of the crown. There was a reversal between the sloth species in the relative importance of lianas in the tree crown and exposure of the crown to direct sunlight.

Selection of trees with large crowns. Sloths of both species tended to use trees with large crowns, both on the sample area and elsewhere. We estimated the size of tree crowns by the cross-sectional area of each crown (crown depth × crown diameter). Total cross-sectional area of the trees on the sample areas was about 35,000 m^2 per ha, and the sum of the cross-sectional area of the crowns of all trees which sloths used was about 40 percent of the total for all trees (Montgomery and Sunquist, 1975), although the sloths used only about 25 percent of the trees on the sample areas.

Almost 90 percent of all trees on the sample areas had crowns which measured 200 m^2 or less in cross-sectional area (Table 8). For three-toed sloths, 37 percent of radiolocations were in the 12 percent of trees which had crowns with cross-sectional areas greater than 200 m^2. Selection of larger tree crowns by two-toed sloths was less obvious, but 29 percent of the radiolocations of two-toed sloths on the sample areas were in trees with larger crowns. On other parts of BCI, about 40 percent of radiolocations of both species of sloth were in trees with crowns larger than 200 m^2 in cross-sectional area (Table 8).

Selection of trees with lianas in their crowns.— Sloths of both species tended to avoid using trees which lacked lianas in their crowns, two-toed sloths selected trees with the most lianas, and three-toed

Table 8.—The frequency with which trees having various crown sizes, as measured by the cross-sectional area of the crown, were found on sample areas on BCI, and the use that sloths made of trees with crowns of various sizes. On the 2 sample areas, 298 trees having 15 cm or greater dbh were measured, and the cross-sectional area of each crown was estimated by multiplying the crown diameter by its depth. Sloths were radiolocated on the sample areas a total of 687 times. For comparison, the sizes of the crowns of trees in which sloths were radiolocated a total of 2253 times elsewhere on BCI are shown.

	Cross-sectional area of tree crown (m^2)			
	0–200	*200–400*	*400–600*	*600–800*
Percent of 298 trees on sample areas	88	10	2	0
Percent of 629 radiolocations of three-toed sloths on the areas	53	35	12	0
Percent of 58 radiolocations of two-toed sloths on the areas	71	12	14	3
Percent of 1877 radiolocations of three-toed sloths on BCI	61	27	9	2
Percent of 376 radiolocations of two-toed sloths on BCI	57	22	5	16

$\chi^2 = 787$; 2df; $p < 0.01$

$\chi^2 = 60$; 2df; $p < 0.01$

$\chi^2 = 13$; 2df; $p < 0.01$

$\chi^2 = 372$; 3df; $p < 0.01$

Table 9.—The frequency with which trees having various quantities of lianas growing in their crowns were found on sample areas on BCI, and the use which sloths made of trees with various amounts of lianas in their crowns. On the 2 sample areas, 298 trees having 15 cm or greater dbh were examined, and the amount of lianas in their crowns was scored on a scale of 1 = none to 4 = many. Sloths were radiolocated on the sample areas a total of 687 times. For comparison, the amount of lianas in the crowns of trees used by sloths elsewhere on BCI, as indicated by a total of 2253 radiolocations, is shown.

	Lianas in tree crown				
	None	*Few*	*Some*	*Many*	
Percent of 298 trees on sample areas	49	17	13	21	
				$\chi^2 = 797$; 3df; $p < 0.01$	
Percent of 629 radiolocations of three-toed sloths on the areas	9	19	48	23	
				$\chi^2 = 83$; 3df; $p < 0.01$	$\chi^2 = 55$; 3df; $p < 0.01$
Percent of 58 radiolocations of two-toed sloths on the areas	3	7	24	65	
Percent of 1877 radiolocations of three-toed sloths on BCI	22	26	28	23	
				$\chi^2 = 444$; 3df; $p < 0.01$	
Percent of 376 radiolocations of two-toed sloths on BCI	6	9	17	69	

sloths tended to use trees with only moderate amounts of lianas. Almost 50 percent of the 298 trees on the sample areas lacked lianas in their crowns (Table 9), while some 20 percent of them had many lianas growing in and through their crowns. Only 9 percent of the radiolocations of three-toed sloths and 3 percent of the radiolocations of two-toed sloths on the sample areas were in trees without lianas. There was thus an obvious avoidance of trees lacking lianas. Two-toed sloths were radiolocated 65 percent of the time in the 21 percent of trees which had many lianas; however, three-toed sloths were radiolocated in those trees only 23 percent of the time. About 50 percent of the radiolocations of three-toed sloths were in the 13 percent of trees that had only moderate amounts of lianas in their crowns.

Elsewhere on BCI (Table 9), two-toed sloths showed a much stronger tendency to use trees with the most lianas in their crowns, while three-toed sloths used mainly trees with moderate amounts of lianas. On BCI as a whole, sloths of both species tended to avoid using trees that lacked lianas.

Selection of trees exposed to sunlight. Sloths of both species selected trees that had a large portion of their crowns exposed to direct sunlight. Sixty percent of all trees on the sample areas grew in shade, with less than 25 percent of their crown exposed to direct sunlight (Table 10). Sloths avoided using those trees, but selected the 35 percent of trees which had three-fourths or more of their crown exposed to sunlight. Two-toed sloths were radiolocated 90 percent of the time in trees on the sample areas which had a large portion of their crown exposed to sunlight, while three-toed sloths were radiolocated in those trees 85 percent of the time. Sloths radiolocated on other parts of BCI selected trees with crowns exposed to sunlight as well, and avoided trees which grew in shade (Table 10).

SELECTION FOR NONTAXONOMIC ATTRIBUTES WITHIN TREE SPECIES. There were probably interactions among tree species and the various nontaxonomic attributes of trees, which influenced the choices which sloths made in their differential use of trees. For 2 tree species (Table 11) we compared the frequency of sloth use of the trees with differences among the trees of a species in 2 nontaxonomic attributes, presence of lianas and exposure of the crown to sunlight.

Three-toed sloths tended to use *Anacardium excelsum* and *Alseis blackiania* trees with moderate amounts of lianas in their crowns, although trees with many lianas and those without lianas were also present on the sample areas (Table 11). Two-toed sloths chose *Anacardium excelsum* trees with large amounts of lianas in their crowns, out of proportion to the number of trees of that species that had large amounts of lianas.

There were relatively few *Anacardium excelsum* trees on the sample areas whose crowns were not exposed to sunlight (Table 11). In spite of the lack of trees growing in shade, sloths of both species spent significantly more of their time than expected in trees whose crowns were in direct sunlight. Likewise, three-toed sloths tended to use *Alseis* trees differentially in response to crown exposure to sunlight.

HABITAT SELECTION AND BEHAVIORAL THERMOREGULATION. The tendency of three-toed sloths to use trees with crowns exposed to sunlight, and which also contained masses of lianas, was related in part to vertical movements which the animals made into and out of direct sunlight as their body temperatures changed. Goffart (1971) reviewed literature concerning body temperatures of captive sloths, including the findings

Table 10.—The frequency with which trees having various amounts of their crowns exposed to direct sunlight were found on sample areas on BCI, and the use which sloths made of trees with various amounts of exposure to sunlight. On the 2 sample areas, 298 trees having 15 cm or greater DBH were categorized as to exposure of the crown to sunlight if viewed from directly above. Sloths were radiolocated on the sample areas a total of 687 times. For comparison, the amount of exposure of the crowns of trees used by sloths elsewhere on BCI, as indicated by a total of 2253 radiolocations, is shown.

	Percent of crown exposed to sun				
	0–25	*25–50*	*50–75*	*75–100*	
Percent of 298 trees on sample areas	60	4	2	35	
				$\chi^2 = 737$; 3df; $p < 0.01$	
Percent of 629 radiolocations of three-toed sloths on the areas	9	2	4	85	
				$\chi^2 = 77$; 3df; $p < 0.01$	$\chi^2 = 1$; 3df; n.s.
Percent of 58 radiolocations of two-toed sloths on the areas	5	3	2	90	
Percent of 1877 radiolocations of three-toed sloths on BCI	15	8	6	62	
				$\chi^2 = 32$; 3df; $p < 0.01$	
Percent of 376 radiolocations of two-toed sloths on BCI	10	13	3	75	

Table 11.—Selection of individuals of 2 tree species on the basis of nontaxonomic attributes. *Anacardium excelsum* trees were apparently selected for by three-toed sloths on the Allee area, but selected against on the Lutz area; trees of that species were apparently selected for by two-toed sloths on the Lutz area. *Alseis blackiania* trees were selected against by three-toed sloths on the Lutz area. Two-toed sloths were located in *Alseis* trees only 7 times.

	Lianas in tree crown				*Percent of crown exposed to sun*			
	None	*Few*	*Some*	*Many*	*0–25*	*25–50*	*50–75*	*75–100*
Percent of 20 *Anacardium* trees	30	20	5	45	10	0	5	85
Percent of 91 radiolocations of three-toed sloths in *Anacardium* trees	12	36	15	36	0	0	1	99
Percent of 117 radiolocations of two-toed sloths in *Anacardium* trees	1	3	15	81	2	0	2	96
Percent of 18 *Alseis* trees	33	17	22	28	67	0	0	33
Percent of 27 radiolocations of three-toed sloths in *Alseis* trees	0	4	70	26	44	0	0	56

that (1) deep body temperature of *Bradypus cuculliger* and *B. infuscatus* varies within wide limits (27.7 to 35.5°C) according to ambient temperature at various times of day (Kredel, 1928; Herbig-Sandreuter, 1964; Eisentraut, 1932), or as ambient temperature is deliberately changed (Britton and Atkison, 1938; Kredel, 1928; Irving et al., 1942); (2) body temperature changes with exercise (Irving et at., 1942); and (3) when exposed to direct sunlight, sloth body temperature rises (Britton and Kline, 1939; Kredel, 1928) and continued exposure to direct tropical sunlight without the opportunity for escape from it may result in a 4 to 6°C rise in deep body temperature and eventual death (Britton and Atkinson, 1938).

We took selected measurements of the microenvironment at the sloth's surface, of internal body temperature of the sloth, and of selected sites in the forest canopy near the sloth. We equiped a total of 4 three-toed sloths with a telemetry device that measured and broadcast sunlight intensity and ambient temperature at the sloth's surface. Similar devices were used to measure and broadcast sunlight intensity and ambient temperature at the top of the forest canopy and 10 m below the surface at a site which was no more than 100 m from the sloth and usually less than 25 m from it. At the same time, we measured the sloth's deep body temperature with a telemetry device inserted into the sloth's rectum through the anus. Because the sloths defecated only about once each week, we were able to obtain serial data from the same animal for several days. When the sloth defecated, the internal temperature telemetry device was passed with the feces, and it was necessary to recapture the sloth to replace it.

During the times when the telemetry devices were in place, we recorded the sloth's deep body temperature, the temperature and sunlight intensity at the sloth's surface, the ambient temperature and sunlight intensity at the surface of the forest canopy, and the temperature and sunlight intensity 10 m below the canopy surface. Measurements of these environmental variables were made once each half hour. Activity by the animal was detected by changes in signal strength from the transmitters (Sunquist and Montgomery, 1973), and recorded continuously on a strip-chart recorder. We also noted the presence of clouds in the sky, and whether or not rain was falling.

We then compared the measurements of temperature and sunlight intensity to determine whether three-toed sloths changed their locations relative to gradients of sunlight intensity and ambient temperature, in response to changes in their internal temperatures.

Deep body temperatures of free-living two-toed and three-toed sloths fluctuated on a daily basis, with maximum temperatures on each date usually occurring at midday and minimum temperatures between midnight and dawn (Table 12). The maximum daily temperature differential recorded for the two-toed sloth was 7.3°C, while for a three-toed sloth it was 7.2°C. The sloths maintained a temperature differential with the environment at all times. They were 7° to 11°C warmer than the coldest ambient temperature measured in shade at their coldest time of day, and from 3° to 11°C warmer than the shade temperature at their warmest. Maximum sloth body temperatures were apparently lower on days when it rained before or at midday.

Body temperatures were apparently little affected by the normal activity of the animals, and continued to fall at night even though the sloths were active (Figure 1). By contrast, three-toed sloths which were forced to be active showed increased body temperatures (Irving et al., 1942). Sloth body temperatures were affected by rainfall, and they usually were reduced as the result of heavy rains, particularly when the rain came during daylight hours.

Three-toed sloths behaviorally thermoregulated by moving in the canopy to places where the light intensity at their body surface was increased when they were cold and decreased when they were warm and their temperature was still increasing. This conclusion is based on the radiotelemetric data on sloth body temperature, ambient temperature, and sunlight intensity at both the surface of the sloth and at 2 levels of the forest. It is also based on observations of the sloths while we measured temperature and light intensity. We show 2 examples of behavioral thermoregulation. In the first (Figure 2), the sloth was in a place where little sunlight could reach it during the period from dawn until 0800, and the sloth's body temperature was low. Ambient temperature began to rise at dawn, and by 0800, when the sloth became active, had increased by about 4°C over the nighttime low. The sloth became active at 0800, and moved to a place in the canopy at which the level of sunlight reaching it was about midway between the sunlight intensity at the top of the canopy and the intensity 10 m below the canopy surface. Following this move, the sloth's body temperature increased by about 6°C, and the sloth remained inactive until after sunset. As the light intensity decreased in the afternoon, the sloth's body temperature dropped. It continued to drop even while the sloth was active for about 3 hours after sunset.

In the second example of behavioral thermoregulation by a three-toed sloth (Figure 3), the cold sloth became active just after sunrise and moved to a place

Table 12.—Minimum and maximum deep body temperatures of free-living sloths on BCI, and minimum and maximum ambient temperatures measured 10 m below the surface of the rain-forest canopy within 100 m of each sloth. The times at which the temperature occurred are shown.

		Minimum temperature (°C)				*Maximum temperature (°C)*				
				Time				*Time*		
Sloth number	*Date*	*Ambient*	*Sloth*	*Ambient*	*Sloth*	*Ambient*	*Sloth*	*Ambient*	*Sloth*	*Remarks*
Two-toed sloth (Dry Season)										
13	15 II 73	22.2	33.3	0500	0700	30.0	40.6	1000	1200	
	16 II 73	23.6	33.8	0100	0800	30.0	37.8	1130	1330	
Three-toed sloth (Dry Season)										
58	15 II 73	22.2	32.2	0500	0600	30.0	37.8	1000	1200	
	16 II 73	23.6	30.5	0100	0000	30.0	37.5	1130	1130	
6	19 II 73	22.2	31.7	0300	0600	30.5	36.7	1400	1400	
	(Wet Season)									
2[1]	22 VIII 72	21.1	32.2	0130	0730	26.1	33.9	1630	0000	Heavy rain 1030–1200
	24 VIII 72	22.2	31.7	0330	0600	33.6	36.9	1130	1530	Partly cloudy all day
28	28 VIII 72	22.2	32.2	0030	0230	28.9	36.9	1230	1400	Cloudy; rain 1430–1800
	29 VIII 72	22.5	29.4	0000	0400	31.9	37.8	1200	1330	Partly cloudy
55	28 VIII 72	22.2	31.1	0030	0730	28.9	36.1	1230	1300	
	29 VIII 72	22.5	30.0	0000	0630	31.9	37.2	1200	1330	
	30 VIII 72	23.3	32.2	0600	0630	31.1	35.3	1000	1230	Cloudy; rain 1230–1500

[1] Pregnant female.

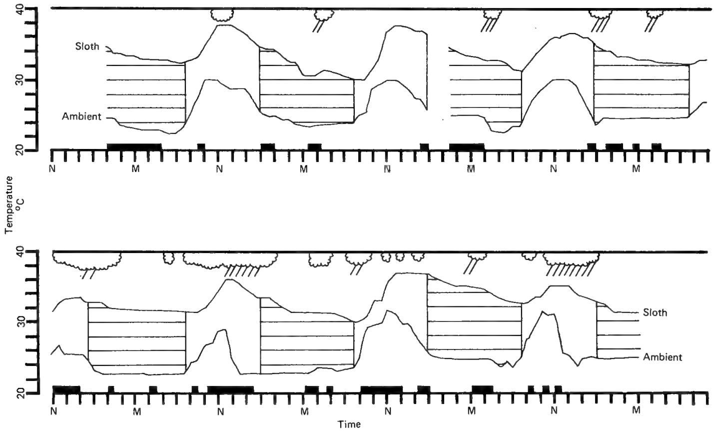

Figure 1. The daily cycle of deep body temperature in three-toed sloths, in response to daily changes in ambient temperature and sunlight intensity. Darkness is indicated by cross-hatching of the area between the lines indicating sloth and ambient temperature. Clouds and rainfall are indicated above the line for sloth temperature, and times when the sloth was active are indicated by the black bars below the line for ambient temperature. Noon is indicated by N, and midnight by M.

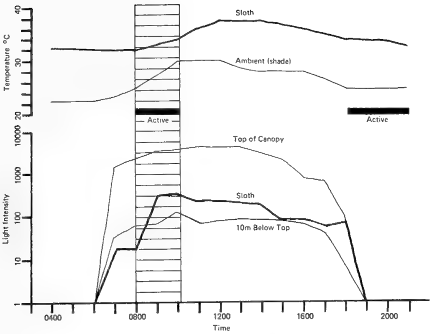

Figure 2. Behavioral thermoregulation by the three-toed sloth occurred between 0800 and 1000 when the cold sloth moved in the canopy of the rain forest in such a way as to increase light intensity at its body surface. See text for additional details.

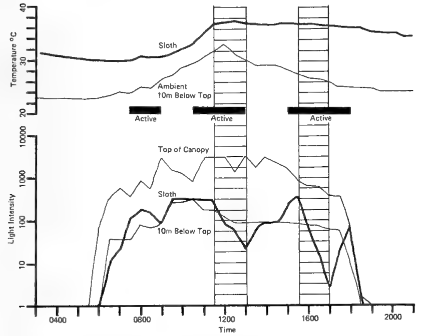

Figure 3. Behavioral thermoregulation by a three-toed sloth occurred between 0600 and 0800 when the cold sloth became active just after sunrise and moved to a place where it was in more intense sunlight. Thermoregulation occurred again between 1130 and 1300 when the warm sloth moved into shade, and again between 1500 and 1700 when the cooling sloth moved into intense sunlight. See text for additional details.

where it was in more intense sunlight. It remained there as its temperature rose, but became active again and moved out of the intense sunlight at about 1130. In this more shaded place, its body temperature remained almost constant. As the afternoon light decreased and the ambient temperature dropped, the sloth again became active and moved to a place with more intense sunlight. However, the animal's body temperature began to decline toward the nighttime low, possibly because the late afternoon sun was not strong enough to warm the sloth.

Large tree crowns exposed to direct sunlight were chosen by both kinds of sloth, perhaps in relation to a need for sunlight to maintain or elevate body temperature during the day, but two-toed sloths also chose trees with masses of lianas which would conceal them while they slept and warn them of the approach of potential predators.

There were 2 major differences in the apparent reasons why sloths of the 2 species selected the trees which they did, and these may help to explain why three-toed sloths maximized use of trees with exposure to sunlight and chose trees with only moderate amounts of lianas in their crowns. On the other hand, two-toed sloths apparently attempted to maximize use of trees with large masses of lianas in their crowns, perhaps at the expense of exposure of the tree crown to direct sunlight.

Two-toed sloths may have chosen trees with masses of lianas primarily to gain protection from predation. Two-toed sloths were inactive during daylight hours, and when we climbed to recapture them were often found asleep deep within a mass of lianas. While they slept in such a location, it was very difficult for us to approach the animal without alerting it to our presence, because the small interlaced branches of the lianas transmitted motion caused by our presence to the sloth. The movements of any potential arboreal predator large enough to kill a two-toed sloth would surely have alerted the sloth as well, giving it the opportunity to attack the predator or to flee through the mass of lianas and out of the tree. Protection and concealment from potential avian predators was provided by the mass of lianas as well.

Three-toed sloths, on the other hand, were often active during daylight hours, and we saw them while they were inactive or active in exposed locations. The trees they used tended to be those which lacked the masses of lianas that gave concealment and early warning to two-toed sloths. The reaction of a three-toed sloth to our presence in the tree was quite different from that of two-toed sloths. Three-toed sloths rarely either attacked us or attempted to flee, until we were actually in the process of capturing them and had touched them with the capture equipment. Most three-toed sloths showed no reaction to our presence until we had captured them, and then they struggled only briefly until we had managed to grasp all their limbs in one hand. Three-toed sloths were obviously not programmed to either flee from a potential predator or to attack it until it has actually touched or grasped the sloth.

There are other major differences in the anatomy and behavior of the 2 sloth species which suggest that they have been under different selection pressures as concerns predation, and have evolved very different ways of reacting to predators. Two-toed sloths, for example, have long, sharp-pointed teeth which are the positional and functional equivalents of the canine teeth of carnivores. These teeth meet in such a way that they are self-sharpening, and each has a very sharp point at all times. The two-toed sloth, when excited, attempts to pull objects to its mouth with its forearm and to bite. Furthermore, after a two-toed sloth became alerted in a tree, it often attacked by moving rapidly toward us down a branch, swinging its foreclaw when it came within range, and attempting to bite. Three-toed sloths are much more docile and never initiated an attack, although they would swing a forearm at us if we agitated them. They have no teeth adapted for piercing bites. The teeth have nearly flat surfaces, and none of them are particularly pointed. They almost never attempted to bite us, even when they were being handled rather roughly.

Differences in the need for sunlight and shade to maintain behavioral thermoregulation provide another reason why sloths of the 2 species may have selected trees with more or less lianas in their crowns. Sloths of both species showed daily fluctuations in body temperature which occurred in direct relation to ambient sunlight intensity (see also McNab, 1978). Thus, their body temperatures were usually highest at about midday.

Three-toed sloths behviorally thermoregulated by changing their location in the forest canopy so as to increase sunlight intensity at their body surface when they were cold and to reduce sunlight intensity when they were warm. Two-toed sloths probably did not make such adjustments in their positions relative to sunlight, as indicated by their almost complete lack of activity during daylight hours (Sunquist and Montgomery, 1973). We saw sloths of both species basking in sunlight with their abdomens facing the sun and their limbs extended. Two-toes sloths, however, were not usually in direct sunlight, but were within masses of lianas.

Three-toed sloths probably depended on sunlight to raise their body temperature each day, and were unable to maintain high body temperatures at night. Particularly on days when it was rainy at midday, the animals failed to achieve a high body temperature. Did this lower body temperature affect the rate at which they digested their food? Little is known of the effect of lowered body temperature on the action of the gut flora of ruminantlike animals, but we may suppose that the rate at which the members of the flora carried out their actions on the leaf material in the gut was reduced whenever the sloth's deep body temperature fell at night. This being the case, the overall rate at which food passed through the sloth's gut would depend in part on the amount of sunlight which the animal could receive during the day, and the consequent elevation in body temperature which it could achieve. It seems apparent that the sloth could run the risk of starvation if it faced several days in a row during which the sunlight intensity was reduced at midday, particularly when rain also fell during the morning hours.

During the rainy season in Panama, particularly during the months of October, November, and early December, it is often cloudy all day and rain falls during daylight hours. It is also during that season that few trees have new leaves (Leigh and Smythe, 1978), and perhaps most of the leaves available to sloths as food are difficult to digest. Sloths could choose more digestible leaves to try to offset the depressing effect of cloudy days and rain on rates of digestion, but only when young leaves are available.

There is an apparent increase in sloth mortality during those months, which affects adult as well as juvenile three-toed sloths. More than 60 percent of all sloths found dead on trails on BCI over the years were found during October, November, and December, although those are the months when fewest people visit the island.

DIGESTION OF LEAVES BY THREE–TOED SLOTHS. Young leaves were digested at the highest rates, older leaves, which were digested fastest tended to be from tree species which ranked highest in use by some three-toed sloths, and rates of digestion of all leaves were lower than rates at which ruminants and other mammals digest their food.

We measured rates at which free-living three-toed sloths fitted with gastric fistulas digested leaves of various species and developmental ages. Dr. M. Busch assisted with design of the fistula devices, performed the surgery to place the devices in the sloths and other veterinary tasks associated with maintaining them, and assisted with all aspects of field work for this portion of the study.

Four three-toed sloths were captured on the Bohio peninsula across the ship channel from BCI during August and September 1974. Each sloth was radio-marked so that we could recapture it when necessary to conduct postoperative examinations, and to recover and measure leaf samples through the fistula.

The gastric fistula device had a base 2.5 cm long with a flared end 3 cm in diameter, which was placed within the stomach. A second flared portion above the end formed a 5-mm wide groove into which the gastric wall and linea alba were sutured to hold the device in place. The other end of the device was fitted with a plug, which was screwed into place to close the opening into the sloth's stomach. Two stainless steel baskets were attached to the plug, and hung into the sloth's stomach on a short chain. Samples of leaf for each digestion trial were placed in these baskets and lowered into the sloth's stomach through the fistula before the opening was closed with the plug. A flap of skin covered the fistula device before the sloth was returned to the field.

Sloths were recaptured at intervals of 5-7 days, and a new digestion trial began at each recapture. The experiment was designed so that we could use a portion of a standard leaf in all the digestion trials, and compare the rates of digestion between the standard and other leaf samples. The standard leaf was from *Poulsenia armata,* and a single leaf was large enough to provide samples for all 13 digestion trials. Leaves from *Lacmellea panamensis* were also used in every trial. Those leaves were too small to allow a single leaf to provide a sample for each trial, however, and 5 leaves collected from the same tree at the same time were used.

A *Poulsenia armata* leaf sample and a *Lacmellea panamensis* sample were placed in 1 of the 2 baskets in every trial. Into the other basket, we put a sample of leaf from the tree in which the animal was recaptured and from as many of the lianas in that tree as possible. We used samples of leaves of different developmental age from the tree where the sloth was captured, when those leaves were available.

Each leaf sample was cut into a recognizable shape (circle, diamond, square), weighed, and wetted with water before being placed in the basket. Digestion was incomplete in all cases, and we were able to recognize all the samples when they were recovered from the sloths.

The standard leaves were kept dry, and the dry weight of standard samples was determined by weighing them before each was placed in a sloth. Leaves from the other trees and the lianas were fresh, and it was necessary to estimate the dry weights of samples from them. Dry weights of the leaf samples were estimated by weight changes in samples of the same leaves, which remained outside the sloth and which were dried before being weighed again. Samples were dried in an oven at 45°C. After the partially digested samples were recovered from a sloth's stomach, they were rinsed, dried for 1 week or more, and then weighed. Rates of digestion were estimated by the percentage change in leaf weight per unit time.

In all, we estimated the rates of digestion of leaves from 12 species of tree, including the 2 species used as standards, and of 7 liana species. We also used leaves of various developmental ages from each of three trees.

Table 13.—Rates of digestion of *Poulsenia armata* and *Lacmellea panamensis* leaf samples by free-living three-toed sloths.

		Percent digested per day		
Sloth number	*Days in sloth*	*Poulsenia armata*	*Lacmellea panamensis*	*Lacmellea/ Poulsenia*
1	5.04	4.17	5.57	1.34
1	5.70	3.56	5.21	1.46
1	6.69	3.44	5.05	1.47
2	5.75	4.43	6.29	1.42
2	8.12	3.61	7.35	2.04
3	5.20	4.94	6.82	1.38
3	6.00	3.20	4.75	1.48
3	6.04	2.66	3.91	1.46
3	6.60	2.88	6.48	2.25
3	7.04	3.49	8.56	2.45
4	5.06	2.77	6.01	2.17
4	6.00	1.88	5.53	2.94
4	6.50	5.02	6.37	1.27
Mean		3.54	5.99	1.86

Leaves of *Lacmellea panamensis* were digested at an average of about 1.9 times the rate of digestion of *Poulsenia armata* leaf used in the same digestion trial (Table 13). *Poulsenia armata* leaf samples were digested at rates ranging from 1.9 percent to 5.0 percent per day, with an average of 3.5 percent per day, while leaf from *Lacmellea panamensis* was digested at rates ranging from 3.9 percent to 8.6 percent per day, averaging 6.0 percent per day. There was considerable trial-to-trial variation, but no consistent differences among the 4 sloths in the rate at which each sloth digested the leaves of either standard species in different trials.

Leaves of the 19 plant species were digested at rates which ranged from 0.20 to 13.4 percent per day among the species. The lowest digestion rate was for the leaf of a palm *Oenocarpus panamense,* and the highest rate was for the young leaf of *Ficus insipida,* which was digested at a rate one-third greater than any other leaf tested.

We compare the rates of digestion of young and old leaves from the same tree for 3 species (Table 14). In all 3 cases, young and medium-aged leaf was digested at a higher rate than old leaf from the same tree. The greatest difference in rate of digestion of young and old leaf was for *Cordia alliodora,* where young leaf was digested at more than 3 times the rate of old leaf from the same tree.

Table 14.—Rates at which old, medium-aged, and young leaves collected from trees at the same time were digested in the same trial.

	Percent per day digested			
Tree species	*Old*	*Medium*	*Young*	*Young/old*
Cordia alliodora	0.96	—	3.10	3.23
Ficus trigonata	9.32	—	13.14	1.41
Cecropia peltata	6.12	8.65	7.09	1.16

The rates of digestion of the leaves used in each trial were compared with the rate at which the *Poulsenia armata* standard leaf sample was digested in the trial, and these indices to relative digestibility were ranked (Table 15). Leaf from the palm *Oenocarpus panamense* was digested at only about 0.05 times the rate at which the standard leaf was digested, while old leaf from *Ficus trigonata* was digested nearly twice as fast as the standard. About one-third of the tree species had leaves which were digested at higher rates than the standard.

Leaves which were digested at the higher rates tended to be those from trees which ranked high in use by some radiomarked three-toed sloths on BCI (Table 15). The 3 tree species whose leaves were digested at the highest rates ranked fourth or higher in total use of tree species by sloths, in 10 of the possible 27 cases. *Lacmellea panamensis* trees were rare in the forest (Table 2), and did not occur on the home range spaces of most sloths. When they did occur, they ranked relatively high in the sloth's use of tree species. *Cecropia peltata* trees were also rare on the portion of BCI where the radiomarked sloths lived, and were not used by any of the 9 sloths. The 6 tree species which ranked lowest in rate of digestion included only 1 case in which the use rank was 4 or higher, of a possible 54. Most of the 9 sloths were found in trees of those 6 species rarely, if at all.

Only 2 of the tree species that were included in the digestion trials were trees that sloths selected for or against on the sample areas (Table 2). *Lacmellea panamensis,* which had one of the higher rates of digestion in the trials, was selected for on the basis of use by 1 sloth, while *Hyeronima laxiflora,* which showed nearly the lowest rate of digestion, was selected

Table 15.—A comparison of the rates at which leaves of 12 tree species were digested by 4 free-living three-toed sloths, and the ranking of those tree species in the total radiolocations of 9 other three-toed sloths on BCI. The rank of digestion was based on comparing the ratios of the rate at which leaf from the tree species was digested to the rate at which *Poulsenia armata* leaf was digested in the same trial. Mean ranks of tree species use were calculated by ignoring animals that had not been radiolocated in that tree species, indicated by a dash.

			Rank of use of the tree species by each three-toed sloth									
Tree species	*Percent digested per day*	*Digestion rank*	*#2*	*#5*	*#6*	*#8*	*#19*	*#21*	*#25*	*#27*	*#31*	*Mean Rank*
Ficus trigonata	9.32	1.89	12.0	2.0	16.5	1.0	2.5	—	10.5	20.5	26.5	9.2
Lacmellea panamensis	5.99[1]	1.86[2]	—	—	4.0	3.5	—	—	—	2.0	—	3.2
Cecropia eximia	3.79	1.37	2.0	11.5	2.0	3.5	2.5	3.0	10.5	6.0	12.5	5.1
Protium panamense	4.72	1.32	32.0	—	—	29.0	21.0	—	—	—	—	27.3
Cecropia peltata	6.12	1.10	—	—	—	—	—	—	—	—	—	—
Poulsenia armata	3.54[3]	1.00	3.0	11.5	6.0	21.5	7.0	4.0	2.0	1.0	12.5	8.6
Spondias radlkoferi	3.42	0.99	—	25.0	—	—	—	—	—	—	—	25.0
Protium tenuifolium	4.11	0.98	—	—	—	—	18.5	—	—	5.0	26.5	16.7
Lacistema aggregatum	1.77	0.94	—	—	—	—	—	—	—	—	—	—
Cordia alliodora	0.96	0.36	25.5	17.5	—	—	18.5	12.0	—	20.5	26.5	20.1
Hyeronima laxiflora	0.87	0.17	4.0	17.5	16.5	29.0	—	17.5	—	—	20.5	17.5
Oenocarpus panamense	0.20	0.05	—	—	—	—	—	—	—	—	—	—

[1] Mean from 13 digestion trials; the range was 3.91 to 8.56 percent per day.

[2] Mean from 13 digestion trials; the range was 1.27 to 2.94.

[3] Mean from 13 digestion trials; the range was from 1.88 to 5.02 percent per day.

for on the Allee area on the basis of a large number of radiolocations of the 1 sloth which used it.

Lacmellea panamensis trees were used in about 7 percent of the total radiolocations of three-toed sloths on BCI (Montgomery and Sunquist, 1975). We estimated that 1 small tree of the species was used by three-toed sloths to the extent that 20 percent of its annual leaf production was cropped by them. Trees of the species were rare; only 3 of the 298 trees on the sample areas were *Lacmellea panamensis* (1 percent). Thorington (1975) identified only 1 *Lacmellea panamensis* tree of 981 total trees 60 cm dbh and greater which grew on 5 ha of the part of BCI on and near where our radiomarked sloths lived. He identified a total of 29 *Hyeronima laxiflora* trees on the same 5 ha.

Lacmellea panamensis was a tree species whose mature leaves were highly digestible, and the use made of the few trees of this rare species probably reflected the ease with which the leaves could be digested. Trees of the species were primarily used by adult female sloths when they needed high levels of energy for carrying dependent young, and by growing young also needing high rates of energy input. Adult female three-toed sloths were radiolocated in *Lacmellea panamensis* trees 52 times, and adult males 12 times. A total of 40 of the 52 locations of adult females (77 percent) were of sloths that were carrying a dependent young, and an additional 8 percent were of females in advanced stages of pregnancy.

Newly independent three-toed sloths whose mothers had used *Lacmellea panamensis* trees while they carried them about tended to use *Lacmellea* trees after they were socially weaned. One of the 2 young sloths whose mothers were radiolocated in *Lacmellea* trees before social weaning was located 15 times after social weaning before it died; 14 of those locations were in *Lacmellea panamensis*. The other independent young was located in *Lacmellea* 10 of 48 times (21 percent) during the 3 months after social weaning.

Adult female three-toed sloths used *Lacmellea panamensis* trees in all months except October and November, but use of the species was concentrated in the dry season (December to April), when 33 of the 52 locations were recorded. During the dry season, all radiolocations of adult females in the species were of those which carried young on their chests. The radiolocations of adult males in *Lacmellea* tended to be in late dry season, with 11 of the 12 locations recorded during March and April.

The leaves of *Hyeronima laxiflora* were relatively indigestable at the time of year when we conducted the digestion trials (mid-wet season), but may have changed with seasons and been replaced with more digestible leaves in dry season.

Hyeronima trees were used by relatively few sloths, although they were more common than *Lacmellea* trees in the forest. Such use of *Hyeronima* as occurred was seasonal, taking place only during a short period of the dry season. Twenty of the 21 radiolocations of adult females in the species were during February, March, and April, as were 9 of the 13 locations of adult males.

Hyeronima laxiflora ranked fourth in use by adult female sloth number 2, and all radiolocations of that sloth in *Hyeronima* were in a single tree. *Hyeronima* trees were used by an additional 4 females and by 4 adult males. No other adult female was radiolocated in *Hyeronima* more than once, and no male more than 4 times. One of the independent young used *Hyeronima* once.

Eighteen of the total 36 radiolocations of sloths in *Hyeronima* were in a single tree. That tree, used primarily by sloth number 2, who was located there 17 times, may have been selected for attributes other than tree species. It had all of the nontaxonomic attributes selected for by three-toed sloths. It was over 20 m tall with a large crown fully exposed to sunlight; the crown contained many lianas, and we identified 6 liana species from it.

Leaves of *Cecropia eximia* trees, once thought to be the primary, if not the only, source of food for three-toed sloths (Beebe, 1926; Lundy, 1952), were digested at a daily rate about one-third higher than the rate at which the standard leaf of *Poulsenia armata* was digested (Table 15). Leaves of the species may have been less digestible in other seasons when radiomarked female sloths made less use of *Cecropia* trees. Use of *Cecropia eximia* by female sloths was highly seasonal, and was concentrated in mid-to late-wet season. Only 14 locations were made in dry season, representing 12 percent of the 120 total locations of adult females in *Cecropia eximia* trees. During August and September, females were located in *Cecropia eximia* trees 72 times (60 percent), and during October and November 30 times (25 percent).

Cecropia eximia trees were used in about 8 percent of the total radiolocations of three-toed sloths on BCI, and ranked highest in total use of tree species (Montgomery and Sunquist, 1975). No three-toed sloth had *Cecropia eximia* as a modal species, but most adult females used trees of this species at a moderate-to-high rate. Most of the radiomarked three-toed sloths made use of *Cecropia eximia* trees during the study, with 7 adult females located in them a total of 120 times and 3 adult males a total of 20 times. *Cecropia eximia* ranked fourth or higher in tree species use for 5 of the 9 sloths (Table 15), and the lowest rank of tree use among the 9 sloths was 12.5.

There was a strong tendency for females which were in mid- to late-stages of pregnancy to use *Cecropia eximia* trees. About 37 percent (44 of 120) of the radiolocations of adult females in *Cecropia eximia* were of pregnant sloths, and 24 percent of all radiolocations of pregnant sloths were in *Cecropia eximia* (44 of 183). *Cecropia eximia* trees formed 0.3 percent of the 981 trees with 60 cm dbh and more on 5 ha of BCI (Thorington, 1975), and were not found on the Allee and Lutz sample areas. In contrast to *Lacmellea panamensis,* adult female sloths carrying young tended not to use *Cecropia eximia.* Only 17 of the 120 radiolocations of adult female three-toed sloths in *Cecropia eximia* trees were of females carrying dependent young.

As illustrated by the examples provided by these 3 tree species, the differential use of tree species may have been related to the relatively high digestibility of mature leaves of rare trees (*Lacmellea*), perhaps to the seasonal presence of digestible young leaves on a tree whose mature leaves were relatively indigestible (*Hyeronima*), or the more constant availability of leaves whch were of moderate digestibility, and on trees which were common in the forest (*Cecropia*). These examples do not exhaust the possible effects of differential digestibility on the use of tree species.

RATE OF PASSAGE OF FOOD THROUGH THREE–TOED SLOTHS. The efficiency with which food is digested is in part dependent on the length of time food is retained in various parts of the gut (Bauchop, 1978; Parra, 1978). Thus, retention time was a major parameter in the sloth's digestive process. We estimated the rate at which food passed through three-toed sloths by measuring the rate at which colored glass beads fed to wild sloths passed through them and appeared in their feces. A. Lang Elliot helped with this portion of the study.

Free-living three-toed sloths defecated once every 8 days, on the average, and passed 56 g dry weight of feces per defecation (Montgomery and Sunquist, 1975). Each of 5 free-living sloths was radiolocated daily, recaptured at the beginning of the field experiment in which we estimated rates of food passage and defecation, and was recaptured within 2 days after each time it defecated. A small radio-transmitter, approximately twice as large as each sloth fecal pellet, was inserted into the sloth's rectum through the anus at each recapture. This transmitter was passed with the feces whenever the sloth defecated, and allowed us to time the interval between defecations and to recover the feces from the forest floor.

A three-toed sloth descends to the forest floor about once each 8 days, digs a shallow depression in the forest floor with its tail, and defecates a mass of fecal pellets into this depression. By carefully digging out the fecal mass associated with a transmitter, we collected all the fecal pellets that had been passed by the sloth during a known time interval.

A total of 5 three-toed sloths were given 3-mm-diameter glass beads so that we could estimate the rate at which food passed through the animals. Beads of a different color were given to each animal at successive recaptures, so that beads from different times could be distinguished in the feces. Beads were poured down a rubber tube that had been inserted into the sloth's stomach through the mouth and esophagus. Some beads stuck in the tube, and we were not always able to introduce all the 80 beads of a color as we had hoped. The number of beads fed to a sloth at any 1 time ranged from 16 to 80 (Table 16). Beads were recovered from sloth feces and counted by looking for ones exposed at the surface of pellets, and by macerating all the pellets in each fecal mass.

Colored beads began to appear in sloth feces 6 days after being fed to an animal (Table 16), and were still being recovered 26 days after being fed to 1 sloth. Although fewer than half the 80 beads which had been fed to that sloth had been recovered when the experiment was terminated after 26 days, beads were still being passed at a nearly constant rate. Beads passed through three-toed sloths at an average rate of 1.9 percent per day, with a range in passage rates of 0.25-4.61 percent per day.. The variation in passage rates was not readily attributable to individual differences in rate of food passage, or to changes in rate with increased time after beads were fed.

Rates of food passage through three-toed sloths are thus so slow that they can be measured in days, whereas those rates for other herbivores are usually measured in hours. As measured by the rate at which glass beads passed through sloths, the rate of food flow through three-toed sloths is certainly the slowest recorded for a mammal, and is similar to or slower than the rate at which food passes through a tortoise (Parra, 1978). When converted for comparison, our measures of the rate of food passage indicate that 2 1/2 days would be required for passage of 5 percent of the markers and 50 days for passage of 95 percent of them. Comparable times for domestic cattle are 20 hours and 120 hours.

DIGESTIVE UTILIZATION OF LEAVES. We used the rate at which leaves of various tree species were digested (Table 15), and the rate at which glass beads passed through sloths (Table 16), to model the utilization of leaves of various kinds by the three-toed sloths. In our

Table 16.—Basis for estimating the rate of passage of food through three-toed sloths as 1.9 percent per day. Colored glass beads, 3 mm in diameter, were introduced into the stomachs of wild, radiomarked sloths. Feces passed by these sloths were recovered by radiolocating small radio-transmitters that had been inserted into the sloths' rectum, and which were passed when the sloth defecated about once every 8 days. Beads of each color in each fecal mass were recovered and counted. Daily rate of food passage was estimated by dividing the percent of the remaining beads recovered from each fecal mass by the number of days during which that fecal mass was accumulated by the sloth. T indicates the total number of beads of the color, and R indicates the number remaining.

Sloth number	*Days after beads were introduced*	*Cumulative total beads passed*		*Beads passed during defecation interval*		*Daily passage rate during defecation interval (% per day)*
		N/T	*%*	*N/R*	*%*	
247	6	4/50	8.0	4/50	8.0	1.33
225	6	4/59	6.8	4/59	6.8	1.13
225	7	1/40	2.5	1/40	2.5	0.36
243	8	8/80	10.0	8/80	10.0	1.25
244	8	10/80	12.5	10/80	12.5	1.56
243	10	2/80	2.5	2/80	2.5	0.25
225	12	6/16	37.5	6/16	37.5	3.12
225	13	8/40	20.0	7/39	17.9	2.99
243	17	25/80	31.2	17/72	23.6	2.62
243	19	18/80	22.5	16/78	20.5	2.28
243	24	31/80	38.7	6/55	10.9	1.56
243	26	38/80	47.5	20/62	32.2	4.61

model, we assumed (1) that each charge of leaf disappeared from the sloth's gut through an integrated combination of digestion and defecation and did not interact with the next charge of food, (2) that the rate of digestion and the rate of defecation remained constant during the entire time a charge of food remained in the animal, and (3) that the mean rate of 1.9 percent per day at which glass beads passed through sloths was a good estimator of the rate at which all leaf passed through the sloth.

When the rates at which old and young leaf from the same tree species are removed from a sloth's gut are compared (Figure 4), 2 advantages for the sloth in eating young leaf become apparent. First, the total time which is required for the gut to clear a significant portion of the leaf and make way for additional leaf intake is very much shorter for young leaf. In approximately 12 days, half the new leaf has left the sloth's gut through a combination of digestion and defecation, but nearly twice that long is required to clear the gut of a comparable amount of old leaf.

Second, and perhaps more important, the proportion of the leaf that is digested as opposed to passing on through the animal is considerably greater for young leaf. By the time that 50 percent of old *Cordia alliodora* leaf clears the sloth's gut, only 17 percent of the leaf has been digested. For new leaf, 32 percent of the leaf has been digested by the time 50 percent of it has cleared the gut.

The gain to a sloth from eating mature leaves of *Lacmellea panamensis* is considerable, but a sloth might put itself in danger of starvation by eating the relatively indigestible leaves of some species, such as *Hyeronima laxiflora* (Figure 5). The rate at which leaf clears the gut in three-toed sloths is very much lower than for other mammals (Parra, 1978), even for relatively digestible species. Approximately 8 days were required to clear the gut of 50 percent of *Lacmellea panamensis* leaf, but the sloth had digested 40 percent of the leaf in 8 days. By eating relatively digestible leaves, the sloth could maintain a flow of food and still digest a portion of the leaf intake.

By eating relatively indigestible leaf like the mature ones of *Hyeronima laxiflora,* a sloth might be in danger of starving with a full stomach because of low rates of food flow and because only a small portion of the food in the gut could be digested. Approximately 25 days were required to clear the gut of 50 percent of such leaf, and even then only 16 percent of it had been digested.

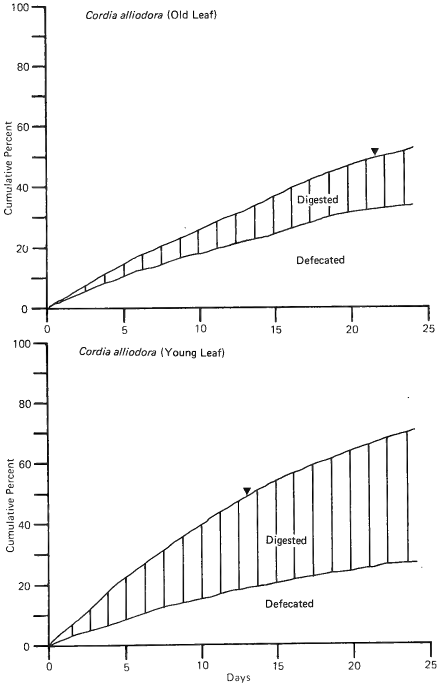

Figure 4. Contrast between the amounts of leaf which would be digested and defecated per unit time when a sloth ate old and young leaf of the same species. The time at which 50 percent of the leaf had been passed out of the gut through an integrated combination of digestion and defecation is indicated by the black arrow for each kind of leaf.

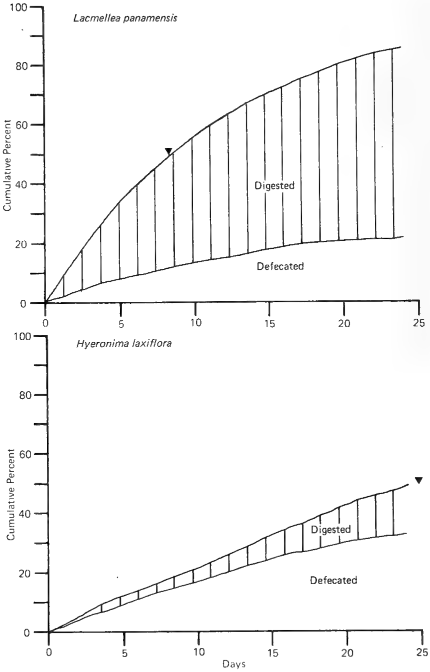

Figure 5. Contrast between the amounts of leaf which would be digested and defecated per unit time when a sloth ate relatively digestible old leaf of *Lacmellea panamensis* and when it ate relatively indigestible old leaf of *Hyeronima laxiflora*. The time at which 50 percent of the leaf had been passed out of the gut through an integrated combination of digestion and defecation is indicated by the black arrow for each kind of leaf.

CAPTIVE FEEDING EXPERIMENT. We attempted to maintain a young three-toed sloth on BCI, by feeding it a diet which alternated between old leaves of *Cecropia eximia* and old *Lacmellea panamensis* leaves. The lack of success we had in maintaining the animal in captivity illustrates the problems which a sloth or other arboreal folivore might face if it chose to feed from a tree with relatively indigestible leaves.

The sloth was a juvenile, approximately 8 months old on the basis of body size. It thus had probably been socially weaned about 2 months before we captured it (see following). Susan Smith fed and cared for the sloth in captivity. She fed the animal with a spoon 2 or 3 times per day, using leaf which had been dried, ground into meal, and rehydrated immediately before each feeding. The rehydrated leaf powder contained 70-80 percent water, and formed a viscous mixture suitable to being fed with a spoon.

We quantified the flow of food through the sloth by weighing the leaf which the animal ate at each feeding and by drying and weighing the feces. We also evaluated assimilation of the food by weighing the sloth before and after each time it fed.

The sloth readily adapted to being fed in this manner, and we were able to feed it to satiation throughout the experiment. Total daily food intake averaged 7.8 gm (SD 2.73 gm), and there was no correlation between the leaf species which was fed

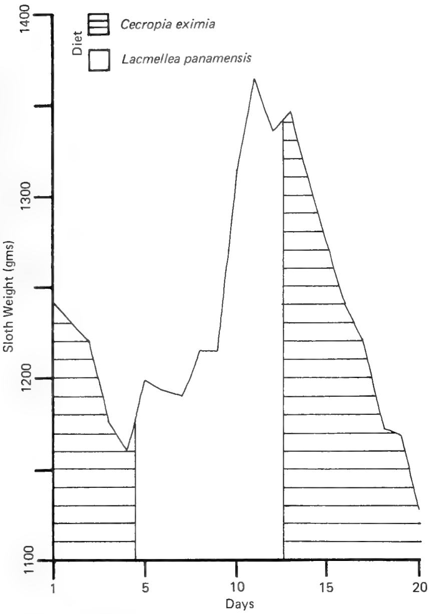

Figure 6. Changes in body weight of a young captive three-toed sloth fed on an alternating diet of powdered, rehydrated leaf of *Cecropia eximia* and *Lacmellea panamensis*. *Lacmellea* leaf was about 1.6 times as digestible as *Cecropia* leaf. The sloth died at the end of the experiment.

and the amount eaten. The difference between food input and feces outflow was greater when *Lacmellea* was fed, averaging 9.8 gm per day for Lacmellea leaf, and 4.9 for *Cecropia*; because of the small number of measures the difference was not significant. However, the difference may indicate that *Lacmellea* leaf was digested more completely than *Cecropia* leaf.

We began the experiment by feeding powdered old *Cecropia* leaf for the first 4 days (Figure 6). During this time, the sloth's weight decreased steadily, and it lost a total of about 100 gm (8 percent of its initial weight). We then changed the diet and maintained the sloth for the next 7 days on rehydrated *Lacmellea* leaf. The sloth steadily gained weight for a total of about 200 gm (approximately a 17-percent increase). We then again fed rehydrated *Cecropia* leaf, and continued to do so until the sloth died 7 days later. The animal lost almost 20 percent of its body weight, and at the end of the experiment weighed approximately 150 gm less than at the beginning of the experiment 20 days earlier.

During the time the sloth was fed *Cecropia eximia*, it was unable to gain sufficient energy to maintain its body weight, probably because the leaf material could only be digested slowly. *Lacmellea panamensis,* a more digestable leaf (Table 15), was probably digested at a higher rate, and the animal was able to extract enough energy to grow. While the sloth was fed *Cecropia* during the 7 days before it died, it could not extract sufficient energy from the food to maintain body weight. It died, probably of starvation, because we fed it leaf from the wrong species of tree.

SOCIAL INFLUENCES ON SELECTION OF TREES. Sloths of both species were usually solitary, except for mothers and their dependent young (see following), and males and females when they met briefly for breeding (Beebe, 1926; Montgomery and Sunquist, 1975). The home range spaces of sloths of the same and of different species overlapped and some sloths used the same trees, although usually at different times. We radiolocated two-toed and three-toed sloths in the same tree at the same time, on rare occasions, but only very rarely found sloths of the same species in a tree on the same date.

It is probable that adult sloths had little influence on the choice of trees made by other adult sloths which lived in the same area of the forest. Most sloths of both species regularly changed from tree to tree, with two-toed sloths changing trees on about 90 percent of successive dates, and three-toed sloths changing on about 60 percent of them (Sunquist and Montgomery, 1973). Most sloths visited even their modal tree irregularly, and behavioral exclusion of other sloths would have been difficult. For example, three-toed sloth number 202 was absent from her modal tree for at least 33 days during a period while we radiolocated her daily, and three-toed sloth number 208 was absent from her modal tree for at least 23 days at a time. A sloth was usually in its modal tree less than 20 percent of the time (Montgomery and Sunquist, 1975), and most of the trees which it used were used for only 1 or 2 days during the study. There remains the possibility that it was not necessary to exclude other sloths because the tree was only suitable for use, as a food source or otherwise, when the sloth was there. This does not seem possible because the nontaxonomic attributes of the tree probably did not change significantly, except perhaps with a change in season or otherwise when deciduous plants lost their leaves, during the interval between visits which the sloth made to the tree. Also, the modal tree species was usually represented on a sloth's home range space by several individuals and the sloth could not use all of them simultaneously. Furthermore, in order for a sloth to use trees only when they were suitable for use, as for example when they had leaves which were edible, would have required the sloth to monitor all of the potential trees on its home range space, and program its movements in such a way as to be in certain trees when they were suitable for use. Such a strategy of continual monitoring of potentially usable habitat resources (Montgomery and Lubin, 1977) might occur in more mobile species, such as howler monkeys on BCI (Milton, 1978). Three-toed sloths did not move about in a way which would have provided the information necessary to choose among all trees on their home range space for each move which they made.

It thus seems unlikely that the set of trees which one sloth used were not used by other sloths because they were not inherently suitable. It remains possible, however, that suitability of a tree with particular reference to the digestibility of its leaves, was characteristic for an individual sloth and did not apply to all sloths which might have used the trees.

The major social influence on the selection of trees by three-toed sloths was through the social inheritance of species preferences and home range space, which occurred when each young sloth was socially weaned by its mother. Each mother three-toed sloth gave her young the opportunity to learn which trees to use, and may have influenced the tree species preferences of the young. At the time of social weaning, she left the portion of the home range space where she had reared her young, and moved to a different portion of the forest. She thus reduced competition for food for her young in 2 ways. Because the tree species preferences of each three-toed sloth tended to be unique, she may have reduced competition with other three-toed sloths living in the same area by giving her own species preferences to her young, and in moving away from the area she reduced the competition which would have resulted between mother and young had she remained on the area where the young was reared.

One adult female three-toed sloth was captured while pregnant, and 3 others while each was carrying a small young on her chest. These females were radiomarked and located regularly while each carried its young about, and until after each of the young became socially independent of its mother. We also radiomarked each of the 4 young before it became independent, and radiolocated it regularly until after it was separated from its mother. When we captured a young sloth which was still with its mother, we estimated its age by comparing its body size to a growth curve plotted from measurements of young sloths of known age.

Each adult female three-toed sloth was usually either pregnant or carrying a young on her chest, as indicated by repeated captures and examination of a total of 11 radiomarked adult females. The gestation period of the three-toed sloth was estimated as 4-6 months on the basis of sizes of embryos (Wislocki, 1927), and our data indicate that it lasts for 5-6 months. For 6 radiomarked females, reproduction occurred at approximately yearly intervals. Two females were known to be pregnant or to have given birth at about the same time of year in 4 successive years, 1 female in 3 successive years, and another reared young during the same season in 2 successive years. For each female, pregnancy and birth took place during the same months of the year, with about 6 months devoted to each pregnancy and the following 6 months to rearing the single young (Figure 7).

Young three-toed sloths were nutritionally weaned and had ceased to nurse by the time they were 3 to 4

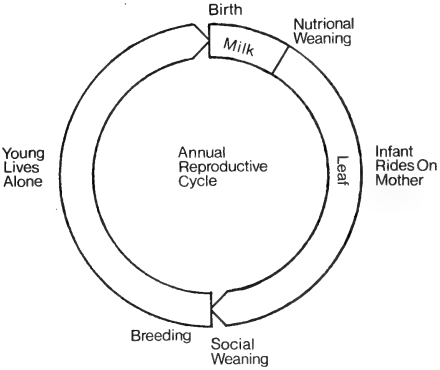

Figure 7. Schematic summary of the relationship between a mother three-toed sloth and her young during the annual reproductive cycle. The young feeds on leaf which it can reach within a radius of its body length from the mother, until it is about 6 months old; the mother carries the infant at all times. After social weaning, the young remains on the portion of the mother's home range space which she used while carrying the young about, but the mother goes to another part of the forest and remains there for 6 months while she is pregnant. Young sloths socially inherit both trees on the mother's home range space and tree species preferences. This social system is the basis for minimizing competition among the three-toed sloths which live in an area, while maximizing competition with other arboreal folivores.

weeks old. Three-toed sloths less than 2 weeks old were seen nursing, and milk could be expressed from the nipples of 3 females until each of their young was about 3 weeks old. We could not express milk from the nipples of 12 mother sloths whose young were more than 4-6 weeks old, and the nipples had lost the appearance of being suckled.

Young three-toed sloths began feeding on leaves before they were nutritionally weaned. Three-toed sloths 2 weeks of age and older were seen eating leaves, including both fragments of leaf which were on the mother's lips and leaves of trees from which the mother was feeding. Beebe (1926) described young three-toed sloths clawing at their mother's mouth until it opened and then licking at bits of leaf which were there. He felt that the mother regurgitated partly digested leaves for the young.

After a young three-toed sloth was nutritionally weaned, it continued to depend on its mother for mobility for an additional 5 months (Figure 7). During the 6 months while the mother carried her young about, she made all choices in location of the mother-young pair. These choices of location included the individual trees, the tree species, and the portion of the plants which both mother and young used for feeding, resting, and all other activities. While the mother fed on leaves, the young usually also fed on leaves near the mother. Presumably, those leaves were from the same species of plant as were chosen by the mother as food. While feeding, the young maintained physical contact with the mother, holding into her coat with at least 1 foot. Feeding by the young was thus restricted to plant parts which were within a radius of about 30 cm of the mother's body. During the 6-month period while the young was carried by its mother, the young learned both food preferences and the locations of trees where it could obtain the leaves that it used as food.

After a mother had carried her young for about 6 months, she abruptly left it. The continued separation of mother and young from that time on constituted social weaning. In all 4 cases where we radiolocated both mothers and their young, the mother left her young in a tree and continued to move away from it for 2 weeks or more, while the young remained in or near that tree for at least 5 days. After remaining in or near the last tree which it shared with its mother, the young began to move from tree to tree. As it moved, the young gradually expanded its range of movements into the area which had been used by the mother and young before social weaning. During this time, the mother moved away and used a different part of the forest than she had used while carrying her young.

Each independent young remained in the portion of the forest in which it was reared, used many of the same trees which its mother had used, and used primarily the same tree species to which it had been exposed before social weaning. We did not radiolocate either mother sloths or independent young every day, and thus probably did not know about every tree used by the animals. In spite of this lack of data, 3 of the independent young were each radiolocated more than 58 percent of the time in trees which we knew the mother had used while carrying her young (Table 12). In total, more than 40 percent of radiolocations of independent young were in trees which their mothers had used prior to social weaning. Fewer than 10 percent of trees in which the young sloths were located after social weaning were more than 20 m from the nearest tree in which we had radiolocated the young while it was with its mother. By contrast, fewer than 5 percent of all 137 radiolocations of the 4 mother sloths after they socially weaned their young were in trees where we had radiolocated them while they carried their young. More than 80 percent of the trees in which they were found after leaving their young were 50 m or more from the nearest tree in which they were radiolocated while carrying their young. Of the trees chosen by each of the 4 young three-toed sloths after social weaning, most were of species in which the mother and young had been radiolocated. More than 60 percent of the radiolocations of each of the 4 independent young were in trees of species which had been used by their mothers while carrying them about (Table 17).

As indicated, three-toed sloths, when considered as a species rather than as individuals, were generalists in terms of the large number of tree species they used. As individuals, however, each of them specialized on a few species, and the species on which each individual specialized differed from sloth to sloth even when the animals lived in the same part of the forest.

The social inheritance of home range space, and particularly of tree species preferences, described earlier, indicates the mechanism by which these individual specializations on a few tree species were maintained in the population. The preference for each set of tree species is passed down from generation to generation through each mother sloth to her young, thus each genealogy of three-toed sloths tends to have a different set of tree species preferences from other genealogies of sloth which live in the same area. High rates of mortality of newly independent young, combined with long-distance dispersal of the young males which survive, act to reduce the probability that a young sloth will be brought into competition

Table 17.—**The influence that locations used by mother sloths and their choice of tree species had on the trees and tree species used by young three-toed sloths after they became socially independent of their mothers. The 4 mother sloths were radiolocated on a total of 263 of the 418 dates, or 63 percent of the time while they each carried a young. After the young were socially weaned, they were radiolocated a total of 131 of the 296 dates when they were available (44 percent). For the young sloths after social weaning, the percent of the trees and tree species used that had been used by the mother and young before social weaning is shown.**

Before social weaning (mother and young)				*After social weaning (young only)*					
					Trees used		*Species used*		
Mother's number	*Radio-locations/ dates*	*Total trees*	*Total species*	*Radio-locations/ dates*	*Total trees*	*Percent used before SW*	*Total species*	*Percent used before SW*	*Percent of locations in species used before SW*
208	121/161	25	20	15/29[1]	2	100	2	100	100
219	69/139	24	18	16/27[2]	6	6	6	67	62
227	30/63	11	10	60/143[3]	11	7	9	55	85
231	43/55	20	17	40/97[4]	14	50	14	64	82

[1] Young died 35 days after social weaning.

[2] Young survived at least 27 days after social weaning, then died within 5 months.

[3] Young survived at least 18 months after social weaning.

[4] Young died 97 days after social weaning.

with its older siblings, or that the mother sloth will compete with it when she returns to that portion of the forest to rear her next young. Obviously, one of the female young born to a three-toed sloth must survive and remain on the home range space if the genealogy is to maintain itself in a particular area, and if the tree species preferences are to be maintained.

Competition between the mother and her newly independent young is reduced when the mother leaves the portion of the forest where she reared the young, and while she lives in the other portion of the forest during the next 6 months. The mother thus uses a different set of trees for rearing her young than she does when the young are independent of her.

The young female which survives and ages probably increases the total number of trees which she uses, until her home range space is as large as the mother's home range space and perhaps contains as many trees as the mother's space. The mother's home range space must have included enough trees in 2 separate portions to provide space for rearing the young during part of each year and being away from it during the other part of each year, and the young female will eventually have the same space requirements. It is tempting to suppose that the young female will in turn rear her young in the portion of her home range space which she inherited, and use the portion of the home range space which she develops after social weaning as the place to go when each of her own young becomes independent.

During the expansion of her home range space, the young female probably chooses trees that are of species which were used by her mother, and thus species which the young animal prefers to use.

We can reconstruct the mechanism by which social inheritance of home range space and species preferences can act to give sloths of each genealogy different tree species preferences even though they share the same areas of the forest. The selective forces which drive such a system are not apparent, however. We speculated elsewhere (Montgomery and Sunquist, 1975) that a part of the life history strategy of the three-toed sloth was to maintain higher population densities in order to remain both cryptic and sedentary but still maximize opportunities to meet for mating.

A corollary of the tendency for each sloth to use a different set of trees and tree species, even though home range spaces overlapped, is that competition between sloths for food and living space is minimized, while competition between sloths and other leaf-eating, arboreal animals is maximized. Other things being equal, we might expect that three-toed sloth population densities would increase at the expense of the other animals. Even if the sloths did not compete with other species and affect their population densities, an unlikely event, sloth population densities should be maximized in a system where competition between sloths is decreased. Three-toed sloth population density should increase up to some limit which would approach the maximum cropping rate which all or most of the trees with edible leaves in an area could sustain, almost regardless of the species composition of the forest in which the sloths lived. Under such a system sloth population density might be higher in more tree-species-rich forests and lower in forests with fewer tree species, because the tree species-poor forest would not allow for the packing in of so many sloth genealogies.

To date, sloths have been censused in only 2 forests, both in central Panama. The forest on BCI was relatively tree species-rich and had about 8.5 three-toed sloths per ha (Montgomery and Sunquist, 1975). The other forest, a tract of mature premontane rain forest at about 1000 m elevation on Cerro Azul, approximately 50 km from BCI, had a different tree species composition, but was also comparatively tree species-rich. We estimated that there were 6 to 7 three-toed sloths per ha there (Montgomery and Seymour, in preparation), using the same census technique which we developed on BCI. The three-toed sloth populations in the 2 areas were not demonstratively different in either composition or density. A census of sloths in a tree species-poor habitat needs to be done.

Three-toed sloths can live at high population densities and use a very wide range of tree species because their social system allows packing of individuals of different sloth genealogies into environments rich in tree species. Three-toed sloths should be able to out-compete other vertebrate folivores which attempt to share the food resources of such an environment. If those potential vertebrate competitors have sharply defined preferences for a few tree species, then one or more sloths might use individuals of those tree species in each part of the specialist's home range space, and feed there while the specialist is absent. A specialist vertebrate folivore in a tropical forest environment rich in tree species must have a large home range space in order to include enough individuals of its preferred species to insure an adequate supply of the resource which they represent. Furthermore, the folivore must defend its resources against others of the same species which might invade the home range space and deplete the resource. Population densities of the specialists would thus tend to be low, relative to the population densities which three-toed sloths can maintain by being generalists with very reduced intraspecific competition. A vertebrate arboreal folivore with more general food or species preferences which attempts to compete with three-toed sloths would be at a disadvantage because it would need to compete with sloths of many genealogies, each of which might compete with it for one or more of the tree species it tried to use. The generalist might bring more competitive pressure to bear on sloths of 1 or a few genealogies, but in so doing would tend to become a specialist. In addition, most of the vertebrate arboreal folivores which have been studied are group-living primates which defend their home range space against others of their species, and the other, more solitary forms such as the koala (see Eberhard, 1978) are in obvious intraspecific competition for food or living space. A species which has evolved a means for reducing intraspecific competition will have an advantage in interspecific competition with a species which attempts to use the same resource, because it can reach higher population densities with the same resource base.

Those generalist vertebrate folivores which are sympatric with sloths are characterized by including fruit as a major part of their diet, or including fruit as well as leaves. Howler monkeys probably eat about equal amounts of leaf and fruit (Milton, 1978), while captive two-toed sloths and porcupines (*Coendou*) are regularly fed fruit as a part of their diet (Merritt, 1976; Crandall, 1964). Iguanas include food in their diet, but are probably able to digest mature leaves as well (Rand, 1978). Because iguanas are able to utilize the leaves of many tree species, they probably represent the major competitor for the three-toed sloth. However, they lack a social system of the type which would reduce intraspecific competition.

If three-toed sloths respond to environments which are low in tree species diversity by showing lowered packing of individuals because fewer genealogies can be accommodated, and thus have lower population densities, other vertebrate arboreal folivores might show increases in population density because the competition with sloths is reduced, or might show a shift to more folivorous food habits. Thus, animals like howler monkeys and iguanas may live at higher population densities and eat more leaves in habitats which are poor in tree species diversity and which have low populations of three-toed sloths.

It has been proposed that the lack of radiation of New World primates and other mammals into the arboreal folivore niche was because the edentates occupied the niche early, and were successful in preventing representatives of other groups from occupying the niche (Eisenberg and McKay, 1974; Eisenberg and Thorington, 1973). The social system which we describe above for the three-toed sloth, and its effect on the generality in tree species use and on maximizing sloth population density in the face of competition, may help to explain the mechanism by which the edentates prevented other arboreal folivores from evolving.

Summary

This paper describes and characterizes the kinds of habitat which radiomarked two-toed and three-toed sloths selected on Barro Colorado island, Panama Canal zone. Habitat selection by the sloths was evidenced by the choices which individual radiomarked animals made from among the large number of trees of many species and diverse growth forms which grew on each sloth's home range space. In any small area of forest on BCI, a sloth had available to it a very large number of tree species from which to choose. These trees showed a range of nontaxonomic attributes such as crown size as well, and trees with various attributes were likewise interspersed. Home range spaces of sloths were usually less than 2 ha in total area, and we radiolocated some individual three-toed sloths in 50 or more trees of 30 or more species.

Sloths probably avoided using tree species when individuals of those species were rare in the forest. Sloths differentially used tree species which grew on the study area at moderate to high densities.

Three-toed sloths, when considered as a species, were generalists with respect to the large number of tree species which they used. Three-toed sloths were radiolocated in 40 of 91 tree species which grew on 2 sample areas. The apparent statistical selection of tree species by three-toed sloths as a whole resulted from the selection of only a few of the trees by individual sloths. There were no apparent general preferences for the same tree species by most three-toed sloths.

Liana species diversity was very high, and most lianas of a species were found in only 1 of the crowns of trees which we sampled. We sampled 39 trees, of which 11 had no lianas in their crowns; the remaining 28 trees contained a total of 55 liana species. Habitat selection by three-toed sloths on the basis of presence or absence of a particular liana species was unlikely.

Radiomarked sloths of the 2 species tended to use trees which were similar with respect to nontaxonomic attributes, and about 20 percent of the trees used by three-toed sloths were also used by two-toed sloths. Three-toed sloths tended to choose trees more for the degree to which the tree crown was exposed to sunlight, while two-toed sloths tended to choose trees with masses of lianas in their crowns. Three-toed sloths may have attempted to maximize 3 nontaxonomic attributes in the following order of importance: exposure of the crown to sunlight, mass of lianas in the crown, and size of the tree crown. Two-toed sloths maximized the mass of lianas and exposure of the tree crown to sunlight.

The tendency of three-toed sloths to use trees with crowns exposed to sunlight was related in part to the vertical movements which the animals made in the forest canopy into and out of direct sunlight as their body temperature changed. Deep body temperatures of free-living sloths fluctuated on a daily basis, with maximum temperatures on each date usually occurring at midday and minimum temperatures between midnight and dawn. Maximum sloth body temperatures were lower on days when it rained and was cloudy. Three-toed sloths behaviorally thermoregulated by moving in the canopy to places where the light intensity at their body surface was increased when they were cold and decreased when they were warm and their temperature was still rising.

A three-toed sloth probably ran the risk of starvation if it encountered several days in a row when sunlight intensity was reduced at midday, particularly when it rained during the morning. This was because the overall rate at which food passed through the sloth's gut probably depended in part on the sloth's body temperature, which in turn depended on the amount of sunlight which reached the animal.

Based on rates of digestion measured in free-living sloths which had been fitted with gastric fistulas, young leaves were digested at the highest rates, and older leaves which were digested fastest tended to be from tree species which ranked highest in use by some sloths. Rates of digestion of all leaves by sloths were much lower than rates at which other herbivorous mammals digest their food. The differential use of tree species shown by the sloths may have been related in part to the relatively high digestibility of mature leaves of some rare trees such as *Lacmellea panamensis*, and perhaps to the seasonal presence of digestible young leaves on trees whose mature leaves were relatively indigestible (*Hyeronima laxiflora*), or the more constantly available leaves which were of moderate digestibility (*Cecropia eximia*).

We estimated the rate at which food passed through three-toed sloths by measuring the rate at which colored glass beads fed to wild sloths passed through the animals and appeared in their feces. Rates of food passage through three-toed sloths were so slow that they were measured in days, whereas those rates for other herbivores are usually measured in hours. Approximately 50 days would have been required for the passage of 95 percent of markers.

We used the rates at which the leaves of various tree species were digested, and the rate at which glass

beads passed through sloths, to model the utilization of leaves of various kinds by three-toed sloths. There were 2 advantages for a sloth in eating young leaf. First, the total time which was required for the gut to clear a significant portion of the leaf and make way for additional leaf intake was very much shortened when compared with the time for old leaf to clear the gut. Second, and perhaps more important, the proportion of the leaf that was digested as opposed to passing on through the gut and leaving the animal as feces was considerably greater for young leaf. By eating relatively indigestible leaf, a sloth might be in danger of starving with a full stomach because of low rates of food flow and because only a small portion of the food in the gut could be digested.

An adult sloth had little apparent social influence on habitat selection by other sloths which overlapped its home range space. The major social influence on the selection of trees by three-toed sloths was through the social inheritance of home range space and tree species preferences which occurred when each mother sloth gave her young the opportunity to learn which trees to use and influenced the tree species preferences. At the time of social weaning, she left a portion of her home range space to the young and moved to a different part of the forest from where it had been reared; the young used many of the same trees which the mother had used, and fed on primarily the same tree species to which it had been exposed before social weaning.

The social inheritance of home range space, and particularly of tree species preferences, indicates the mechanism by which these individual specializations on a few tree species were maintained in the population. The preference for each set of tree species is passed down from generation to generation through the pathway mother to daughter, thus each genealogy of three-toed sloths tends to have a different set of tree species preferences from other genealogies of sloth which live in the same area.

A corollary of the tendency for each sloth to use a different set of trees and tree species, even though home range spaces overlap, is that competition between sloths for food and living space is minimized while competition between sloths and other arboreal folivores is maximized. Sloth population density might be higher in a more tree species-rich forest and lower in a forest with few tree species, because the forest with few tree species would not allow for packing in of so many sloth genealogies.

The social system which we describe for three-toed sloths can act to maximize sloth population density, and may have been a major factor in the success of sloths in competing with other potential arboreal folivores. This may help to explain why an edentate has been so successful as the arboreal folivore in the neotropics, whereas several species of primates occupy the same or a similar niche in the Old World tropics.

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Comparative Morphology, Food Habits, and Ecology of Some Malaysian Arboreal Rodents

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Introduction

Note:

In conducting the research described in this report, the investigators adhered to the "Guide for Laboratory Animal Facilities and Care," as promulgated by the Committee on the Guide for Laboratory Animal Resources, National Academy of Sciences, National Research Council. The opinions or assertions contained herein are the private views of the authors and are not to be construed as official or as reflecting the views of the Department of the Army or the Department of Defense.

Peninsular Malaysia has a land area about the size of Florida. Habitats vary from primary rain forests, with their more than 2000 species of trees (Corner, 1951), to essentially monocultures of rice fields, oil palm, or rubber estates. Forests are represented in various stages of succession as a result of selective timbering or clear cutting. Although the primary forest probably will not quickly regenerate to its original form, selective cutting rather than clear cutting retains most nearly the original physiognomy of the forest. Selective timbering usually eliminates the slow-growing hardwoods. When clear cutting is done, the fast-growing trees first become prevalent. Depending on how extensive the clear cutting was, the forest may never regenerate to its original species structure. Even primary rain forests, however, differ greatly from one area to another. In some areas, primary growth is very high, with emergent trees over 60 m and a few 65 m or more. Other forests, especially at the higher elevations, are not so tall.

Very little primary forest remains in Malaysia, particularly in the lowlands. Before World War II, it was estimated that 70–80 percent of the peninsula was covered by primary forest (Wyatt-Smith, 1954). Forests which represent mixtures of original flora and secondary growth are still very prevalent as a result of the government-regulated "forest reserve" system which permits only partial timbering of areas designated as forest reserves.

Review of Malaysian Mammals

Many of the 200 species of mammals known to occur on peninsular Malaysia are dependent on the forest. Various species respond in different ways to alterations of the forest habitat. Cutting of the forest appears to reduce the population sizes of some species and to enhance those of others. This phenomenon will be demonstrated later with various species of flying squirrels.

A brief survey (Medway, 1969) of the fauna of the peninsula reveals that of the nonvolant species, 9 are primates, including 3 species of langurs, 3 macaques, and 3 gibbons. Four species of "primitive primates" occur along with 12 species of tree squirrels, 2 ground squirrels, and 11 flying squirrels. There are 26 species of rats and 3 porcupines. Carnivores include 2 mustelids, 3 otters, 11 civets, 5 mongoose (including *H. urva*, not recorded by Medway), 7 cats, a bear, and a dog. Four deer, a goat, 2 species of wild oxen, a tapir, an elephant, 2 pigs, and 2 species of rhinoceros comprise the grazers and browsers. Insectivores number 7 species. There are a few specialized species such as the scaly anteater (*Manis*) and the flying lemur (*Cynocephalus*) (which neither flies nor is a lemur; it glides and is not closely related to any other group of mammals). The goat (*Capricornis*), 3 of the squirrels, (*Tamiops, Dremomys, Callosciurus flavimanus*), 3 of the rats (*Rattus fulvescens, R. inas, R. edwardsii*), and the mole *Talpa* appear to be confined to the highlands (above 1000 m), although many of the lowland species also occur in the highlands. Eight species of rats (*Mus musculus, Rattus rattus, R. exulans, R. tiomanicus, R. norvegicus, R. argentiventer, Bandicota indica, B. bengalensis*), the house shrew (*Suncus*), and 1 mongoose (*Herpestes auropunctatus*) appear to be more recently introduced than other species (Harrison and Quah, 1962). Except for the exotics, most of the mammals are forest species.

Of the lowland forest species, 42 can be considered arboreal. These include mainly squirrels (all but *Rhinosciurus* and *Lariscus*), the flying squirrels, 3 rats (*Chiropodomys, Hapalomys, Pithechir*), the tree shrews, the slow loris, the "flying lemur," the marten, and 4 of the civets (*Prinodon, Paradoxurus, Arctogalidia, Arctictis*). Many of the terrestrial rats, cats, civets, and the bear are actually more or less scansorial.

Table 1 summarizes various classifications of the mammals of Malaysia. Of the arboreal species only 1, *Martes*, is a strict carnivore. The macaques, gibbons, tree shrews, slow loris, some of the civets, *Pithechir, Chiropodomys, Hylopetes* (2 sp.), and perhaps some of the other flying squirrels or tree squirrels are omnivores. The langurs and *Cynocephalus* seem to be obligatory folivores. Some of the flying squirrels, *Petaurista* (2 sp.) *Aeromys, Pteromyscus*

Table 1.—Various classifications of Malaysian mammals.

	Number of species	*Percent*
Bats	82	41
Canopy	44	22
Ground and Aquatic	74	37
Total	200	100
Canopy Species (Including 2 Highland Squirrels)		
Carnivores	1	2
Omnivores (Class* 1)	14	32
Herbivores/Frugivores/Some Insects (Class 2)	4	9
Herbivores/Frugivores (Class 3)	17	39
Folivores (not obligate) (Class 4)	4	9
Folivores (Class 5)	4	9
Total	44	100
	Malaysia	*Worldwide**
Arboreal Herbivores	15%	(4%)
Arboreal	22%	(4%)
Percent Herbivorous among Arboreal	45%	(16%)
Percent Arboreal among Herbivores	66%	(19%)

*Based on mammalian genera (see Eisenberg, 1978).

can subsist on leaves although they eat fruits when they are available.

From this brief overview it is apparent that the arboreal component of the mammalian fauna is very significant in Malaysia. The bats were not considered in this analysis because none of them are folivores. Yet they comprise nearly half of the mammalian species and most of them occupy arboreal roosts. Moreover, some are frugivorous and probably compete heavily with the arboreal herbivorous/frugivorous rodents. We have seen encounters between one of the most common fruit bats, *Cynopterus,* and one of the most common flying squirrels, *Iomys,* while both were feeding in fruit trees (figs) at night. Curiously, the alarm calls of *Cynopterus* and *Iomys* are nearly identical, a sort of 2-note bugling. It is tempting to speculate on the survival value of this convergent call in these markedly unrelated mammals, which appear often to share feeding sites at the same time.

Of the nonvolant species in Malaysia, about 36 percent are arboreal; 15 percent are both arboreal and herbivorous. Of all the herbivore species, about half are arboreal and of the arboreal species about two-thirds are herbivorous. This stresses how important these modes of life are among the mammals of Malaysia and probably reflects the history of prevalence of forests in the area.

The Flying Squirrels

No mammals in Malaysia are more dependent on an arboreal mode of life than the flying squirrels, with the possible exception of the "flying lemur," *Cynocephalus.* Flying squirrels are difficult to trap, partly, perhaps, because of their arboreal habits. Among approximately 100,000 mammals trapped by the Institute for Medical Research in Malaysia since 1948, only a dozen or so were flying squirrels. Most of the trapping was done on the ground or low in the vegetation. The majority of the flying squirrels trapped were in traps placed on trees. The sparse trapping record led mammalogists to believe these species were rare. Later, collections were made by capturing animals in their arboreal nest cavities (Muul and Lim, 1971). These collections indicated that most of the flying squirrels, at least, were quite common but not predisposed to entering traps. Continued collecting throughout Malaysia has given us a great deal of new information about the biology of flying squirrels, particularly in those areas in which intensive collecting was done. The areas were chosen for intensive collecting because they were destined to be deforested for agricultural purposes, and our collectors worked ahead of the woodcutters. In one such area in the state of Johore over 2000 flying squirrels were collected.

Degree of folivory

The flying squirrel group serves well for the purpose of comparing various degrees of herbivory or folivory, since among the 11 species occurring on the peninsula nearly all classes, as defined by Eisenberg (1978), are represented (Table 2).

While peninsular Malaysia has an abundance of species of flying squirrels, additional species are found in Sumatra and Borneo. Two smaller species of *Petaurillus* occur in Sarawak (Chasen, 1940); a large *Petinomys (hageni)* occurs on Borneo (Medway, 1965), Java, and Sumatra (Chasen, 1940), and a medium-sized *Petinomys* in Sumatra and Java (perhaps also in Borneo); *Aeromys thomasi* occurs on Borneo (Medway, 1965). Thus, Borneo has the most diverse flying squirrel fauna—14 species—and lacks only 1 species occurring elsewhere in the archipelago, *Petinomys* (misidentified as *Hylopetes* by Chasen, 1940) *sipora* of Sumatra. Java has the fewest number (6) of species of flying squirrels, perhaps because it is nearly entirely deforested, having had a long history of intensive agriculture. Conversely, Borneo is the least disturbed area (until just recently) with the most extensive tracts of uninterrupted forest anywhere in Southeast Asia. Not much is known about

Table 2.—Comparison of various degrees of herbivory or folivory among the 11 species of flying squirrels occurring on peninsular Malaysia. (Classes as defined by Eisenberg, 1978.)

	Class					
Species	*1*		*2*	*3*	*4*	*5*
Petaurillus	X	or	X			
Iomys	X	or	X			
Petinomys setosus	X	or	X			
P. vordermanni	X	or	X			
Hylopetes lepidus				X		
H. platyurus				X		
Petinomys genibarbis				X		
Pteromyscus pulverulentus				X		
Aeromys tephromelas				X		
Petaurista petaurista					X	
Petaurista elegans					X	

Table 3.—Species of flying squirrels found in the archipelago arranged according to size and degree of herbivory. Matrix denotes classes of herbivory (see Eisenberg, 1978)

	Size of classes by head and body length in mm										
Species	*Less than 80*	*80–90*	*90–100*	*100–110*	*110–140*	*140–170*	*170–200*	*200–240*	*240–300*	*300–400*	*Over 400*
Petaurillus hosei	1 or 2										
P. emiliae	1 or 2										
P. kinlochii		1 or 2									
Petinomys setosus			1 or 2								
P. vordermanni			1 or 2								
Hylopetes platyurus				3	3						
H. lepidus					3	3					
Iomys horsfieldii						1 or 2					
Petinomys genibarbis						3					
Pteromyscus pulverulentus								3			
Petinomys hageni								3			
Aeromys thomasi									3		
Petaurista elegans										4	
Aeromys tephromelas											3
Petaurista petaurista											4

the biology of the Bornean flying squirrels, but we could provisionally classify *Petaurillus emiliae* and *P. hosei*, both pigmy flying squirrels, in Class 1 or 2. *Petinomys hageni* and *Aeromys thomasi* are probably Class 3.

In Table 3 the species of flying squirrels found in the archipelago are arranged according to size and degree of herbivory. The smaller sized species tend to be less herbivorous and the largest are the most herbivorous.

Farther north from the Sunda region additional species are found, but little is known of their biology. The genus *Petaurista* is the most widespread and occurs from Kashmir through India, Sri Lanka, Burma, China, Thailand, Indochina, and Formosa. To the north this genus occurs in Korea and Japan. All of the species are large, exceeding 400 or 500 mm head and body length. All of the species seem to be in Class 4, as is *Aeretes* of China. In Thailand, 2 additional *Hylopetes* are found and are probably Class 3. *Eoglaucomys* of Kashmir and *Petinomys fuscocapillus* of Sri Lanka are probably Class 3. *Belomys* of Thailand has teeth similar to that of the larger *Trogopterus* farther north, but nothing is known of their diets. This leaves only the large *Hylopetes nigripes* of Palawan and the large *Petinomys* of Mindanao. Little is known about either. In Afganistan and Kashmir the large *Eupetaurus* occurs, but is known only from a few skins and only 2 skulls. The teeth in *Eupetaurus* are nearly hypsodont and the molars are not unlike those of beavers.

Digestive tract

We have internal morphological data only for flying squirrels occurring on peninsular Malaysia (Figures 1 through 7). Table 4 includes species in which cecal length has been measured. The length of the cecum correlates well with the type of diet. Excluded from Table 4, but appearing in Figure 7, is *Petinomys genibarbis*. Nothing is known of its diet in the wild state. It has a cecum approximately 140 mm in length, and on the basis of this we have placed it in Class 3 (Table 2).

In *Petaurista*, the most folivorous genus, the abdominal cavity is long, approximately 2/3 or 3/4 of the total body length. The long cecum is thrice folded upon itself and the large intestine is also very long. The intestinal wall is thin.

In addition to the long cecum, the 2 species of *Petaurista* have cheek teeth which are usually worn flat, with cingula and rings of enamel that form complex designs in the surface depending on the amount of wear. No cusps, as such, are present. Such flat teeth probably result from grinding action

Table 4.—Comparison of cecal lengths in various species of flying squirrels and correlation with type of diet.

Species	*Cecal length (mm)*	*Class*	*Diet*
Petinomys setosus	5	1 or 2	seeds & fruit
Petinomys vordermanni	4	1 or 2	seeds & fruit
Iomys horsfieldii	15	1 or 2	fruit & seeds
**Hylopetes platyurus*	70	3	seeds, fruit, leaves, insects
**H. lepidus*	86–120	3	seeds, fruit, leaves, insects
Pteromyscus	140	3	seeds, fruit, leaves
Petaurista	over 250	4	leaves, fruit, seeds

*See Muul and Lim, 1971.

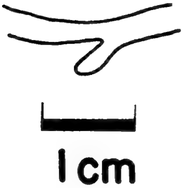

Figure 1. Cecum of *Petinomys setosus.*

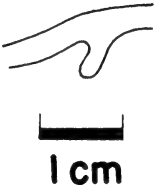

Figure 2. Cecum of *Petinomys vordermanni.*

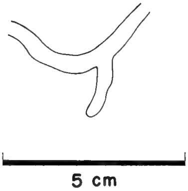

Figure 3. Cecum of *Iomys horsfieldii.*

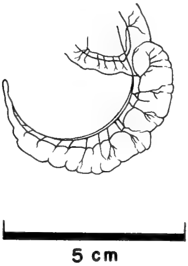

Figure 4. Cecum of *Hylopetes platyurus.*

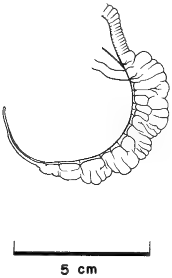

Figure 5. Cecum of *Hylopetes lepidus.*

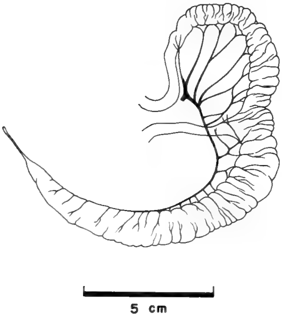

Figure 6. Cecum of *Pteromyscus pulverulentus.*

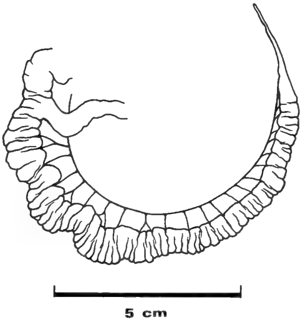

Figure 7. Cecum of *Petinomys genibarbis.*

and attest further to a herbivorous diet. The other large species, *Aeromys tephromelas,* has smaller, more cuspidate teeth. *Aeromys thomasi* has nearly flat teeth, something between those of *Aeromys tephromelas* and *Petaurista.*

The smaller squirrels have typical sciurid, cuspidate teeth, although in most of the species the cheek teeth are more complex and more varied among species than among the Sciurinae. There do not appear to be any obvious correlations between tooth structure and diets, except in *Petaurista* and *Aeromys thomasi. Pteromyscus,* for example, has a fairly large cecum (about 140 mm) but quite complex teeth, which are used to chew leaves and also fruits and seeds. In the rest of the species the teeth function mainly in a "mortar and pestle" fashion. Such teeth are fairly generalized and occur in nearly all of the Sciuridae. On a worldwide basis, *Belomys* in Thailand, and *Trogopterus* farther north, have very complex teeth, but nothing is known of the significance of their structure.

In most species the incisors are well developed. However, the small *Petinomys setosus* and medium-sized *Pteromyscus* often have blunt lower incisors. Captive *P. setosus* placed hard, shelled nuts into their water dish for a few days before attempting to open them. *Petaurista* and *Pteromyscus* have further adaptations for a folivorous mode of life. Both have proportionally longer fingers than do the other flying squirrels. *Petaurista* are often observed in the wild state to use their hands to pull small branches toward them or from overhead. Usually only one hand was used. Captive *Petaurista* and *Pteromyscus* when handled could draw blood from the animal handler's arm by simply grasping the skin with one hand, squeezing and penetrating the claws into the skin. Their grip is strong. The other flying squirrels (groups 1–3) would attempt to scratch, but not grip.

All of the flying squirrels were adept at using the tail as a balancing organ. It usually hung below the animal during feeding, or folded over the back when the animal had all 4 limbs available for support.

Habitats

Although forests in Malaysia are represented in all stages of regeneration, the primary forest seems to support a different assortment of species than do the secondary or regenerating forests. This is particularly evident in the arboreal species, and especially in the flying squirrels. This subject will be treated in more detail elsewhere. Table 5 includes a summary of our findings regarding flying squirrels in peninsular Malaysia. Note that the prevalence of *Hylopetes lepidus* in primary through secondary forests is replaced by *Petinomys vordermanni* in more disturbed, replanted areas. Among the medium-sized species, *Pteromyscus* is similarly replaced by *Iomys.* As forests are cut, *Petaurista elegans* is replaced by *P. petaurista.* Apparently as the forest changes through man's activities, some species populations decline, but others increase. In fact, the areas which had the

Table 5.—Habitat utilization by flying squirrels in Malaysian forest types.

Species	*Primary forest*	*Partially cut primary forest*	*Secondary forest*	*Fruit/rubber* mixtures*
Petaurista elegans	+ +	+		
Pteromyscus pulverulentus	+ + +	+		
Petinomys setosus	+ +	+	+	+
Aeromys tephromelas	+	+		
Hylopetes lepidus	+ + + +	+ + +	+ + +	+
Petaurista petaurista	+	+ +	+ +	+
Hylopetes platyurus		+	+	+
Iomys horsfieldii		+	+ +	+ + +
Petinomys genibarbis			+	+
Petinomys vordermanni		+	+	+ + + +
Petaurillus kinlochii				+

\+ less than 10 percent of total catch of flying squirrels.
\+ + 10–20 percent.
\+ + + 20–50 percent.
\+ + + + more than 50 percent.
* Pure stands of rubber had very few flying squirrels.

highest densities of *P. petaurista* were those which were nearly clear-cut of the primary forest, save for scattered fruit trees left as relicts. As long as distances between trees were short enough for the squirrels to glide from one to another, populations of *Petaurista* thrived, even in villages. *Petaurista* are efficient gliders, losing only one-fifth to one-tenth of their elevation for a unit of horizontal distance. Thus, from a 30 m height they can travel at least 150 m horizontal distance. The nongliding giant squirrels, *Ratufa,* are not found in such situations. In villages *Petaurista* is considered a pest, along with *Iomys,* to the fruit crops. Not only fruits are taken at all stages of development, but also flowers and leaves (*Petaurista* only). *Iomys* is sometimes a pest of coconut plantations.

Only *Petaurista elegans* was found at elevations above 1500 m in peninsular Malaysia. *Hylopetes lepidus* and *Petaurista petaurista* were collected up to 1000 m. *P. elegans* seems to replace *P. petaurista* at high elevations, as well as in deep forests.

Table 6 summarizes the litter sizes of the flying squirrels in peninsular Malaysia. No correlation is evident between the degree of folivory and litter size. The large squirrels, whether markedly folivorous evident between the degree of folivory and litter size. The larger squirrels, whether markedly folivorous (*Petaurista*) or not (*Aeromys*), had single young. *Petinomys genibarbis* seems to be an exception, but it is a peculiar case. The gestation period is quite long, over 53 days. Its young, unlike those of the other Petauristinae, are born with their eyes open, fully furred, claws developed, and they are also precocial in their behavior. They can climb the first day and eat solid food. *Pteromyscus,* which are larger than *P. genibarbis,* have 1 or 2 more altricial young, but not as altricial as those of the rest of the smaller flying squirrels.

The highest productivity (litter size × litter frequency) appears to be in *Petinomys vordermanni* and *Iomys horsfieldii,* neither of which are abundant in the deep forest but seem to take advantage of temporary situations, such as in villages and plantations. The nests of *P. vordermanni* are poorly constructed, which may contribute to its faster population turnover. The slowest turnover is among the large species, such as *Petaurista* and *Aeromys.* Both species breed infrequently and the single young requires a long time for full development (3–4 months or more). Large numbers of *Petaurista* are shot in fruit plantations to keep them from eating the fruits. Nevertheless, the populations of *Petaurista* seem to maintain themselves and will probably continue to do so unless hunting pressure is increased or the tall trees in which they nest are cut down.

Table 6.—Comparison of litter sizes for the 11 species of flying squirrels in peninsular Malaysia.

Species	*Litter size (mode)*	*Range*
Petaurista petaurista	1	1
Petaurista elegans	1	1
Aeromys tephromelas	1	1
Petinomys genibarbis	1	1
P. setosus	2	1-2
P. vordermanni	2	1-3
Hylopetes lepidus	2	1-3
H. platyurus	2	1-2
Pteromyscus pulverulentus	2	1-2
Petaurillus kinlochii	2	2
Iomys horsfieldii	2	1-4

Summary

Most of the forest rodents in Malaysia are arboreal or at least scansorial. Among them folivores are few, but are morphologically well adapted for obtaining, processing, and digesting a leaf diet. All of the rodent folivores also eat fruit and other plant products when these are available, and some can live in the laboratory even in the absence of foliage in their diet. In the folivorous Petauristinae, the digestive tract includes a greatly elongated cecum which is an offshoot from the small intestine. The abdominal cavity is also elongated and in some species the cecum is approximately 3 times the length of the abdominal cavity and is thrice folded upon itself. In related species which do not habitually consume leaves, the cecum is reduced in size or is rudimentary. The teeth in some folivorous rodents are large and heavily crenulated, with the crowns flattened from grinding action during chewing. The teeth of nonfolivores are cuspidate and often smaller in proportion to the skull length. The fingers of the folivorous Petauristinae are extra long and are used for grasping and pulling overhead limbs closer during feeding while the animal rests on a larger limb. The long tail hangs under the limb and is used to maintain balance.

The folivorous Petauristinae occur in both primary and secondary forests and at all elevations, although there are species replacements altitudinally and according to habitats. Reproductive rates and probably population turnover rates are lower in folivores when compared to the nonfolivore Petauristinae. The folivorous Petauristinae populations can maintain themselves, sometimes in large numbers even in marginal habitats and in habitats greatly modified by activities of man.

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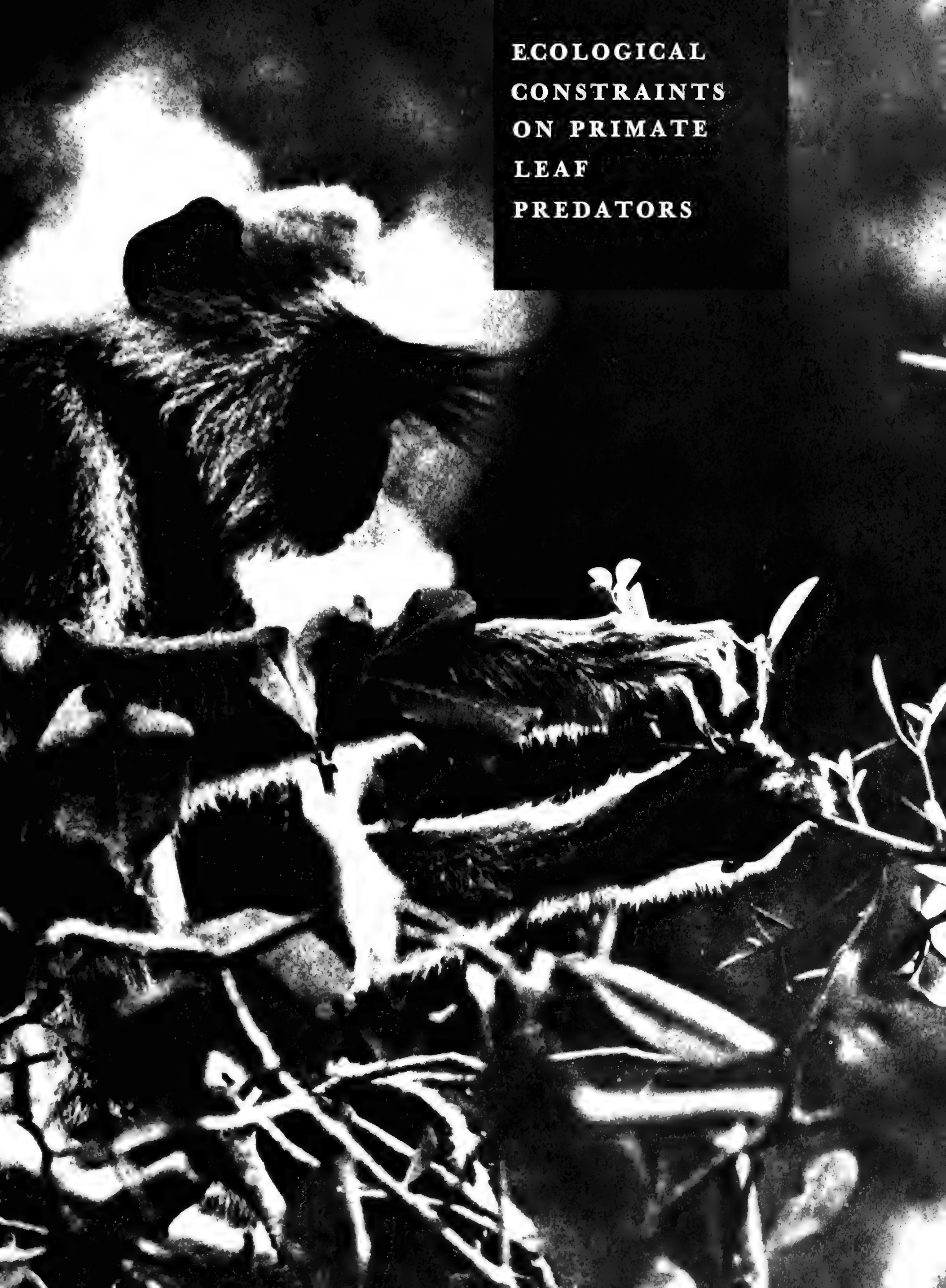
Presbytis entellus selectively feeding on leaves. (Photo by C. M. Hladik)

ECOLOGICAL CONSTRAINTS ON PRIMATE LEAF PREDATORS



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Adaptive Strategies of Primates in Relation to Leaf-eating

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Introduction

The most specialized of the primates are the folivores. Among the living prosimians—Platyrrhine and Catarrhine monkeys—two major types of gut specialization for processing leaves have evolved as follows:
(*1*) Large cecum or wide colon in *Lepilemur, Pro-*

pithecus, Avahi, Indri, some Platyrrhine monkeys like *Alouatta* and, to a lesser extent, for Catarrhines like *Gorilla, Symphalangus,* and some Cercopithecidae. In this type of gut, bacterial fermentation provides at least a partial hydrolysis of cellulose and hemicelluloses occurring after the absorption of the largest part of the soluble sugars, fats, and amino acids.

(2) Sacculated stomach in *Presbytis, Colobus,* and *Nasalis,* where the bacteria and flagellae affect the food at an early stage of digestion. This is followed by selective absorption as the digesta move down the gut.

Not only gut morphology, but different strategies of adaptation to the environment which involve behavior and sociology are also important characteristics of leaf-eaters. These feeding strategies related to folivory affect many primate species—in addition to those whose staple food is leaves—because in natural conditions, leaves are the main source of protein for most of the large frugivorous primates.

Several examples are presented below, with a comparison of the ecological niches of these leaf-eating primates in different natural systems.

Prosimians as Folivores

A specialized prosimian folivore.

The sportive lemur, *Lepilemur leucopus,* which lives in the south of Madagascar, provides a rare example of a specialist for leaf-eating among the primates (Figure 1). This nocturnal species, which feeds mostly on crassulescent leaves, reingests a part of its fecal material, just like the rabbit which practices "caecotrophy" (Taylor, 1940). Such a peculiar behavior is unique among the primates (Charles-Dominique and Hladik, 1971), but the other features related to the folivory of the sportive lemur are typical of the other folivorous primates.

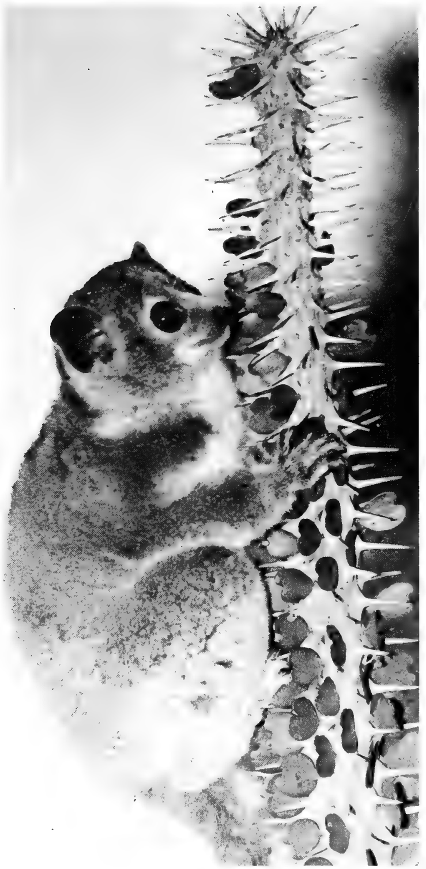

Figure 1. *Lepilemur leucopus* on a Didiereaceae (*Alluaudia ascendens*) from which the leaves can be used as a staple food.

The mechanism of digestion of the leaves has been investigated (Hladik et al., 1971). Table 1 shows the progress in concentration and deconcentration of the main components of the leaves during the twofold cycle of ingestion and reingestion by a sportive lemur. The food ingested in natural conditions was a mixture of leaves and flowers of two species of Didiereaceae, no other leaves being available during the dry season. This food was fairly rich in protein (15.1 percent), but poor in lipids (2.7 percent) and reducing sugars. The ratios of hemicelluloses to lignocellulose indicates that very few hemicelluloses are hydrolyzed after the animal begins feeding at night. There is an increase of this ratio in the cecum, showing that a part of the cellulose is rapidly hydrolyzed. The hemicelluloses are slowly hydrolyzed afterwards and absorbed in the colon where the ratio of hemicelluloses to lignocellulose is progressively reduced.

A large part of the food decomposed in the cecum passes quickly and forms "feces" that could be compared to the "caecotrophes" of the rabbit, containing a high proportion of protein. These particular feces are eaten and pass a second time through the small gut, where absorption of the soluble components resulting from bacterial fermentation occurs. The feces reingested by the sportive lemur have no special shape characteristics, as in the case of the

Table 1. Composition of food and ingesta in the digestive tract of *Lepilemur leucopus*. (From Hladik, *et al.*, 1971.)

	Composition (percent of dry weight)			
	Protein	*Lignocellulose*	*Hemicelluloses*	*Ratio of Hemicelluloses to Lignocellulose*
Natural food ingested (mixture of leaves and flowers of *Alluaudia ascendens* and *A. procera.*)	15.1	24.1	13.6	0.56
Stomach content (at night)	10.3	43.0	23.1	0.54
Caecum content (at night)	45.8	17.5	49.3	2.8
Beginning of the colon (at night)	35.4	29.0	34.5	1.2
Beginning of the colon (afternoon)	36.0	39.9	21.6	0.54
End of the colon (afternoon)	26.9	45.6	20.6	0.45

rabbit, and they are difficult to identify in the stomach content; but the ramified short-chain fatty acids with uneven numbers of carbon atoms that we found in the stomach content can be used as a tracer to demonstrate the reingestion since they are typical of bacterial action and are formed in large quantities in the cecum.

In *Lepilemur,* the adaptation for folivory includes not only morphological and physiological features, but also the very peculiar behavior for a primate, *caecotrophy*. This strategy allows a more complete absorption, in the small gut, of all the soluble substances resulting from bacterial fermentation. Thus, an animal of 600 g of body weight survives on the poorest diet observed among primates. In terms of the calories available in the raw foodstuff before the effects of bacterial fermentation are considered, there is an intake of only 13.5 Kcal per day (Charles-Dominique and Hladik, 1971).

Socioecology and diet of lepilemur

The utilization of leaves as a staple food involves a social strategy of habitat utilization which is a common characteristic of most of the leaf-eating primates (Hladik, 1975). These convergent socio-ecological patterns are shared by the primate species of different taxonomic groups in which the social organization itself might be more or less complex according to the level of evolution.

Lepilemur has one of the most primitive types of social organization (Charles-Dominique and Hladik, 1971; Hladik and Charles-Dominique, 1971, 1974). The adult males occupy exclusive territories with respect to each other, but the territories of one or more adult females are included in each male's territory. The social groups are thus very small and simple, consisting of 1 adult female with 1 or 2 offspring maintaining periodical contact with 1 male.

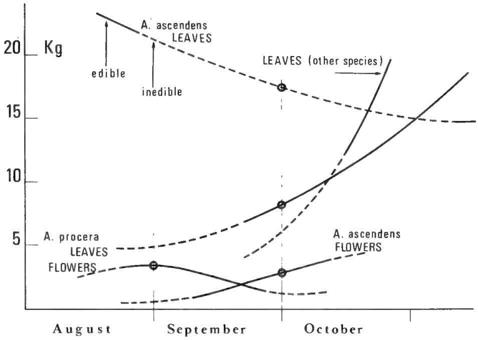

Figure 2. Variations in the food available in the supplying area of one *Lepilemur* during the period of maximal drought.

Territories of *Lepilemur* generally cover less than 0.2 hectare, which allows very high population densities. We recorded 350 *Lepilemur* per km^2 in the Didiereacae bush habitat, and 810 per km^2 in a gallery forest (biomasses of 2.1 kg/hectare and 4.9 kg/hectare respectively).

In the bush habitat, we surveyed the trees along a transect and calculated the average quantity of food available for one *Lepilemur,* during the period of maximal drought (Figure 2). Two species of Didiereacae—which look like big cacti—*Alluaudia procera* and *A. ascendens* form the main part of this bush and produced at this time most of the food available. In these particular conditions, a calculation with good accuracy was fairly simple to perform. We found an average for each animal of 1.6 times the minimum food necessary for survival (Charles-Dominique and Hladik, 1971). Even among nonfolivores (cf. Smith, 1968), a mammal cannot stay in an area where very little food above the minimum requirement is available.

The above calculation applies only to a period of about 2 months during which a minimum of food is available for *Lepilemur*. Just after that period (Figure 2), new leaves start growing and the stock of potential food is thus rapidly increased. One can suspect, nevertheless, that the size of the territory of *Lepilemur* was selected in relation to the food available during the worst drought periods. This is an inclusive strategy for the species, allowing the maximal efficiency of land use (maximum biomass) without any loss of population during the periodic seasons of minimum food production.

The territorial behavior of *Lepilemur* maintains the population density at an optimum level. The territories are stable, with precise boundaries defended by the owner, who utters loud calls and makes other displays, but rarely directly fights against intruders. With nightfall, the sportive lemurs leave their "nests" located in hollow trunks or in the thickest parts of the bush, and start calling in duets: 2 animals, one on each side of a territorial boundary, together give a series of short, successive calls (Charles-Dominique and Hladik, 1971). The necessity of using sounds for marking boundaries might appear obvious for a nocturnal species, if we suppose that they cannot see the intruders clearly; but it has been demonstrated by Pariente (1974) that *Lepilemur* can see accurately in the light levels of his nocturnal environment. The loud calls for territorial marking may be correlated with the fact that a leaf-eater does not have to move very much to find his food, and thus has only a few occasions for visual displays along territorial boundaries. The sounds are more efficient, especially in small territories. This might explain why vocal display has been selected for in many other leaf-eating primates and why they have many convergent traits.

Other folivorous prosimians

There are several types of dietary specializations among the different prosimian species. The lemurs evolved from a primitive type whose diet included at least a large part of insects and some fruits (Charles-Dominique and Martin, 1970). This primitive animal was probably small and resembled either *Galago demidovii* (weighing 60 g and now living in the evergreen forest of continental Africa), or *Microcebus murinus* (also weighing about 60 g and adapted to different biotopes in Madagascar).

Although fruits are the main food resource for most of the prosimians, leaves are utilized by many species even if they are less specialized than *Lepilemur* or have evolved divergently. Ingesting leaves, at least in small quantities, might be a primitive trait of prosimian feeding behavior since *Microcebus murinus* was observed in natural condition feeding on *Uapaca* leaves (Martin, 1972). Only the large lemur species, nevertheless, utilize leaves in large quantities. This follows the general principles of energetics (McNab, 1978; Parra, 1978) and allometry in body proportions (Grand, 1978). Leaves must be retained in large quantity and for a long time to allow the processes of fermentation. The largest forms are generally the more folivorous, as shown by some examples recently studied in the field.

In places where they lived in sympatry (southwest forests for Madagascar), *Lemur fulvus* and *Lemur catta* feed partly on the leaves of different plant species. Considering the records of individual activity (which are not exactly the true proportions of foodstuffs in the diets), Sussman (1972, 1974) found 89 percent of leaf-feeding by *L. fulvus* and 44 percent by *L. catta*. Body weight for both species is around 2.5 kg. For both species, the food choices may vary according to the vegetation available in different biotopes—*L. catta* diet is described by Jolly (1966) in the gallery forest of the south of Madagascar—but it always includes a fraction of leaves.

Propithecus verreauxi, living in different types of vegetation, has been observed by Richard (1973, 1978). According to the place and the season, this indriid of about 3 kg body weight may feed on large amounts of leaves. Some larger species of *Propithecus*, living in the rain forest of Madagascar and weighing up to 6 kg, also use large amounts of leaves in their diet (Petter, personal communication), but no precise data are available to compare these larger species with the smaller *P. verreauxi*.

The largest of the living lemurs, *Indri indri* (Figure 3), weighs about 9 kg, and inhabits the rain forest of the eastern coast of Madagascar. It feeds mainly on leaf material (Pollock, 1975). From 40 to 70 percent of the feeding observations involve young leaves and buds. Fruits comprise 25 percent of the feeding observations while seeds comprise about 10 percent. Pollock observed the *Indri* occasionally coming to the ground to ingest pieces of dead wood and earth. This phenomenon of geophagy is a common trait of many species of primates which use leaves as staple food (Ripley, 1970; Hladik and Hladik, 1972; Hladik, 1973; Oates, 1974). Geophagy is not related to the mineral composition of the diet but probably its physical structure (Hladik and Gueguen, 1974).

Figure 3. The indri (*Indri, indri*) is the largest of the living lemurs and the most folivorous among them. (Photo by J. J. Petter)

Among the prosimian species, different aspects of gut morphology can be related to leaf-eating. Maximum development of both the cecum and colon is found in the Indriidae (Hladik, 1967), while among Lepilemuridae, only the cecum is expanded.

Body weight and diet in relation to the composition of the natural substances

The adaptations to leaf-eating concerning gut and also tooth morphology (Kay and Hylander, 1978) have to match the environmental conditions. The different foodstuffs available in natural conditions have a range of composition (Table 2) fairly similar in different environments. As a consequence, the range of body size of the prosimians, as well as higher primates, is in relation to the natural diet.

The smallest species have diets yielding the maximum energy, made up of insects and fruits. Whenever several sympatric species of primates include insects in their diet, an individual of any given species foraging in the same area can obtain approximately the same quantity of insects per unit time (Hladik and Hladik, 1969; Charles-Dominique, 1971). Thus the small species (60 to 250 g) like *Galago demidovii, Arctocebus calabarensis, Loris tardigradus,* etc., can fill their stomachs with insects. Larger species cannot obtain enough insects during 1 day (or 1 night) of foraging and they have to fill their stomachs with a complementary type of food, such as fruits, gums, or leaves. For example, *Galago alleni, Perodicticus potto, Nycticebus coucang* (body weight 200 g to 1000 g) or higher primates such as *Saguinus geoffroyi* (500 g) have a diet of insects and fruits. All of the small primates catch as many insects as they can, which makes up 25 percent of the food intake for the small forms but no more than 10 to 20 percent for the larger forms. Leaves can be utilized by a few highly specialized forms of 600 to 1200 g, such as *Lepilemur* and *Hapalemur* (Petter et al., 1977).

The largest species of primates are frugivorous or folivorous. Species weighing up to 2 or 3 kg may use both fruits and insects. For example, *Cebus capucinus* includes 20 percent of insects and other prey in its diet (Hladik and Hladik, 1969). The proportion of insects in the diet of larger primates is generally lower, since the maximum weight of insects collected is limited by their relative abundance. However, the total food intake becomes larger for the larger primate species. Fruits yield an average of only 5 percent protein and the variations between the fruits of different species are small (see Table 2).

The small proportion of insects (5 to 20 percent) included in the frugivorous diet of a large primate is generally not sufficient to increase the protein content above a total of 7.5 to 10 percent of the total dry weight. Such a rate is considered insufficient for a mammal, the minimum for domestic animals being 12 percent protein. Thus, in natural conditions, frugivorous primates around or above 2 kg of body weight are faced with the necessity of finding a complementary protein source. Leaf material is this complementary substance available *ad libitum* in the natural environment. The protein content of mature leaves reaches 10 to 20 percent and the buds and young leaves used by most of the primates contain 25 to 35 percent protein, with the maximum of 55 percent observed in the shoots of a leguminous tree (Hladik et al., 1971; Hladik and Viroben, 1974; Hladik et al., in press; A. Hladik, 1978).

Thus, any large primate species utilizes leaves as the main source of protein because there is no other efficient alternative. If on the one hand *Cebus capucinus* or *Macaca sinica* (3 kg) ingests only 15 percent of green vegetal material (Hladik and Hladik, 1972), then on the other hand, by contrast, larger species like *Ateles geoffroyi* and *Alouatta palliata* (6 and 8 kg) may utilize even more leaves and buds (20 and 40 percent respectively of the total ingested; Hladik and Hladik, 1969). This large proportion of leaves and buds is necessary to compensate for the low amount of protein in a frugivorous diet without any animal food supplement. The diets of *Lemur* and *Propithecus,* described in the previous section,

Table 2.—**Some examples of the composition of natural substances eaten by primates in different environments. (After Hladik, *et al.*, 1971, and Hladik unpublished data concerning Sri Lanka [1800 analysis] and Gabon.)**

		Percent dry weight		
	LEAVES	*Protein*	*Soluble Glucids*	*Lipids*
GABON	*Baphia leptobotrys,* shoots	55.0	—	—
(rain forest)	young leaves	36.3	20.1	2.2
	mature leaves	26.1	—	1.3
	Ongokea gore	19.3	24.9	1.2
	Gilbertiodendron dewevrei	10.2	13.5	0.7
PANAMA	*Cecropia* sp.	12.5	24.6	2.1
(rain forest)	*Ceiba pentandra,* shoots	25.3	19.5	1.2
SRI LANKA	*Glycosmis pentaphylla,* young leaves	31.5	5.6	3.1
(dry forest)	*Walsura piscidia,* young leaves	19.5	8.3	1.5
	Adina cordifolia, mature leaves	11.8	7.8	7.3
	Alangium salvifolium, shoots	26.2	10.3	2.6
	FRUITS			
GABON	*Nauclea diderrichii*	4.5	47.2	5.3
(rain forest)	*Aframomum giganteum*	8.2	48.8	11.1
	Musanga cecropioides	8.8	31.5	6.3
	Pseudospondias longifolia	7.5	17.4	0.6
PANAMA	*Dipteryx panamensis*	4.4	41.5	1.4
(rain forest)	*Cecropia peltata*	5.0	36.4	2.3
	Ficus insipida	4.5	30.1	3.5
	Spondias mombin	2.8	57.4	0.7
SRI LANKA	*Drypetes sepiaria*	2.8	52.5	7.1
(rain forest)	*Ficus benghalensis*	8.4	6.8	18.1
	Syzygium cumini	6.6	4.1	2.2
	Garcinia spicata	6.2	30.6	20.3
	INSECTS			
GABON	mixed insects from litter	70.2	0.5	3.5
(rain forest)	adult Sphingidae	65.6	1.8	16.3
	Caterpillars (An 15)	62.3	6.4	21.2
	Ants with nest (*Macromiscoides aculeatus*)	29.0	20.0	4.2

consist basically of this same type of fruits and leaf combination.

Foraging for insects may be useless for large primates, since the protein reward would be too small compared to the time and energy required in searching for insects. We do not know exactly why some intermediate-sized diurnal lemurs, such as *L. catta,* have retained the strategy of feeding only on fruits and leaves without utilizing some insects. Could it result from competition with birds? For the largest species of lemuriformes, such as *Indri indri,* the leaf material is the only resource available in large quantity and the fruits and seeds can be considered as a complement for carbohydrates.

This very broad generalization about food composition and primate body weight applies only to the major size categories. Many variations in the diet are related to the combination of more subtle factors like socio-ecology which must be considered in more detail.

Biomass and supplying area

In the different rain forests where data have been fully collected (Leigh and Smythe, 1978; A. Hladik, 1978), leaf production is approximately the same. Other food resources such as buds and young leaves, fruits, etc., are available in smaller quantities, but the order of magnitude is probably similar. In the tropical forests of dry zones, the production is lower than that in the rain forest (approximately half the leaf production; Hladik and Hladik, 1972).

The biomasses of the different primate species are ultimately limited by the food resources. The maximum biomass may be high for a species that feeds on ubiquitous resources like the leaves of the common tree species, or low for a species using scarce resources like leaf flushings and fruits, or even very low for a species that relies on the products of secondary producers, such as insects. Thus, a comparison of the maximum biomasses for a species is a fairly good indicator for the general diets of the different *copus* reaches 5 kg per hectare in the gallery forest of the south of Madagascar, while *Microcebus murinus*, feeding on insects and fruits, accounts only for 0.25 kg per hectare (Charles-Dominique and Hladik, 1971).

To complement this general information, it is necessary to calculate the total food available for 1 individual nocturnal prosimian or for 1 group of diurnal primates and to determine to what extent the local resources are shared by other individual prosimians or by other groups. Generally there are large overlapping parts common to different home ranges (Figure 4). Consider 3 adjacent primate troops, A, B, and C. Let us define 3 classes of habitat utilization: Class 1, 2, and 3. The core area (or territory) will be referred to as Area 1 for groups A, B, and C. In Area 1, each troop has exclusive utilization of all the resources. In the overlapping parts (Area 2), any two groups, such as A and B, share the resources. It has been demonstrated (Hladik and Hladik, 1972) that each group can use an equivalent amount of the food available in a type 2 area. When the ranges of three groups, A, B, and C overlap (defined as a class 3 area), one-third of the resources is available for each group. We define the "supplying area" (*surface moyenne exploitée*) as area 1 + half of area 2 + one-third of area 3 + etc. for a given troop. The larger the home range in relation to "supplying area," the greater the sharing of scattered food resources occurs. This will be shown below by the feeding and social strategies of different prosimian and higher primates.

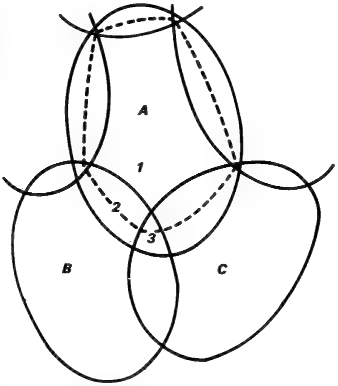

Figure 4. The "supplying area" of group A, as determined by the limits of the home ranges of the other groups (*see text*), is delineated by the broken line.

Socio-ecology and folivorous diet among prosimians

As with morphological structures, the behavioral and social characteristics of the large, diurnal lemuriform species of Madagascar show different trends and many convergences.

The leaf-eaters, *Indri* and *Propithecus*, form the smallest social units that allow a regular distribution of the population in small territories. The *Indri* live in family groups of 3 or 4 (Petter and Peyrieras, 1974; Pollock, 1975), while the *Propithecus* form larger groups of 4 to 6 and show more tolerance among males and among females (Richard, 1974, 1978).

The melodious vocalizations of the *Indri* permit each group to know the location of its neighbors without moving toward the limits of its territory. These calls may act as a repellent between the groups, and thus maintain the territorial boundaries. *Propithecus verreauxi* of different groups may interact visually (Richard, 1978), but they also have a typical territorial call that they utter early in the morning. Many other primates have a territorial call (Gautier, 1975), but the regular use of this loud vocalization by the leaf-eating primates at the beginning of the period of activity is a characteristic of these small, barely mobile groups. As in the case of *Lepilemur*, the vocal display has been selected for use when visual displays have little chance of being efficient.

In the bush of the south of Madagascar, the diurnal folivorous *Propithecus verreauxi* reaches a biomass similar (4 kg per hectare) to that of *Lepilemur leucopus*, which is folivorous and nocturnal (Charles-Dominique and Hladik, 1971). *Propithecus* feeds on a slightly wider variety of plant species on a relatively larger range (Richard, 1978). The individuals or very small groups of *Lepilemur* utilize the most common plant species, and the relative abundance and regular dispersion of these food resources allow a regular dispersion of *Lepilemur* on small supplying areas.

In the dry forest of the southwest of Madagascar, Sussman (1972, 1974) found a similar clear-cut relation between the ecology and the social organization of the 2 sympatric species of *Lemur, L. fulvus* and *L. catta*. The biomass of *L. fulvus* may be greater than 10 kg per hectare in correlation with a diet including a very high proportion of leaves. This species lives in small groups of from 5 to 10 animals, on a small range (0.75 hectare), and utilizes a small number of common trees (3 species yielded 80 percent of the food). In contrast, *L. catta* lives in larger groups of about 20 animals on a larger range (8.8 hectares), and has a smaller biomass (6 kg per hectare). This correlates with a partly folivorous diet including more fruits. The larger size of the supplying area of this last species is not correlated with the biomass (smaller than that of the previous species), but certainly is correlated with the uneven dispersion of the plant species utilized as food. In fact, Sussman showed that *L. catta* utilizes about twice as many food plants as *L. fulvus*. The very high biomasses that we can deduce from Sussman's observations may reflect the maximum possible utilization of the habitat by the folivorous lemurs, as is the case for the folivorous langurs in a dry forest of Sri Lanka (Hladik, 1977).

Compared to these figures, the biomass of the *Indri* seems very small (around 1 kg per hectare) in the rain forest of the east coast of Madagascar (Petter and Peyrieras, 1974; Pollock, 1975). This must be related to the feeding habits of the *Indri* which eats almost exclusively the young leaves which have attained only about a tenth the weight of their full-grown counterparts (A. Hladik, 1978). Furthermore, young leaf production is not evenly distributed in time. On the other hand, *Indri* feeds on a small number of tree species (82.6 percent of Pollock's feeding records concern 12 species among the 20 common ones out of a set of many hundreds of rain forest tree species).

Platyrrhine Monkeys as Folivores

In Central and South America, the only truly folivorous mammal studied is the three-toed sloth, *Bradypus* (Montgomery and Sunquist, 1975, 1978). Nevertheless, leaves play an important part in the diet of several species of primates.

Howler monkeys

The howler monkey, *Alouatta palliata*, has been described as a folivorous primate in the early literature, owing to superficial observations, but large quantities of fruits are eaten and the leaves can be considered as a complementary part of the diet. We followed a group of howlers during 15 months on Barro Colorado Island, Panama, to make quantitative estimates of the food intake, and obtained a diet including 60 percent fruit and flowers and only 40 percent leaves (Hladik and Hladik, 1969). These round numbers are related to the wet weight and can be considered as low accuracy data (± 5 percent). These data are the only criteria for interspecific comparisons. Even though the feeding times that can be accurately measured are generally not closely related to the food intake by volume (Hladik, 1977), we will compare our data with studies employing time measures. The more recent study of *A. palliata* by Milton (1978) demonstrated the intraspecific variations of the diet of the howler monkey in relation to the local variations of the environment. Her data on feeding (46 percent on fruit and 44 percent on leaves) came from the same group of howlers that we previously observed, and show that the main characteristics of the feeding behavior have been maintained. A small number of food species are selected to form the staple food of that group. *Ficus* is still the main fruit component of the diet.

We discovered that these different *Ficus* species have different amino acid contents in the protein fraction of their fruits and leaves (Hladik, et al., 1971). The mixture of *Ficus* fruits and leaves in the diet of the howler monkey is complemented with many other food species (all of which are not analyzed in such detail), and the data suggest the maintenance of a favorable balance of essential amino acids.

Like any large species of frugivorous primates, the howler monkey (7 to 8 kg) needs the leaf material to maintain a normal level of protein intake and does not intentionally eat any insect or other invertebrate prey. Nevertheless, in the sample that we utilized to calculate the average protein content in the annual diet, we found only 9.6 percent protein.

The variations in the diet of the howler monkey are certainly related to the protein and soluble sugars available in the different food species. Milton (1978) reports that the groups spent 39 percent of time feeding on fairly new leaves and only 5 percent on mature leaves. Glander (1975, 1978) recorded howler monkeys in a relict riverine forest eating new leaves 44.2 percent of the time and mature leaves

19.4 percent. All these records of time feeding are the most accurate data available, but they cannot be compared since they refer to different environments and different samples on which the feeding intake is not predictable. Schlichte (1978) observed the howler monkeys in Tikal, Guatemala, and reported over an interval of 3 months probably the most extreme condition in which they can survive. During his study, the howlers spent 70 percent of their time feeding on fruits of just one species of tree. In this species-poor forest, the animals used only 7 of the 36 species as food sources.

In the rain forest, the feeding strategy of the howler monkey, which is adapted to the fruits and leaves of about a dozen of the common tree species, does not vary to a great extent. Klein and Klein (1975) gave a description of the feeding strategy of *Alouatta seniculus* (in Colombia) which is very similar to that of the howler of Barro Colorado, including the utilization of the immature fruits and leaves of different *Ficus* species.

The maximum biomass of the howler monkey on Barro Colorado Island is about 4 kg per hectare (Hladik and Hladik, 1969). One group of 10 howlers used a supplying area of 15 to 20 hectares. There is a fairly rapid shift in the home ranges of different groups (Chivers, 1969) and, over the long term, one can consider that a very important overlap between the supplying areas of different groups gives access to an important number of scattered tree species for each of the small groups.

The group is of medium size (up to 15 or 20) with little evidence of dominance hierarchy among males. Eisenberg et al. (1972), characterized this intermediate type of social organization as "age-graded male troop," differing little from the smaller "one-male groups" formed by the true folivorous primates. Among the frugivorous-folivorous large lemurs of Madagascar, we also found this type of medium-sized group, except that among lemurs the females were generally less tolerant and the system was closer to a matriarchy.

The loud calls uttered by the howlers, especially at dawn, have an important function in the maintenance of the territory (Carpenter, 1934; Chivers, 1969). When utilizing leaves and very common fruits, like those of *Ficus,* the howler monkeys do not have to travel long distances to feed. Consequently, the loud calls may be the most efficient signaling method they can use.

The choice of a limited number of common food species for complementary nutrients allows the relatively small groups of howler monkeys to share a nonhomogenous environment divided into small home ranges, slightly increased by the overlaps. This feeding strategy of a fruit-and-leaf-eater could not be applied to a primate species using more scattered resources without facing the risk of unequal division of the food resources among the groups.

Spider monkeys

The red spider monkey, *Ateles geoffroyi,* is a typical frugivorous primate, weighing 5 to 6 kg, for whom the leaves (especially the young leaves and buds) are a necessary complement of the diet. In the forest of Barro Colorado, the leaves account for 20 percent, (fresh weight) of the annual food intake of the spider monkey (Hladik and Hladik, 1969).

Ateles geoffroyi utilizes a wider variety of food species than *Alouatta palliata* on Barro Colorado Island, where 80 percent of the total food ingested by *Alouatta* is made up of 14 tree species, while about 25 tree species account for the same proportion of the food of *Ateles.* The supplying area of a group of *Ateles* is also wider (40 hectares; Hladik and Hladik, 1969) and the biomass rarely exceeds 1 kg per hectare. Very similar differences were observed by Klein and Klein (1975) between *Alouatta seniculus* and *Ateles belzebuth* in the rain forest of Colombia.

Red spider monkeys obtain most of their protein from leaves. They choose the young leaves and shoots with high protein content—for example, *Poulsenia armata* or *Ceiba pentandra* shoots containing 25.3 percent protein (dry weight). They eat some mature leaves and petioles of *Cecropia,* which contains only 12.5 percent protein, but the leaf petioles are generally selected for their high mineral content (Hladik and Gueguen, 1974). The fruits selected by *Ateles* are richer in soluble glucids than the few species utilized by *Alouatta* (Hladik, et al., 1971). The utilization of food sources that yield more nutrients but are not so common as those resources used by *Alouatta* correlates with the smaller biomass of *Ateles* and its larger home range.

There is a considerable interindividual tolerance and a splitting of *Ateles* populations into subgroups (Klein and Klein, 1975). This behavior trait correlates with the use of scattered food sources.

Capuchin monkeys

The white-throated capuchin, *Cebus capucinus,* is sympatric with the 2 former species on Barro Colorado Island, and is a smaller cebid weighing about 3 kg. It obtains a large part of its dietary protein from insects and small invertebrate prey for which it forages. Nevertheless, 15 percent (wet weight) of its diet consists of leaves, shoots, and other green vegetal material. This intake is completed by 65 percent fruit and 20 percent invertebrate and vertebrate prey (Hladik and Hladik, 1969). The average composition of the annual food intake includes, by dry weight, 8.8 percent animal protein and 5.6 percent vegetable protein (Hladik, et al., 1971).

This primate species selects the richest parts of a set of food plants that includes more than 40 tree species. The capuchins form large groups with a more obvious social hierarchy than in the above New World species (Oppenheimer, 1968), and their biomass in the rain forest of Barro Colorado reaches only 0.5 kg per hectare. To gather their food, concentrated in small areas over a very wide range of 90 hectares, the capuchins have to travel long distances every day. They have frequent contacts with the neighboring groups; these contacts involve aggressive displays, but no use of loud territorial calls.

Rufus-naped tamarin

The rufus-naped tamarin, *Saguinus geoffroyi,* is a small callitrichid weighing only 0.5 kg. It feeds on fruits and insects, with animal prey accounting for 30 percent (fresh weight) of its diet. Nevertheless, about 10 percent of its diet includes leaves and green plant material. The protein intake of the tamarin includes 16 percent animal protein and 4.6 percent plant protein (dry weight). Obviously, leaves are not very important as a nutrient, but the fact that the tamarins belong to an early diverging group of New World primates and do eat some leaves may suggest that the adaptation to a diet complemented by leaves is a primitive trend which has been amplified in the different primate radiations.

Cercopithecids Tending to Folivory

Near Makokou, Gabon, at the field station of the C.N.R.S., 17 species of primates live in sympatry. Among them are different examples of leaf-eaters, but the only true folivorous mammals of the Gabonese rain forest are the flying squirrels (3 species of *Anomalurus,* 1 of *Idiurus,* and 1 of *Zenkerella*), and the tree hyrax, *Dendrohyrax dorsalis.* This last species, subjected to a short field study (Richard, 1964), showed the relative stability of small individual territories and the use of loud calls probably as a spacing behavior. *Dendrohyrax* was observed in a pen defecating always at the same place.

The small nocturnal prosimians of the Makokou forest include 5 species which have been studied during 7 years by Charles-Dominique (1971, 1975). Their diets include none or very few leaves. A very small proportion of leaves is utilized by *Galago demidovii,* one of the less specialized forms. Two other prosimian species feed on the gums of trees and lianas. For *Euoticus elegantulus,* gums account for 75 percent of the food intake (Charles-Dominique, 1977). These gums are compounds of pentoses and are highly polymerized. They yield roughly the same nutrients as fruits, but necessitate bacterial fermentation, as for digestion of leaves. In this respect, the wide cecum of *Euoticus* has a converging shape and may be compared to the cecum of *Lepilemur* (Charles-Dominique and Hladik, 1971).

Cercopithecinae of Gabon

Among the 8 species of frugivorous Cercopithecidae living in the rain forest near Makokou, the smallest one, *Miopithecus talapoin* (1 to 2 Kg) eats the largest proportion of insects. According to Gautier-Hion (1971), only 8 percent of leafy material was found in the stomach contents. A large band of 115 talapoins lives on 140 hectares with a biomass of around 1 kg per hectare.

Different species of *Cercopithecus* (*C. pogonias, C. cephus,* and *C. nictitans*) can be classified in a range of body weights from 2 to 7 kg. All of them eat fruit complemented by leaves and insects in different proportions. These monkeys may form polyspecific groups sometimes joined by the talapoins (Gautier and Gautier, 1969) and use a large supplying area. There are slight but clear-cut differences in the diets of these three species of *Cercopithecus. C. pogonias* includes with fruits an average of 14 percent insects and 2 percent leaves; *C. cephus* utilizes 10 percent insects and 8 percent leaves; *C. nictitans,* the largest species, is also more folivorous, with 8 percent insects and 28 percent leaves (all results from dry weight of stomach contents from Gautier and Gautier, 1975). The total biomass of the polyspecific association described by the Gautiers reaches about 2 kg per hectare, which proves the equal efficiency of this system of fruit-and-leaf-eaters, compared with the systems in other types of environments where the food resources are not so scattered.

The DeBrazza monkey, *Cercopithecus neglectus,* inhabits the river banks of the Makokou forest and forms small groups of about 4 individuals (Gautier, personal communication). Its diet includes some leaves, fruit, and seeds, and is still subject to analysis. It might be similar to that of the black colobus, *Colobus satanas,* living in the coastal forest of Cameroon (McKey, 1978). The population density of *Cercopithecus neglectus* is very high, and the biomass may reach 4 kg per hectare (after Gautier and Gautier, personal communication). The small groups are barely mobile and are in a small territory. A loud vocalization (a kind of booming typical of other *Cercopithecus* species but more developed in *C. neglectus*) is used at regular intervals. These characteristics of the social structure might be only a convergence toward the social forms shown by leaf-eating primates. The convergence is also evident in a comparison of the digestive system (Hladik and Chivers, unpublished data), and in the fact that they feed on certain types of food with a high fiber content, such as *Gilbertiodendron dewevrei* leaves, which contain only 10.2 percent protein and 13.5 percent sugars (Table 2) and are not eaten by the other primate species.

Two *Cercocebus* species, *C. albigena* and *C. galeritus,* inhabit the Makokou area. In fact they occur in sympatry, but the geographic area of 1 species extends toward the east and west, while the other (*C. galeritus*) extends only towards the east. *C. galeritus* was the subject of a detailed field study (Quris, 1975), showing that its habitat is almost exclusively limited to the fringe of forest along the rivers. A group of 10 to 15 has a home range of about 200 hectares extended in a long strip of 4 to 8 km along a river. There are important overlaps in the ranges of 2 groups and the supplying area is about 100 hectares. The diet of *C. galeritus* is made up of fruits complemented by 13.9 percent leaves and 2.8 percent insects (dry weight of stomach contents, after Quris, 1975). The feeding strategy is similar to that of the larger species of *Cercopithecus,* since the leaves serve as the main protein complement in an environment where the food sources might be equally scattered. The body weight of *Cercocebus* is about 10 kg and the biomass 1.5 kg per hectare (these figures are maximum biomasses in the areas effectively utilized by the primates, not in the whole rain forest including different types of environments).

The mandrill, *Papio sphinx,* is the largest of the Cercopithecidae living in Gabon. Its diet includes fruits, seeds, insects, and a certain quantity of leaves. Large groups of mandrills utilize a very large supplying area (Jouventin, 1975). The field conditions did not permit a detailed study of the feeding strategy, but one can expect that the leaves play an important part in the amino-acid balance, as shown below for the chimpanzee.

Two species of the Colobinae, the black and white and the black *Colobus,* also occur in the forest of Gabon. These folivorous monkeys have been hunted for years; they are still scarce and we do not have good data concerning their ecology. Examples of the ecology of the Colobinae are presented in subsequent sections.

Comparative data from East Africa

A comparison can be established between the primate ecology in the rain forest of Makokou (typical of West Africa) and in the Kibale forest (as an example of East Africa) where detailed field studies have been carried on by T. T. Struhsaker and coworkers (Struhsaker, 1975, 1978; Rudran, 1978; Waser and Floody, 1974; Oates, 1974). The Kibale forest is higher in elevation (1450 m) than the Makokou forest (500 m) and its ecosystem as determined by the number of all species is slightly less complex.

The folivorous monkeys account for the largest part of the biomass of the Kibale forest: *Colobus badius* (17.6 kg per hectare) and *Colobus guereza* (0.6 kg per hectare; figures after Struhsaker, 1975). The red colobus, *C. badius,* eats a small amount of fruit (4.8 percent of the feeding observations), which may represent a larger fraction of the actual food intake by weight. *C. badius* utilizes the young leaves of a limited number of tree species (10 species account for 75.4 percent of feeding observations; Struhsaker, 1978). Groups of 50, which include several males, range over 15 to 20 hectares. Conversely, the black and white colobus, *C. guereza,* forms groups of about 10 concentrated in small areas (2.75 hectares) where they feed almost exclusively on 3 food plants (69 percent of the feeding observations), among which 1 species, *Celtis durandii,* accounts for 48.5 percent (Oates, 1974). Shoots and young leaves account for 58 percent of intake. This less mobile species uses a booming roar which may serve to space the groups (Clutton-Brock, 1975). The difference in the biomass data of Struhsaker between the 2 *Colobus* species is due to the unequal distribution of *C. guereza,* which is located in drier places than the *C. badius* in this nonhomogenous environment. The maximum biomasses of *C. guereza* found in dry areas may be equal or higher (18 kg per hectare; Oates, 1974) than that of *C. badius.* As shown previously, the higher the maximum biomass (considered in an homogenous environment), the higher the proportion of ubiquitous food resource in the diet, since leaves are more abundant than fruits and mature leaves are more abundant than shoots and young leaves.

The 3 *Cercopithecus* species of the Kibale forest, *C. ascanius, C. mitis,* and *C. lhoesti* (1.6, 1.3, and 0.1 kg per hectare respectively), can be compared to the species of the Makokou forest in terms of feeding strategy and resulting biomasses (Struhsaker, 1975; Rudran, 1978). All of these species are frugivorous and use a large amount of leaves.

Cercocebus albigena forms groups of 15 ranging on 34 hectares (Waser and Floody, 1974) in the Kibale forest. The species biomass for the whole area is 0.6 kg per hectare (Struhsaker, 1975), but the maximum biomass is quite similar to that of *C. galeritus* in the Makokou forest.

The chimpanzee, *Pan troglodytes sweinfurthii,* is sympatric with all the previous species in Kibale, with a biomass of 0.3 kg per hectare.

Anthropoids as Folivores

Chimpanzees and gorillas are still abundant in the rain forest of the Makokou area, but the study of the wild populations of these anthropoids is not yet possible and very few direct observations have been published. These protected animals are extremely shy owing to the recent and continuing hunting pressures. In the field station of Makokou, we worked on anthropoids reintroduced into their natural environment on different islands along the Ivindo River. The ecological studies of semitame animals allowed a very detailed inventory of the diet of the chimpanzee, *Pan troglodytes troglodytes* (Hladik, 1973).

Chimpanzees

The average annual diet of the chimpanzee contains (in fresh weight) 28 percent leaves, shoots, and stems; 68 percent fruits and a few seeds; and 4 percent insects or small prey. When we investigated the composition of these foodstuffs, it was clear that the importance of leaves and shoots was balancing the amount of proteins in the diet (Hladik and Viroben, 1974). In the regular daily intake, leaf proteins are combined with some insect protein. Among the chief plant species eaten throughout the year, the amino acids are partly complementary; for instance, the leaves of *Baphia leptobotrys* contain very small amounts of leucine and threonine, while the shoots and stems of *Hypselodelphis violacea* have larger proportions of these amino acids in their protein. The relative proportion of histidine, leucine, lysine, and threonine is, nevertheless, too low in the protein of the whole plant fraction owing to an excess of valine (Table 3). The small amount of animal protein, from ants of different species, seems to just compensate this lack, but the diet would have a lack of cystine if the insects were not mixed with the plant protein.

Even in populations of chimpanzees which hunt for small-sized game (Teleki, 1973), leaf-eating is compulsory. This is necessary because the protein intake over a year from game is very low and prey is often not available to subadults (Wrangham, personal communication). This explains why the chimpanzees can afford to work for hours to gather the tiny leaf buds of *Baphia leptobotrys* (Figure 5) which weigh 0.05 g but contain 55 percent protein (dry weight).

Table 3.—Comparison of the relative proportions of the essential amino-acids in the vegetal and animal food samples accounting for most of the dietary protein ingested by the chimpanzee, *Pan troglodytes troglodytes,* in the forest of Gabon. The percentages of essential amino-acids are related to their sum. The "total average" is calculated according to the importance of each sample in the diet of the chimpanzee. (From Hladik and Viroben, 1974.)

Amino-acids	*Stems of Hypselodelphis violacea*	*Leaves of Baphia leptobotrys*	*Ants nest of Macromiscoides aculeatus*	*Ants and grubs of Oecophylla longinoda*	*Total average*	*Protein of egg as reference*
Cystine	4.55	7.7	2.7	1.75	5.86	4.8
Histidine	4.75	2.85	9.0	6.55	4.28	4.55
Isoleucine	10.95	11.5	11.3	12.4	11.59	10.4
Leucine	20.25	13.5	19.2	22.1	16.23	16.7
Lysine	10.45	8.65	12.9	15.0	10.36	13.9
Methionine	4.6	2.7	3.4	3.5	3.10	6.1
Phenylalanine	11.45	8.65	8.1	7.6	8.69	11.55
Threonine	11.75	7.9	11.3	10.2	9.01	9.25
Tyrosine	6.05	9.0	8.7	8.4	8.57	9.25
Valine	15.2	27.6	13.4	12.4	22.34	13.5

Figure 5. Chimpanzee, *Pan troglodytes troglodytes*, in the rain forest of Gabon, collecting the tiny shoots of *Baphia leptobotrys* (55 percent of protein content).

Figure 6. Gorillas reintroduced on a small island near Makokou. As leaf-eaters, they need a large amount of bulk and practice coprophagy whenever the leaves and stems are not available in sufficient quantity.

They feed throughout the year on *Baphia* leaves which yield 21.3 to 36.3 percent protein varying with the season. The geophagy which is regularly practiced by the chimpanzee, as well as by many folivorous primates, may facilitate the absorption of the leaf tannins (Hladik and Gueguen, 1974).

The supplying area of the forest-living chimpanzees is very large (Reynolds and Reynolds, 1965) in relation to the distribution of the trees producing large amounts of fruits. Nevertheless, the biomass is about 1.5 kg per hectare, very similar to that of the other primates using leaves as a complement for a frugivorous diet.

Gorillas

An adult gorilla (*Gorilla gorilla*) weighs about 4 times as much as a chimpanzee and can reach 200 kg; it is no longer arboreal at this stage. It feeds mainly on leaves and stems with fruits always being a smaller fraction of the diet. The main field studies concern the mountain gorilla, *G. gorilla beringei* (Schaller, 1963; Casimir, 1975; Fossey and Harcourt, 1977), but little is known about the lowland gorilla, *G. gorilla gorilla,* which may utilize more fruits in addition to the leaves (Sabater Pi, 1966; D'Arcy and Hladik, in preparation). Schaller described more than 100 plant species utilized by the mountain gorilla and watched some regular sequences of geophagy. A limited number of plant species accounts for a large amount of the food intake and, for long periods, bamboo shoots of *Arundinaria alpina* formed 90 percent of the diet of a group (Casimir, 1975). These bamboo shoots, rich in tryptophane, are a good complement for the protein of the leaves and bark of the other food species with which they are mixed in small quantity throughout the rest of the year.

The diet of *Gorilla* involves a large amount of bulk (lignin, cellulose, etc.) and some correlative differentiations of the digestive tract. The wild specimens examined have a relatively larger hindgut than all the species of primates that feed on fruits and leaves (Chivers and Hladik, in preparation). As a consequence of this adaptation, a large volume of fodder is required for a normal behavior. Coprophagy may be practiced under conditions of low food availability. For example, some reintroduced gorillas, living on too small an island near Makokou, destroyed most of the lianas and edible trees. As a result they were not able to find enough leaves to feed on. Every day, they ate their feces which contain much fiber (Figure 6) and perhaps some protein to recycle, as is the case for *Lepilemur*. In Rwanda, *G. g. beringei* also eats its fecal material when bad weather does not allow sufficient foraging time (D'Arcy, personal communication).

According to the field data of Schaller (1963) and those of Fossey and Harcourt (1977), the biomass of the mountain gorilla may vary from less than 1 kg per hectare to 2 kg. This is small when compared to other folivorous primates, but is probably related to the open type of vegetation. We do not have any comparative data for the rain forest of Gabon.

Hylobatidae

The gibbons and siamang have been studied in the rain forest of Malaya by Chivers (1971, 1973). Their comparative socio-ecology parallels the differences and similarities found among other primates feeding on leaves and fruits (Hladik and Chivers, 1974).

The white-handed gibbon *Hylobates lar,* is the smallest species (4 to 7 kg), feeding on fruits 70 percent of its feeding time. A family group of gibbons has a territory of about 50 hectares; thus the biomass is about 0.4 kg per hectare.

The siamang, *Symphalangus syndactylus,* is the largest species (10 kg). It spends 50 percent of its feeding time eating the leaves and shoots of many trees and vines; thus the amount of fruits ingested is smaller than that of the previous species. Among those fruits, the siamang may eat large amounts of immature fruits of different species of *Ficus.* Its feeding strategy resembles the strategy of the howler monkey; this convergence between the 2 species is also apparent in the ranging pattern. A small family group of siamangs is barely mobile in a small territory of 15 to 30 hectares, and the territorial calls, long-carrying in the rain forest, have a spacing function more apparent than those of the other gibbon species. The territories are separated by a buffering zone which lowers the total density of the siamang population. If we consider only what is effectively the supplying area for the groups in a study area, the maximum biomass may reach 8 kg per hectare (Chivers, 1973).

The socio-ecological patterns related to habitat utilization vary with the relative proportion of leaves in the diet. The siamang is more folivorous than the gibbon and forms small, barely mobile groups, and utilizes the most common food sources (Chivers, 1973). In the forest of Malaya, the leaves are used as staple food by the two sympatric species of *Presbytis, P. obscura,* the dusky leaf monkey, and *P. melalophos,* the banded leaf monkey (Curtin and Chivers, 1978).

The Colobinae

With a sacculated stomach and its associated bacterial flora and fauna of flagellates (Kuhn, 1964), the Colobinae show the best adaptation to leaf-eating among primates. The convergence toward the ruminant type of gut was demonstrated by Moir (1967), and the efficiency of such a system allows the utilization of mature coriaceous leaves as staple food. Nevertheless, all the species of Colobinae observed in the field utilize a certain amount of fruits or some seeds.

The ecology of 2 species of *Presbytis, P. senex* and *P. entellus,* have been investigated with respect to the particular use of the chemical environment. These 2 leaf-monkeys live in sympatry with 2 other primate species, *Macaca sinica* and *Loris tardigradus,* in the semideciduous forest of Polonnaruwa, Sri Lanka (Hladik and Hladik, 1972).

The purple-faced langur

Presbytis senex, the purple-faced langur, has been studied at the Polonnaruwa field station by Rudran (1970, 1973). This is a large species (12 kg) socially organized in "one-male groups" of 5 or 6 monkeys. They always stay in the canopy and do not move very much within a small territory of 3 to 4 hectares. The territorial loud calls of *P. senex* are related to intergroup spacing (Figure 7).

Figure 7. A group of *Presbytis senex* in the forest of Polonnaruwa. This group lives in a very small territory (1 hectare) and resources available are the minimum for survival.

The very high biomass of *P. senex* in Polonnaruwa (14.5 kg per hectare) can be related to a highly folivorous diet based on the most common tree species. This diet includes, in fresh weight, 60 percent leaves and shoots, 12 percent flowers and flower buds, and only 28 percent fruits (Hladik and Hladik, 1972).

One individual *P. senex* eats about 400 kg (fresh

Table 4.—Total food in kilograms (fresh weight) available per year for 1 monkey of the different groups of *Presbytis senex* in Polonnaruwa. (After Hladik and Hladik, 1972.)

	Adina cordifolia		*Schleichera oleosa*		*Other trees*
Groups	*Leaves*	*Flowers*	*Shoots*	*Fruits*	*Leaves*
A	1,300	60	240	65	1,100
B	3,500	160	380	105	2,200
C	2,100	100	420	115	2,200
D	4,700	215	350	100	2,000
E	3,500	160	510	160	2,000
F	1,000	50	200	55	2,800
G	6,500	300	300	85	5,800
H	600	30	130	35	1,000

weight) in 1 year. This is approximately one-tenth of what is available, if we consider the supplying area of each group and divide the total food available by the number of individual monkeys within a supplying area (Table 4). The calculation of the production of the different foodstuffs was made on an area of 54.5 hectares by a systematic recording of all the tree canopies and appropriate measures of production (Hladik and Hladik, 1972).

Eating one-tenth of the food production might be the maximum permissible for a folivore that utilizes a fairly large amount of shoots and young leaves (20 percent of the total food intake), without endangering the food plant population. In fact, in the supplying area of group H, which was reduced by the pressure of the dominant neighboring groups, the annual food available per monkey is less than 2000 kg (Table 4) and some trees of this area (*Alangium salvifolium*) were dying because the young leaves were eaten too frequently. Fitzgerald (1978) also found 1 tree species (*Metrosideros robusta*) killed by overbrowsing by the brush-tailed opossum (*Trichosurus*) recently introduced in New Zealand. The ecological adaptation of this opossum cannot be compared with that of the purple-faced langur because the opossums in the whole area feed too actively on 1 preferred tree species. This is a classical danger of introducing new species. One can expect that, in a similar manner in the past, several tree species have been exterminated when new forms of folivores colonized. The situation of *Presbytis senex* in Sri Lanka is the result of a long-term balance between the food species and the folivores. The tree species actually available are not overbrowsed, except by one group—which obviously will disappear. The normal situation of groups A, B, C, etc., is to maintain territories with little overlap (Rudran, 1970), including an average of 10 times or more of the food actually required.

The territorial system of *P. senex* allows a fairly homogenous distribution of the food resources among the different groups (Table 4). If we consider that the most common food resource may be different for different groups, then the small intraspecific variation of the diet may be related to local variations of the food available. This is the case for the howler monkey, *Alouatta* (Milton, 1978). Only a dozen tree species produce 90 percent of the food ingested by *Presbytis senex* and 2 of them, *Adina* and *Schleichera*, account for half of this food. The homogenous distribution of the common food plants allows each group to get its share in a fairly small supplying area (Hladik and Hladik, 1972). The ecology of the black and white colobus in Africa (Oates, 1974; McKey, 1978) is very similar to that of the purple-faced langur.

The gray langur

Presbytis entellus, the gray langur, inhabits the dry forest of Polonnaruwa, in sympatry with *P. senex*. This big colobine of about 15 kg forms large "age-graded male groups" of 20 to 30 individuals living in territories of 10 to 15 hectares (Ripley, 1967, 1970). There are important differences in the ecology of the 2 langur species, one of the most apparent being the reduced arboreality of the gray langur, which spends much time foraging or resting on the ground.

The diet of the gray langur is less folivorous than that of the purple-faced langur, but it includes more shoots and young leaves. The yearly average in fresh weight is 48 percent leaves, 7 percent flowers, and 45

Table 5.—Annual mean production in Kg (fresh weight) available for one individual of the different groups of *Presbytis entellus* for some of the most common food-producing tree species of the Polonnaruwa field station. [The identification as male or female of some *Drypetes* trees was not possible after the period of production; thus some figures are underestimated.]

	Walsura piscidia shoots	*Drypetes sepiaria*		*Ficus spp. fruits*	*Schleichera oleosa fruits*
		shoots	*fruits*		
North group	40	180	23.5	62.5	30
Central group	20	135	20	262	115
South group	(few)	>50	>10	197	40

percent fruits. Nevertheless, the maximum biomass of *P. entellus* is quite similar to that of *P. senex*, i.e., about 14 kg per hectare. Both species utilize shoots and young leaves. These are available to be cropped only in limited quantity and may be the limiting factor on langur biomass. Many fruits are utilized by the gray langur, when they are available; since they can be replaced by leaves when not available, however, they are not the core of the diet.

There is more variety in the food choices of *P. entellus* as compared to the monotonous diet of *P. senex*. Ninety percent of the food of *P. entellus* is made up of 25 plant species and 6 of them account for half of the total diet (versus 12 and 2 for *P. senex*). Several plant species are eaten by both langur species, but the proportions differ and there is no competition. For instance, the main food plants of *P. senex, Adina cordifolia* and *Schleichera oleosa,* account only for a small amount (4 and 3 percent) in the diet of *P. entellus* (Hladik and Hladik, 1972).

Some of the plant species eaten by the gray langur are not very common and the territorial system of large groups in fairly large areas is necessary to prevent the unequal distribution of unevenly scattered food sources (Hladik and Hladik, 1972). The differences in the spatial distribution of the main food trees used by the 2 sympatric langur species appears clearly in previously published figures (Hladik and Hladik, 1972).

According to what is eaten by the gray langur, the food available was calculated within the "supplying area" of each of the groups living at the Polonnaruwa field station. These total resources, divided by the number of monkeys in each group, are distributed fairly evenly, when taking into account the slight intraspecific dietary variations (Table 5). A system of small territories would have necessitated more overlaps in troop ranges to allow an equal access to the scattered food resources. On the other hand, the system of large groups with large territories is necessary as an antipredator device, to increase the level of vigilance of partially ground living primates (Crook and Gartlan, 1966). The red colobus is the African ecological equivalent of the gray langur, with only slight differences in the ranging pattern (Struhsaker, 1975, 1978).

Food choices and food composition among langurs

In both langur species, the food choices vary throughout the year, according to the food resources available in the different seasons. These annual variations (Figure 8) have been plotted on a graph according to the total food intake (fresh weight) observed at different seasons for *Presbytis senex* and *P. entellus* (Hladik, 1977). In the total annual food intake, *P. senex* utilizes more mature leaves (about 40 percent) than *P. entellus* (20 percent), which eats a higher proportion of shoots and young leaves. It is remarkable that, at any time of the year, the same type of difference characterizes the diet of each of the langur species. *P. entellus* is more frugivorous and eats more young leaves than mature leaves.

P. entellus which includes more species in its food choices is also more selective, choosing the fruits when they are available and the younger leaves instead of the mature ones. As a result, its diet yields more protein, more lipids, and more soluble glucids. But the seasonal variations have a stronger effect on the diet of *P. entellus* than on that of *P. senex*. The results of the analysis of the different food samples (Hladik, et al., in prep.), show the seasonal content in nutrients presents very little variation for *P. senex* (Figure 9), but large seasonal differences in the dietary pattern of *P. entellus*. In *P. entellus,* the rate of protein intake may be as low as 10 percent (dry weight) of the food intake, reaching 16 percent during the rainy season when the leaf buds and flushing

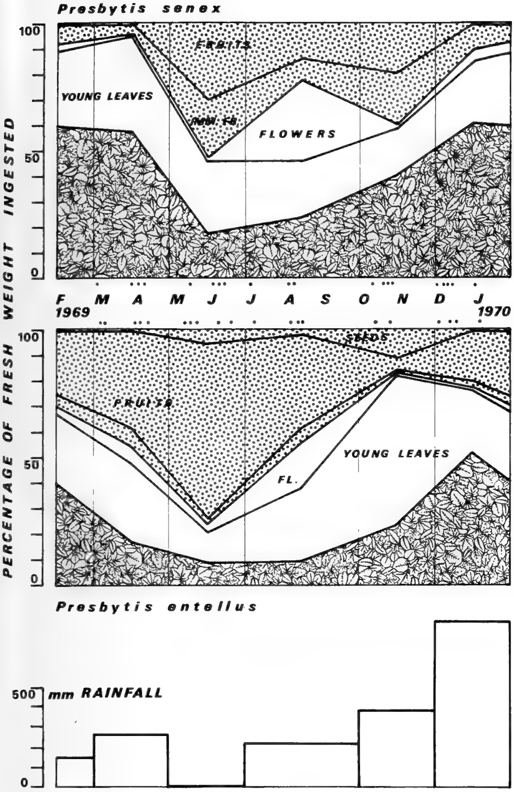

Figure 8. Seasonal variations in the natural diets of *Presbytis entellus* and *P. senex,* in relation to the rainfall which determined food availability during the period of study. Data were collected during continuous daily observations, noted as dots along the time axis. From bottom to top, the food categories are mature leaves; young leaves and shoots; flowers; immature fruits; mature fruits; seeds.

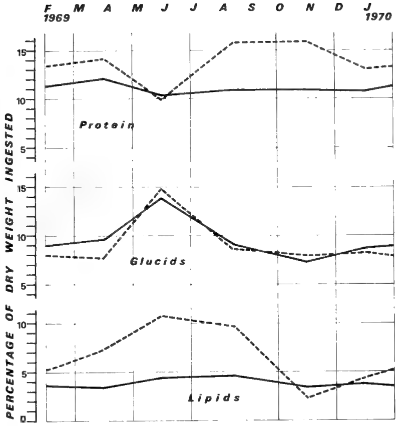

Figure 9. Annual variations in the composition of the diets of *Presbytis senex* (solid line) and *P. entellus* (dashed line).

are very abundant. Conversely, for *P. senex,* the protein content never exceeds 12 percent but is very stable. Similar differences between the langur species appear in the rates of intake of lipids, soluble glucids, and minerals, but the highest average rate is that of *P. entellus.*

As a result, *P. entellus* obtains much more energy from its environment, but it has to spend more energy than *P. senex* to find its more scattered food resources. As is the case for the other leaf-eating primates that feed partly on fruits, the gray langur is more mobile in its ranging and may have more frequent agonistic interactions with the neighboring groups along the territorial boundaries (Ripley, 1967); thus, feeding strategy and social strategy are complementary. The less mobile system of *P. senex* functions with more economy and without any change during the year.

Both langur species eat small amounts of earth. This geophagy which has been observed among most of the primates feeding on large amounts of leaves may have no connection with the mineral nutrition (Hladik and Gueguen, 1974). The mineral content of the earth samples is smaller than the content of the food samples for both sodium and zinc, which are the only elements that might be too low in the total diet.

Conclusions

Primary compounds versus secondary compounds

The selection of the natural food substances by different primate species can be related to their content in primary nutrients (soluble carbohydrates, lipids, and protein). Moreover, many alleochemics (Whittaker and Feeny, 1971; Janzen, 1970, 1978), like tannins, alkaloids, saponins, glycosides, etc., are present in the leaves and in different parts of the plants and some of these chemicals have been selected as repellent or toxic agents against leaf predators. The taste of these chemicals may act directly as a repellent against folivorous mammals. For example, a young gorilla observed in Makokou fed on different liana leaves on which the screening tests were negative (A. Hladik, 1978). A few other leaves had been chewed and then spat out and, for those leaves, the screening tests were positive, showing the possible presence of alkaloids.

Among many species of rainforest plants, the proportion of species with a high alkaloid content is very low (A. Hladik, 1978). Only 2 to 5 percent of the plant species might have high alkaloid levels possibly resulting from selection due to insect predation and may thus be toxic for mammals. In most of the leaves of the rain forests, the small amounts of alkaloids detected by the screening tests are less toxic than coffee is for man.

Tannins are present in some leaves and Feeny (1969) demonstrated in vitro that the binding of tannins with the protein of the leaves prevents their digestion by trypsin. This would not apply to primates with a microbial gut flora, as for example the Colobidae and *Lepilemur*. For the other species, large quantities of tannins may be a deterrent. We also have suggested (Hladik and Gueguen, 1974) that the soil rich in clay eaten in small quantities by most of the folivorous primates may act as an adsorbent of the tannins. This hypothesis originated with the observation of the utilization of clay with acorns by human populations that would otherwise not be able to eat the tannins of the acorn without this preparation.

The selection of secondary compounds as a plant adaptive strategy resulting from predation by insects is well documented (Janzen, 1978), especially for seeds. It is not obvious for leaves and especially for the leaves of the species of the rain forest, but there is another kind of plant adaptive strategy that can be caused by insect predators. This involves plant parts which are very poor in nutrients. These parts will then be positively selected by insect predators which will neglect them and look for other types of food. Thus, the poorest composition will be selected for in different plant species subject to predation. This strategy is complementary to the retention of toxic allelochemics by the plant parts that have a high nutrient content.

The most specialized folivorous primates can utilize those plant species with a low nutrient content, thanks to a physiological (and sociological) strategy such as the system described for *Presbytis senex,* specialized on *Adina cordifolia* leaves; probably the same situation pertains for *Colobus guereza* feeding on *Celtis durandii* leaves (Oates, 1974). These leaves yield very little nutrient (Table 2). The primates, like other mammals, have a territorial strategy that in most cases prevents overbrowsing. This adaptation is probably very recent, and there is probably very little selection for allelochemics due to the activities of folivorous primates.

The small amounts of nontoxic allelochemics in plants might have an important role in primate feeding behavior. The particular taste, even what humans have found to be very bitter or stringent, is a conditioning stimulus which might complement the long-term reaction of the folivorous primates and improve their efficiency in food-searching.

The role of the primary compounds is obvious when we consider the composition of the natural substances selected by the many frugivorous and partly folivorous primates, since the higher the content in soluble glucids and protein, the more positive the food selection by the primates (Hladik et al., in preparation, and unpublished data from Gabon and Madagascar). The secondary compounds have a secondary role in most of the cases on which we have collected precise data. One case, in our Sri Lanka study (Hladik and Hladik, 1972), concerns the fruits of *Strychnos potatorum* eaten by *Presbytis entellus* and not eaten by *Macaca sinica* which, however, eats the leaf petioles of this *Strychnos*. We found some unidentified alkaloid (not strychnine) in the fruits and nothing in the leaves, but very small amounts of alkaloids have been found in the 76 other leaf samples screened (Hladik et al., in preparation). Thus, the monkeys only need to avoid a few toxic plant species; the rest of their strategy is to balance their diet with different amino acids if they do not have a bacterial flora to synthesize those essential nutrients, or to detoxify the rare harmful allelochemics.

Ecological classification of the leaf-eating primates

The primate species can be distributed into 3 grades divided into finer ecological categories, according to their natural diet (Hladik, 1975), Eisenberg (1978) presents a general classification of the Mammalia in which those categories fit.

The first grade (Figure 10) concerns species utilizing the secondary production as a main source of energy. It includes the typical insectivores and different forms utilizing fruits and insects in different proportion.

The second grade concerns the primate species whose diet combines insects (or other prey) and some green plant parts, such as leaves, and eventually some seeds, as a protein complement for fruits. These species are from genera such as *Cebus, Cercopithecus, Macaca, Papio,* and *Pan*.

The third grade concerns species utilizing the primary production only. It includes the frugivorous and folivorous primate species obtaining their proteins

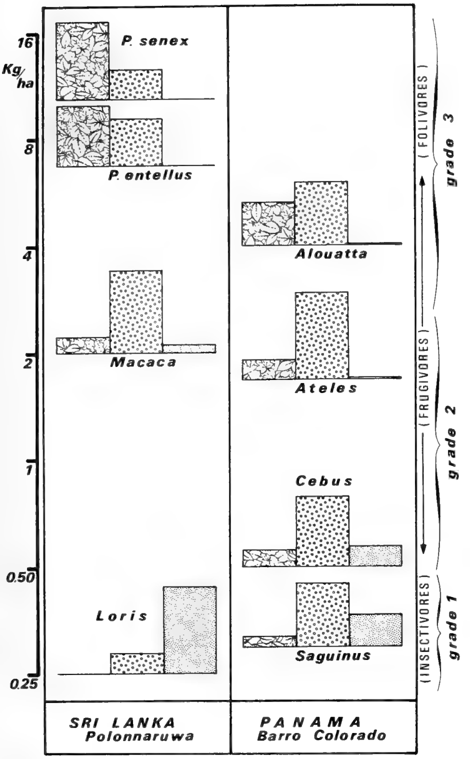

Figure 10. Relationship between the type of diet and the biomasses of primates in two different field stations. The different species are located on a vertical scale, according to the biomass observed in the field. For each species, the diagram represents the proportions of different food categories ingested in one year: leaves (left rectangle); fruits and seeds (central rectangle); insects and other prey (right rectangle). The three grades refer to the ecological classification of the diets presented in the discussion.

essentially from the leaves (*Ateles, Alouatta, Gorilla*). In this category, there is a progressive trend toward forms with either a large cecum and colon (*Lepilemur, Indri*), or a complex stomach (*Presbytis, Colobus*).

The evolution toward a partial or total folivore has occurred in several families of primates and in several parts of the world. In the different radiations, the body weight and the digestive tract have evolved simultaneously. The possibility of utilizing young leaves with a high protein content permitted the emergence of the large primate forms. In the rain forest, the complementarity of leaf phenological patterns of trees and lianas is the main factor on which those primates are dependent (A. Hladik, 1978). The most specialized folivorous primates are adapted to the most ubiquitous resources, that is, the leaves of some common trees that may have escaped insect predation by maintaining a composition with a minimum of nutrients.

There is a limit in the maximum biomass that the folivorous primates can attain. This level is reached when the animals eat about one-tenth of the food available in their supplying area, during a yearly cycle. This condition is the limit for an adequate balance between the food tree species and the monkeys: it has been selected to allow the maximum biomass, as demonstrated for *Lepilemur* and for 2 *Presbytis* species. This level is maintained by the territorial social system. The biomasses of ecologically equivalent species of primates are roughly similar in different forests. This is not surprising when the leaf production is almost the same, as in Gabon (A. Hladik, 1978) and in Panama (Leigh and Smythe, 1978). The folivorous primates crop a very small amount of the total leaf production: about 0.5 percent in the rain forest of Barro Colorado, and 4 percent in the dry forest of Polonnaruwa (Hladik and Hladik, 1972) where the tree species utilized are the most common ones. This low figure for the rain forest is related to the low production of shoots and young leaves and maybe to a selection of a small number of tree species; most of the animal forms are more specialized in the rain forest.

The utilization of common tree species or of the more scattered food sources is another important point correlated with the size of the home range and the extent of the overlaps which allow a homogenous distribution of the food resources in the different supplying areas. Thus, in the different grades (Figure 10) the slight differences in biomasses are related to slight ecological differences, either the proportion of leaves in the diet and/or utilization of common tree species.

It is not possible to say whether the evolution of the social structure resulted from the pressure of the ecological conditions or if the adaptation to the environment followed sociological evolution. It can be said rather that the co-evolution of sociology and ecology was necessary for the emergence of the leaf-eating primates.

Summary

A few specialized forms of primates utilize leaves as a staple food. For many other primate species, includ-

ing apes, the green vegetable fraction of the diet balances in different ways the intake of protein and the possibility for combination with the other available resources.

Among prosimians, *Lepilemur* is presented as an example of extreme specialization for folivory, with a primitive type of social organization and the smallest individual territory. The "supplying area" of the other prosimian genera is correlated with the relative proportion of leaves and fruits in the diet and with the body weight. A general law concerning body weights and diets of prosimians and simian primates is presented and discussed.

The frugivorous-folivorous simian primates show a similar pattern of ecological and sociological adaptations, as exemplified by the genera *Alouatta* and *Ateles* for whom leaves are required to provide adequate levels of dietary protein. A similar feeding strategy is also found in many cercopithecid genera. The "supplying area" and the maximum biomass are thus related to different models of habitat utilization which influence to a large extent the type of social organization.

The feeding behavior of the *Presbytis* and of other folivorous primates depends on primary compounds present in the natural substances. According to the latest data from field and laboratory studies, the secondary compounds play a secondary role in primate ecology.

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Introduction

In May 1970 I began a field study of the behavior and ecology of the red colobus monkey (*Colobus badius tephrosceles*) in the Kibale Forest of Western Uganda. The first phase of this study was completed in March 1972, (Struhsaker, 1975). In late August 1972, I resumed my studies in Kibale, continuing with the work on red colobus in addition to initiating a study on redtail monkeys (*Cercopithecus ascanius schmidti*) in the same study area. This work is still in progress and is part of a long-term study of primate behavior and ecology in the Kibale Forest.

Details on the Kibale Forest and the behavior and ecology of red colobus can be found in my monograph on red colobus (Struhsaker, 1975), but I shall present a brief résumé here for a better understanding of what follows. The Kibale Forest is just north of the equator in Western Uganda at an elevation ranging from 1110 m to 1590 m. The vegetation is extremely varied, but the major study area consists of moist evergreen forest having affinities with both montane rain forest and lowland tropical rain forest. Although much of the vegetation adjacent to the study area is of recent origin, the bulk of the forest in the study area is old and mature. Eight anthropoids live in Kibale: *Colobus badius, Colobus guereza, Cercopithecus ascanius, C. mitis, C. l'hoesti, Cercocebus albigena, Papio anubis,* and *Pan troglodytes.* The red colobus live in multi-male heterosexual groups averaging about 50 in number. Social groups have extensive overlap in home ranges. Intergroup relations vary from extreme tolerance to extreme aggression, but are essentially based upon an intergroup dominance hierarchy. My main study group (CW group), from which most of the data in this report were collected, was smaller than the typical red colobus group and averaged about 20 individuals. Their diet is comprised primarily of buds, young leaves, and leaf petioles.

The purpose of this report is to point out some of the less apparent aspects of *C. badius* feeding ecology and includes a consideration of their ecological stability, relation of activity and diet, "arthropod" feeding, food-item preferences, the relation between food-species preferences and the life-style of these food species, and the importance of floral predation by *C. badius* on fruit production.

Methods

Most of the data reported here were collected from August 1972 through March 1975. During this period, 21 monthly samples were made of the CW group. Each of these samples usually consisted of watching the group for 5 consecutive mornings near the beginning of each month. A total of 454.4 hours of observation was logged with the CW group during this time; combined with my observations of Kibale red colobus prior to August 1972, the total observation time amounts to 2048.1 hours. The morning samples of 1972-1975 included mapping the movements of the group, scoring food items, all social interactions and, for 14 of the monthly samples, scoring individual activity records. The techniques were the same as those described for the 1970-1972 phase (Struhsaker, 1975).

Factors Contributing to Stability

Stability in food habits

The feeding data for 1972-1975 (Table 1) are remarkably similar to those for 1970-1972. In both periods relatively few species accounted for a large proportion of the diet; the 10 most common food species accounted for 75.4 percent of the diet in the 19 monthly samples of 1970-1972 and, although somewhat different in composition, the 10 most common food species of 1972-1975 comprised 72.7 percent of the diet.

Computation of dietary overlap between the 12 monthly samples of April 1971-March 1972 and the 21 monthly samples of August 1972-March 1975 by summing the shared percentages (Holmes and Pitelka, 1968; Struhsaker, 1975) reveals 59.3 percent overlap when species-specific food items are considered. Clarification of this analysis is offered by the hypothetical case where 2 samples are compared for overlap in diet; in *sample I* the diet consisted of 40 percent of leaf buds of species A, 20 percent of flowers of species B, and 40 percent of mature leaf petioles of species C; whereas in *sample II* the diet consisted of 10 percent of leaf buds of species A, 10 percent of flowers of species B, 80 percent of leaf buds, but no mature leaf petioles of species C. The overlap between these two samples is the sum of their shared percentages, which is 20 percent (10 of A, 10 of B, zero of C).

Considering the differences in sample sizes and the lack of adjustment for intermonthly variation in availability of different foods, I feel that the overlap of 59.3 percent in species-specific food items is quite high. In the earlier study a similar analysis of overlap was carried out in which 17 monthly samples were compared. This analysis revealed an intermonthly overlap in species-specific food items which averaged 24.3 percent and ranged from 9.3 to 50 percent.

Consecutive months usually had the greatest percentage overlap and nonconsecutive months had less overlap. Comparison of two large time blocks (1970-1972 versus 1972-1975) increases the percentage overlap, but nevertheless the dietary diversity of red colobus combined with the relatively small samples (20-60 hours per month) makes improbable any greater overlap.

The overlap in plant-food species, regardless of the items eaten, between the 2 study periods was 74.7 percent and the overlap in plant items, regardless of species, was 83.3 percent. Both of these analyses lend support to the suggestion of long-term stability in the red colobus diet.

The dietary stability of red colobus in Kibale is even more evident upon examination of a cumulative list of food species which rises and levels off very quickly (Table 1A). Only 9 new food species were added to the total food list during the additional 454.4 hours of observation in 1972-1975. A similar analysis for the omnivorous redtail monkey yields a curve of very different shape, rising quickly, but not leveling off even after some 550 hours of observation (unpublished data). I think this interspecific difference simply re-

Table 1.—Feeding observations from 21 systematic monthly samples of CW group of *Colobus badius tephrosceles* (August 1972–March 1975). Data expressed as percentages of 2,399 scores

Key to Table 1 with corresponding symbols (*) from Struhsaker (1975, Tables 34 and 35) and (total percentages)

(*)
F? (a) = fruit of unknown age (1.5)
RF (b) = ripe fruit (1.6)
UF (c) = unripe fruit (1.1)
S (d) = seeds (1.4)
Fl (e) = flowers (3.8)
FlB (f) = flower buds (12.1)
LB (g) = leaf buds (14.5)
?YL (h?) = young leaves unspecified age (1.3)
LYL (h2) = large-sized young leaves (11.1)
MYL (h3) = medium-sized young leaves (4.5)
SYL (h4) = small-sized young leaves (5.0)
vSYL (h5) = very small-sized young leaves (1.8)
PLYL (i2) = petioles of large-sized young leaves (0.58)
PMYL (i3) = petioles of medium-sized young leaves (1.4)
PSYL (i4) = petioles of small-sized young leaves (1.3)
P?YL (i?) = petioles of unspecified age young leaves (0.17)
ML (j) = mature leaves (3.3)
PML (k) = mature leaf and leaflet petioles (15.5)
piML (m) = pieces of mature leaves (3.4)
atML (n) = apical tip of mature leaf (1.2)
bML (o) = basal part of mature leaf (0.25)
L? (p) = leaves of unknown age (8.0)
St (r) = young stem tips or stems (0.54)
Ot (s–u) = miscellanous categories (*see* Struhsaker 1975) (4.72)

Food species (and %)	*Food item and %*
Albizia grandibrachteata Taub. (0.041)	Fl 0.041
Albizia gummifera (Gmel.) C.A. Sm. (2.38)	Fl 0.38, FlB 0.33, LB 0.38, ?YL 0.25, LYL 0.38, PMYL 0.041, PML 0.58, Ot 0.041
Aningeria altissima (A. Chev.) Aubr. & Pellegr. (13.7)	UF 0.041, Fl 1.2, FlB 3.6, LB 4.6, LYL 0.13, MYL 0.083, SYL 0.50, vSYL 0.79, PLYL 0.13, PMYL 0.041, PML 2.5, Ot 0.12
Aphania senegalensis (Juss. ex Bernh) Radlk. (0.041)	piML 0.041
Balanites wilsoniana Dawe & Sprague (1.3)	UF 0.083, MYL 0.13, SYL 0.17, PMYL 0.041, PML 0.5, piML 0.083, St 0.29
Bosqueia phoberos Baill. (2.8)	LYL 2.5, MYL 0.13, ML.0.041, PML 0.041, piML 0.041, L? 0.041
Cardiospermum grandiflorum Sw. (0.29)	MYL 0.13, ML 0.083, L? 0.041, St 0.041
Cassipourea ruwenzorensis (Engl.) Alston (0.13)	LYL 0.083, MYL 0.041
Celtis africana Burm. f. (14.8)	FlB 4.9, LB 8.6, LYL 0.13, MYL 0.21, SYL 0.54, vSYL 0.33, PML 0.083, atML 0.041
Celtis durandii Engl. (3.7)	F? 1.3, UF, 0.46, Fl 0.041, LB 0.33, LYL 0.21, MYL 0.46, SYL 0.46, vSYL 0.21, Ot 0.041
Chaetacme aristata Planch. (1.4)	LYL 1.2, ML 0.041, PML, 0.041, Ot 0.13
Chrysophyllum gorungosanum Engl. (0.8)	LYL 0.041, ML 0.17, PML 0.041, piML 0.38, atML 0.21
Cordia millenii Bak (0.42)	MYL 0.083, SYL 0.041, PMYL 0.21, PML 0.041, Ot 0.041
Diospyros abyssinica (Hiern) F. White (0.17)	PML 0.083, Ot 0.083
Dombeya mukole Sprague (3.9)	Fl 0.083, LYL 0.67, MYL 1.4, SYL 0.33, ML 0.50, PML 0.13, piML 0.083, L? 0.63, Ot 0.041
Elaeodendron buchananii Oliv. (0.54)	LYL 0.50, MYL 0.041
Fagara angolensis Engl. (0.041)	MYL 0.041
Fagaropsis angolensis Engl. (0.33)	SYL 0.041, PML 0.13, piML 0.041, atML 0.041, Ot 0.083
Ficus brachylepis Welw. ex Hiern (1.1)	UF 0.13, LYL 0.33, SYL 0.17, ML 0.38, atML 0.083
Ficus capensis Thunb. (0.041)	LYL 0.041
Ficus exasperata Vahl (0.041)	Ot 0.041
Ficus natalensis Hochst. (0.46)	F? 0.083, UF 0.041, LYL 0.21, SYL 0.041, ML 0.083
Funtumia latifolia (Stapf) Stapf ex Schltr. (2.3)	S 0.13, Fl 0.33, FlB 0.21, ML 0.79, piML 0.54, atML 0.083, bML 0.083, Ot 0.12
Illigera pentaphylla Welw. (0.041)	?YL 0.041
Lovoa swynnertonii Bak. f. (2.3)	UF 0.083, LB 0.041, LYL 0.21, MYL 0.083, SYL 1.1, vSYL 0.041, PMYL 0.041, PML 0.63, Ot 0.083

Table 1.—Feeding observations . . ., cont.

Food species (and %)	*Food item and %*
Markhamia platycalyx (Bak.) Sprague (10.3)	Fl 0.54, FlB 1.8, LB 0.29, LYL 0.041, SYL 0.29, vSYL 0.17, PLYL 0.041, PMYL 0.75, PSYL 0.88, PML 5.4, Ot 0.17
Millettia dura Dunn (1.7)	Fl 0.13, FlB 0.13, LB 0.041, LYL 0.29, MYL 0.58, SYL 0.54
Mimusops bagshawei S. Moore (4.8)	RF 0.50, LB 0.041, LYL 0.083, ML 0.54, PML 2.2, piML 0.33, atML 0.58, bML 0.083, L? 0.041, Ot 0.41
Monodora myristica (Gaertn.) Dunal (0.041)	piML 0.041
Newtonia buchanani (Baker) Gilb. & Bout. (9.5)	UF 0.083, Fl 0.33, LB 0.083, ?YL 0.96, LYL 0.96, P?YL 0.041, L? 7.0, Ot 0.041
Olea welwitschii (Knobl.) Gilb. & Schellenb. (0.50)	LYL 0.13, PML 0.29, Ot. 0.083
Pancovia turbinata Radlk. (0.25)	MYL 0.083, vSYL 0.17
Parinari excelsa Sabine (2.9)	LB 0.083, LYL 1.42, PLYL 0.083, PML 0.33, piML 0.25, Ot 0.67
Pinus caribaea (0.083)	ML 0.041, bML 0.041
Premna angolensis Guerke (0.50)	LYL 0.13, MYL 0.083, SYL 0.041, PLYL 0.083, PML 0.083, Ot 0.083
Pseudospondias microcarpa (A. Rich) Engl. (0.25)	FlB 0.083, piML 0.041, Ot 0.041
Reissanta parvifolia (oliv.) Halle (0.38)	UF 0.041, Fl 0.21, FlB 0.041, PML 0.041, atML 0.041
Rhipsalis baccifera (J. S. Mill) Stearn (0.13)	F? 0.041, St 0.041, Ot 0.041
Sapium ellipticum Pax (0.13)	SYL 0.13
Spathodea nilotica Seem. (0.29)	P?YL 0.13, PML 0.17
Strombosia scheffleri Engl. (6.3)	F? 0.041, UF 0.041, S 1.2, Fl 0.21, FlB 0.50, LYL 0.13, MYL 0.13, SYL 0.17, PLYL 0.21, PMYL 0.25, PSYL 0.041, ML 0.041, PML 1.7, piML 1.2, atML 0.041, Ot 0.38
Symphonia globulifera L. (0.17)	S 0.041, LYL 0.083, PLYL 0.041
Teclea nobilis Del. (2.4)	F? 0.041, RF 0.96, UF 0.083, Fl 0.17, FlB 0.42, LYL 0.50, MYL 0.083, SYL 0.083, atML 0.083
Trema guineensis Ficalho (0.42)	LYL 0.041, ML 0.17, L? 0.21
Trichilia splendida A. Chev. (1.4)	Fl 0.13, FlB 0.041, MYL 0.041, SYL 0.21, vSYL 0.083, PSYL 0.42, ML 0.083, PML 0.17, piML 0.25
Urera cameroonensis Wedd. (0.50)	LYL 0.25, MYL 0.083, ML 0.083, PML 0.083
Usnea-like lichen (0.13)	Ot 0.13
Uvaria angolensis Oliv. (0.17)	MYL 0.17
Xymalos monospora (Harv.) Baill. (0.29)	LYL 0.083, SYL 0.041, piML 0.083, Ot 0.083
Epiphyte spp. (0.33)	LYL 0.041, bML 0.041, St 0.17, Ot 0.083
Lichen spp. (0.88)	Ot (0.88)
Liana spp. (0.83)	FlB 0.041, LYL 0.29, MYL 0.083, SYL 0.041, ML 0.21, PML 0.17
Tree spp. (0.42)	LYL 0.041, MYL 0.21, SYL 0.041, PML 0.041, Ot 0.083
Strangler *Ficus* (0.041)	MYL 0.041
Moss sp. (0.38)	Ot 0.38
Probable invertebrate (0.33)	Ot 0.33
From lichen-covered branch (0.041)	Ot 0.041
Ficus sp. (0.083)	LB 0.083

flects a basic phenomenon of rain-forest ecology. Leaves and buds are available more often and for longer periods of time in tropical, moist evergreen forests than are flowers and fruits, which often occur only at very long and infrequent intervals for a given species. Consequently, the complete diet of a folivore is more likely to be available during any given study period than is the complete diet of a highly frugivorous species.

Stability in activity patterns

The red colobus time budget in the 1972–1975 sample was essentially the same as in 1970–1972. Activity records (n = 3,888) were gathered rather uniformly at

Table 1a.—Cumulative number of *Colobus badius* plant-food species

Date of sample	*Hours of observation*	*Cumulative hours of observation*	*Number of new plant-food species*
Sept '70	83.1		24
Oct	112.3	195.4	6
Nov	138.4	333.8	12
Dec	97.8	431.6	2
Jan '71	85.1	516.7	4
Feb	81.8	598.5	3
March	67.7	666.2	2
April	78.1	744.3	0
May	71.5	815.8	1
June	53.6	869.4	1
July	32.2	901.6	1
Aug	68.9	970.5	0
Sept	69.5	1,040.0	0
Oct	57.5	1,097.5	0
Nov	49.3	1,146.8	1
Dec	53.3	1,200.1	0
Jan '72	45.7	1,245.8	5
Feb	43.5	1,289.3	0
March	42.8	1,332.1	0
Sept	17.6	1,349.7	0
Oct	20.3	1,370.0	2
Nov	20.7	1,390.7	0
Feb '73	21.7	1,412.4	3
March	21.9	1,434.3	1
April	21.7	1,456.0	0
May	22.6	1,478.6	1
June	23.1	1,501.7	0
July	23.5	1,525.2	0
Aug	23.5	1,548.7	1
Nov	24.9	1,573.6	0
Dec	23.4	1,597.0	0
Jan '74	22.4	1,619.4	0
Feb	23.0	1,642.4	0
April	20.4	1,662.8	0
May 2-6	23.2	1,686.0	1
May 27-31	23.3	1,709.3	0
Nov	18.5	1,727.8	0
Dec	18.3	1,746.1	0
Jan '75	20.3	1,766.4	0
March	20.0	1,786.4	0
Total			71

Note: The data for September 1970 through March 1971 come primarily from CW group and those from April 1971 through March 1975 come exclusively from CW group.

half-hour intervals from 0700 hours through 1130 hours during 14 monthly samples (January 1973–May 1974) in essentially the same manner as in the first phase of the study. The methodological exceptions were as follows: (1) In the 1972–1975 sample, feeding was subdivided into 3 subcategories which were ingestion, chewing, and foraging. Foraging in turn was subdivided further according to motor patterns employed and substrate foraged in. (2) The behavior pattern referred to as scanning was scored separately. It consists of slowly moving the head back and forth, up and down, or from side to side in obvious visual inspection. In the 1970–1972 sample, this pattern was included with the category of sitting. (3) In the first 3 of the 14 monthly samples all non-foraging behavior was lumped into one category. (4) Scanning was not scored in the first monthly sample, but was tallied in the remaining 13 months.

For each of the 10 sample time periods (0700–1130 hours), a mean value was computed for each activity based on the last 11 monthly scores. These mean values were compared with the mean values for the same time periods in the 12-month sample of August 1970–August 1971. Feeding (ingestion, chewing, and foraging) averaged 38.9 percent (25.7 to 50.3 percent, S. D. 8.18) in 1973–1974 compared to a mean of 45.2 percent (38.0 to 59.4 percent, S.D. 6.36) in the 1970–1971 sample; these differences were not significant ($t = 1.934$, $0.1 > p > 0.05$, 2-tailed). A similar analysis was carried out for resting (sit and scan) and again the differences between the 1973–1974 sample ($\bar{x} =$ 36.8 percent, 23.1–49.3 percent, S.D. 7.43) and the 1970–1971 sample ($\bar{x} =$ 34.6 percent, 21.5–41.3 percent, S.D. 6.05) were not significant ($t = 0.740$, $0.5 > p > 0.4$, 2-tailed).

Stability in home range.

The home range of the main study group remained essentially unchanged during the entire study. Ranging data for 20 monthly samples (August 1972–January 1975) of the CW group of red colobus were analyzed in the same manner as previously described for the 17 monthly samples of November 1970 through March 1972 (Struhsaker, 1975). A grid system comprised of 0.25 ha quadrats was superimposed over the daily range maps and the amount of time spent in each specific quadrat was tallied. In the sample of 1970–1972, consisting of 1107 tally-hours, the CW group used 277 different 0.25 ha quadrats. In the August 1972–January 1975 sample, consisting of 669 tally-hours, they used 175 0.25 ha quadrats. Twenty-two (12.6 percent) of these latter 175 quadrats were "new," i.e., not used in the 1970–1972 sample. These new quadrats were rather uniformly scattered along the periphery of the home range and did not represent a movement into an entirely new area of 22 contiguous quadrats. That these new quadrats did not constitute an important shift in home range is further supported by the fact that only 9.3 percent of the tally time was spent in them; 90.7 percent of the tally time was spent in "old" quadrats also used by the group in the 1970–1972 sample. The distribution of time in these quadrats was much the same in both sample periods.

Overlap in home-range utilization between these 2 periods was computed in the same manner as the percentage overlap in diet. The shared percentages of time spent in each specific quadrat for the 2 sample periods were summed. The percentage overlap in the distribution of time in space for the 1970–1972 and 1972–1975 samples was 47.5 percent. In view of the differences in sample size between the 2 periods, I think this represents fairly extensive overlap and suggests long-term stability in ranging patterns. This conclusion is further supported by an analysis of intermonthly overlap in home range utilization of the 17 months of 1970–1972. In these 136 pair-combinations, the maximum overlap was 34.6 percent (Struhsaker, 1975).

Feeding by Red Colobus

The influence of diet on activity patterns

Assuming that the rumenlike digestive system of red colobus responds to high concentrations of crude fiber and lignin in a manner similar to that of true ruminants, one would expect a slower digestive rate and passage time of meals comprised of high proportions of mature leaf blades than those containing mostly buds or young leaves because older plant growth generally has greater concentrations of fiber and lignin than young growth (e.g., Short, et al., 1974). It is also possible that mature leaves of many of the food trees contain toxic compounds which demand detoxification and thereby lengthen passage and digestion time. If these assumptions are correct, one might expect that the proportion of mature leaf blade in the red colobus diet would have a direct bearing on the feeding and resting aspects of their time budget. This hypothesis should be tested with continuous or nearly continuous observations of specific individual monkeys. The observation conditions at Kibale, however, prohibit adequate longitudinal samples of this nature. Consequently, we must be satisfied for the moment with a less precise test of these relations.

The proportion of the monthly diet comprised of mature leaf blades (including scores of entire blade, pieces of the blade, apical tip and basal part of the blade, but excluding petioles and petiolules) was compared with the proportion of the monthly activity scores made up of feeding (including ingestion and chewing, but excluding foraging) and of resting (including sitting and scanning) for 11 monthly samples (May 1973–June 1974, Table 2). There was no significant correlation between the amount of mature leaf blade in the monthly diet and the proportion of feeding ($r_s = 0.045$, $p > 0.05$) nor the proportion of resting ($r_s = 0.155$, $p > 0.05$). This lack of correlation could be due to the imprecision of the sampling method or to the apparent fact that red colobus generally eat very little mature leaf blade and, consequently, their activity cycle may be relatively unaffected by the small amount they do eat.

Table 2.—Relation between red colobus diet and time budget

Month of sample	*Feeding % of scores*	*Resting % of scores*	*% Mature leaf in diet*
May 1973	32.5	44.3	21.3
June	35.1	33.4	13.1
July	39.4	33.1	13.3
Aug	35.6	40.3	10.0
Nov	32.1	37.8	4.7
Dec	24.9	42.2	11.0
Jan 1974	42.5	32.8	3.3
Feb	31.2	43.2	2.0
April	37.6	30.8	2.1
May	29.8	38.0	11.1
June	34.8	32.4	12.1

Foraging and probable arthropod feeding

Although direct evidence of red colobus eating insects or other arthropods is virtually nonexistent, there are 2 lines of indirect evidence clearly indicating that they do.

The first kind of indirect evidence concerns an activity which I have termed arthropod foraging behavior. Red colobus forage in 2 basic ways. The most common method consists of manual manipulation and visual examination of the leaf or other substrate being foraged. The second and much less common method consists of climbing along the undersurface of a tree branch while hanging in an upside-down posture. Foraging was systematically scored along with other activities for 14 monthly samples (January 1973–May 1974). Arthropod foraging comprised on average only 3.7

Table 3.—Diurnal variation in red colobus feeding behavior

	$\bar{X}$ % *of monthly samples*										
Time of sample	*0700*	*0730*	*0800*	*0830*	*0900*	*0930*	*1000*	*1030*	*1100*	*1130*	$\bar{X}$ *of preceeding 10* $\bar{X}$*s*
Forage	0.56	6.13	1.82	3.15	3.55	4.30	3.26	4.63	4.99	4.97	3.74
Feeding (ingestion and chewing)	49.16	44.85	38.88	39.59	31.43	39.86	29.82	34.43	25.06	21.18	35.43
Scanning	2.99	1.23	2.48	1.20	2.07	1.77	1.13	1.33	2.03	2.30	1.85

N = 3,888 scores; 0700 hours sampled only during 10 months; foraging scored in 14 months; feeding in 11 months, and scanning in 13 months.

percent of the activity scores.[1] The frequency of foraging varied considerably between the sample periods of 0700–1130 hours (Table 3), but does not correlate with the diurnal variation of feeding (ingestion and chewing) ($r_s = -0.345$, $p > 0.05$). Although some of the foraging peaks coincide with feeding peaks, such as at 0730 and 0930 hours, others do not. Some of the latter occur in late morning when feeding is generally at a low level and these foraging peaks (1100 and 1130 hours) may be related to higher temperatures and increased arthropod activity and thereby greater detectability. Scanning, as described earlier, was thought to be related to feeding and/or foraging. However, correlation coefficients show no significant relation between its frequency of occurrence and that of feeding ($r_s = 0.042$, $p > 0.05$) or of foraging ($r_s = -0.285$, $p > 0.05$). Scanning is probably related to other activities in addition to feeding and foraging, such as social spacing and social interactions.

A total of 147 foraging scores were tallied (Table 4). The single most important species-specific substrate was the mature leaf of *Strombosia scheffleri* (36.1 percent). *Strombosia* was also the most important species in which foraging occurred (37.4 percent) and mature leaves, regardless of species, were the most important general substrates in foraging (78.2 percent). That mature leaves constitute the most important substrate for foraging is not too surprising in an evergreen forest. Although having a large crown and being fairly abundant in the study area, *Strombosia* is by no means the most common evergreen species nor the one providing the greatest amount of crown area. It does, however, demonstrate a very high degree of insect damage on its mature leaves, as will be shown in detail later.

The second line of indirect evidence for arthropod feeding is based on the ingestion of small and unidentifiable objects; these, based on the motor patterns of procurement and substrates involved, were judged to be arthropods. These objects were so small that usually they were not visible to the observer and it is possible that on some occasions the objects were plant material rather than arthropods. Of the 2399 feeding scores for the 1972–1975 period, only 62 (2.6 percent) were classified as probable and exclusively arthropods. The majority of these objects were taken with slow movements: 59.7 percent by the slow application of the mouth directly to be substrate, 11.3 percent by removal from the substrate with a slow one-handed pickoff. Only 3.2 percent were obtained with a rapid grab, and the mode of procurement was not noted in 25.8 percent of the cases. These results suggest that red colobus are primarily eating slow-moving or relatively immobile forms of arthropods. This in turn seems related to the reduced thumb of red colobus which hinders manual dexterity and to their heavy body weight which makes difficult stealthful stalking of rapid-moving arthropods.

The single most important species-specific substrates from which arthropods were obtained were mature leaves of *Strombosia* (9.7 percent) and dead leaves of *Parinari* (9.7 percent) (Table 4). Likewise, *Strombosia* and *Parinari* are the 2 most important species, regardless of substrate, for arthropod procurement—and together account for 37.1 percent of the catches. Mature leaves (32.3 percent) were the important substrates, regardless of species, from which arthropods were taken, although branches (25.8 percent) and dead leaves (22.6 percent) were also very important. In

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[1] The mean value of the monthly means for each of the 10 sample time periods, 3.7 percent, is and was computed in the same way as for feeding and resting.

Table 4.—"Arthropod" feeding and foraging data for red colobus; feeding scores collected during 21 monthly samples (August 1972–March 1975) and foraging scores collected during 14 monthly samples (February 1973–May 1974). Data expressed as % of total scores.

Species	*Mature leaf*		*Branch*		*Dead leaf*		*Moss*		*Lichen*		*Large young leaf*		*Monocot epiphyte*		*Total %* *Feeding*	*Total %* *Foraging*
	fd	*fo*	*fd*	*fo*	*fd*	*fo*	*fd*	*fo*	*fd*	*fo*	*fd*	*fo*	*fd*	*fo*		
Parinari	3.2	6.8	1.6		9.7	1.4	3.2	1.4			1.6				19.4	9.52
Strombosia	9.7	36.1	3.2	1.4	3.2		1.6								17.8	37.4
Funtumia	4.8	6.8	1.6	3.4											6.5	10.2
Markhamia	3.2	1.4			3.2			0.7							6.5	2.0
Aningeria	1.6	1.4	3.2	1.4				0.7							4.8	3.4
Fagaropsis	1.6		1.6						1.6						4.8	0
Mimusops	1.6	8.2			1.6										3.2	8.2
Lovoa		1.4	1.6	2.0	1.6										3.2	3.4
Celtis africana		0.7	3.2												3.2	0.7
Olea		0.7	3.2												3.2	0.7
Blighia unijugata Bak.							3.2								3.2	0
Diospyros	1.6	2.7													1.6	2.7
Albizia gummifera		1.4	1.6												1.6	1.4
Dombeya					1.6					1.4					1.6	1.4
Trichilia		0.7	1.6												1.6	0.7
Pseudospondias		0.7	1.6												1.6	0.7
Cordia	1.6														1.6	0
Ficus exasperata	1.6														1.6	0
Newtonia			1.6												1.6	0
Premna	1.6														1.6	0
Aphania		4.1													0	4.1
Balanites		0.7*										0.7			0	1.4
Chrysophylum		1.4													0	1.4
Xymalos		1.4													0	1.4
Symphonia		0.7													0	0.7
Pancovia												0.7			0	0.7
Bosqueia								0.7							0	0.7
Tree spp.		1.4		3.4	1.6	0.7	4.8	0.7	1.6	0.7			1.6	0.7	9.7	7.5
Total	32.3	78.2	25.8	11.6	22.6	2.0	12.9	4.1	3.2	2.0	1.6	1.4	1.6	0.7		

fd = feeding,
fo = foraging
N = 62 feeding scores.
N = 147 foraging scores.
*Large leaf of unknown age

general, the trends of these results correspond well with the trends of the foraging data (Table 4). For example, mature leaves, those of *Strombosia* in particular, were important in both sets of data. There are, however, some notable differences in the relative importance of some species and substrates between the foraging and arthropod-feeding data (Table 4). Some of these differences can be reconciled if one considers another probable source of arthropod food. It has been suggested earlier (Struhsaker, 1975) that feeding scores classed as "pieces of mature leaf" probably included insect galls as well. This suggestion is especially convincing in those cases where the monkey carefully and slowly turns over and examines the undersurface of a series of mature leaves and then slowly applies its mouth to the center of one of these leaves and bites out a very small piece of the leaf. Accepting this class of feeding scores as a source of arthropod food increases the arthropod portion of the red colobus diet by 3.4 percent (Table 1), giving a total of 144 scores (6.0 percent of total). Of these 144 scores, 24.3 percent were from *Strombosia* mature leaves, which compares with a foraging score for the same substrate of 36.1 percent. Moreover, 102 (70.8 percent) of these 144 scores were from mature leaves, which corresponds very well with the foraging score of 78.2 percent. *Funtumia* mature leaves account for 11.1 percent of these scores compared to a foraging percentage of 6.8 percent. The correspondence is similarly improved for the mature leaves of *Mimusops:* 6.3 percent of the arthropod feeding and 8.2 percent of the foraging.

Many nonruminant mammals are dependent on animal food for vitamin B_{12}. It is well established that the microbes in true rumens are capable of producing B_{12} in amounts adequate for their host. Occasionally there may be a deficiency of B_{12} if normal bacterial action does not take place in the rumen owing to heavy loads of internal parasites or nutritional deficiencies (Morrison, 1957). Of the latter, one of the most important concerns cobalt, which comprises 4 percent of vitamin B_{12}. The estimated cobalt requirement of ruminant animals is several times greater (approximately 70-200 times greater) than that included in the required B_{12} of nonruminants. This difference is related to the inefficiency of the biosynthesis of B_{12} in the rumen and to the greater requirement of ruminants for cobalt in order to synthesize a coenzyme form of B_{12} which is involved in an intermediate step in the metabolism of propionic acid. Propionic acid is of greater importance in the energy metabolism of ruminants than in nonruminants (Hayes and Swenson, 1970). Oxnard (1969) provides indirect evidence suggesting that B_{12} is synthesized by microbial symbionts in the rumenlike stomach of two species of langur monkeys which are also members of the subfamily Colobinae. A similar situation may exist for red colobus. Their probable animal (arthropod) food constitutes only 6 percent of the total diet and would seem to be of relatively little importance. If so, why do they spend any time foraging for and feeding on arthropods? The metabolic capabilities of the stomach microbes in red colobus are virtually unknown. It may be that they, like some ruminants, require exogenous sources of B_{12} (Bryant, 1970) or that animal food is ingested to supplement the cobalt requirements of their B_{12}-producing stomach microbes.

Leaf damage by insects as it relates to red colobus food habits

Part of my long-term study at Kibale involves monthly samples of the phenology of 85 individually marked tree specimens representing 11 species. In November 1974, I also began scoring for these same trees the relative leaf damage, presumably and apparently caused by insects. Five classes of damage were scored, ranging from 0 to 4 (maximum damage) (Table 5). *Strombosia* mature leaves generally had the greatest insect damage, and this correlates well with the importance of this substrate as a source of red colobus foraging and arthropod food. Similarly, the incidence of mature leaf damage in *Markhamia* and *Funtumia* corresponds rather well with their utilization by red colobus for arthropod food. In contrast, *Parinari* shows less mature leaf damage than one would expect based on its importance to the red colobus as a source of arthropod food. Apparently, the arthropods that red colobus procure from *Parinari* mature leaves are not feeding on these leaves. Doyle McKey (personal communication) has suggested that insects may be feeding on the petiolar glands of *Parinari* mature leaves. *Celtis africana, Aningeria,* and especially *Celtis durandii* show proportionally much more mature leaf damage than one would except from their role in providing the red colobus with insects. Perhaps the insects exploiting these trees are too mobile or unpalatable for red colobus. *Teclea* fits this pattern to a lesser extent, but its mature leaf damage is generally low. *Lovoa, Symphonia,* and especially *Diospyros* show very little mature leaf damage and are correspondingly little exploited by red colobus for arthropods. Young leaves of all species are virtually undamaged by insects and this relates to the low incidence of foraging and insect-feeding in them by red colobus.

Insect damage to mature leaves does not correlate well with the factor of whether or not red colobus eat

Table 5.—Insect damage to leaves of 84 trees in phenology sample in compartment 30, Kibale Forest, Uganda.

Family	*MATURE LEAVES* *Species and number of specimens in sample*	*Nov. 1974 29 & 30th*		*Dec. 1974 28 & 29th*		*Jan. 1975 27 & 28th*		*March 1975 2 & 3d*		*March 1975 30th*	
Ulmaceae	*Celtis africana* (5)	1.8†	1-4* n = 5	1.8	1-2 n = 5	1.8	1-3 n = 5	1.75	1-3 n = 4	2.2	1-3 n = 5
Rutaceae	*Teclea nobilis* (5)	0.4	0-2 n = 5	1.0	1 n = 5	1.2	1-2 n = 5	1.2	1-2 n = 5	2.0	2 n = 5
Ebenaceae	*Diospyros a.* (10)	0.0	n = 10	0.2	0-1 n = 10	0.0	n = 10	0.9	0-1 n = 10	0.9	0-1 n = 10
Sapotaceae	*Aningeria* (5)	1.2	0-3 n = 5	1.75	1-2 n = 4	1.2	1-2 n = 5	1.2	1-2 n = 5	1.6	1-3 n = 5
Guttiferae	*Symphonia* (5)	0.0	n = 5	0.0	n = 5	0.2	0-1 n = 5	0.6	0-1 n = 5	0.4	0-1 n = 5
Apocynaceae	*Funtumia* (9)	0.89	0-2 n = 9	1.0	0-2 n = 9	1.0	1 n = 9	1.33	1-2 n = 9	1.22	1-2 n = 9
Rosaceae (Chrysobalanaceae)	*Parinari* (10)	0.0	n = 10	0.3	0-1 n = 10	1.1	1-2 n = 10	0.8	0-1 n = 10	1.1	0-2 n = 10
Olacaceae	*Strombosia* (10)	2.1	2-3 n = 10	3.1	2-4 n = 10	1.8	1-2 n = 10	2.4	2-3 n = 10	2.5	2-3 n = 10
Ulmaceae	*Celtis durandii* (10)	2.8	0-4 n = 10	3.0	1-4 n = 10	2.5	1-4 n = 10	1.0	0-2 n = 7	1.4	1-3 n = 10
Bignoniaceae	*Markhamia* (10)	1.7	0-3 n = 10	1.6	1-2 n = 10	1.7	1-2 n = 10	2.1	1-3 n = 10	2.8	1-4 n = 10
Meliaceae	*Lovoa s.* (5)	0.0	n = 5	0.8	0-1 n = 5	1.0	1 n = 5	0.6	0-1 n = 5	1.0	1 n = 5
	YOUNG LEAVES										
	Celtis africana (5)	0.0	n = 0	0.0	n = 2	0.0	n = 1	0.0	n = 2	0.4	0-2 n = 3
	Teclea n. (5)	0.0	n = 5	0.6	0-1 n = 5	0.33	0-1 n = 3	00.0	n = 0	2.0	2.0 n = 1
	Diospyros a. (10)	0.0	n = 8	0.17	0-1 n = 6	0.0	n = 3	0.0	n = 1	1.0	1.0 n = 1
	Aningeria (5)	0.0	n = 3	0.0	n = 5	0.0	n = 3	0.0	n = 3	0.0	n = 2
	Symphonia (5)	0.0	n = 2	0.0	n = 5	0.0	n = 5	0.0	n = 4	0.0	n = 4
	Funtumia (9)	0.0	n = 8	0.0	n = 9	0.0	n = 8	0.13	0-1 n = 8	0.11	0-1 n = 9
	Parinari (10)	0.0	n = 10	0.1	0-1 n = 10	0.1	0-1 n = 10	0.0	n = 2	0.0	n = 5
	Strombosia (10)	0.0	n = 10	1.0	0-2 n = 10	0.5	0-1 n = 2	0.0	n = 0	0.0	n = 2
	Celtis durandii (10)	0.0	n = 5	0.29	0-2 n = 7	0.0	n = 3	0.38	0-1 n = 8	0.43	0-1 n = 7
	Markhamia (10)	0.0	n = 10	0.63	0-2 n = 8	0.88	0-1 n = 5	0.4	0-1 n = 5	0.30	0-1 n = 10
	Lovoa s. (5)	0.0	n = 1	0.33	0-1 n = 3	0.0	n = 5	0.0	n = 5	0.0	n = 5

†mean score, *range of scores

n = no. of specimens having phytophase (mature or young leaves)

statistics based on number of specimens having phytophase

0 = none
1 = very little
2 = little
3 = some
4 = much

these leaves (Table 6). *Funtumia* was the only species, of the 11 considered, whose mature leaf blades were eaten to any extent by red colobus—but the insect damage to its mature leaves was not particularly great. Similarly, exploitation of young leaves from 11 species by insects was low, and does not correlate with the high incidence of red colobus feeding on young leaves ($r_s = -0.268$, $p > 0.05$, from Table 6). The degree of insect damage is clearly and unreliable indicator as to whether or not the leaves of a particular species are eaten by red colobus. This is not surprising in view of the apparent physiological differences in digestion and detoxification between them, and also in view of the ability of some insects to utilize plant toxins for their own toxic defense. One should not completely exclude the possibility that the relatively short period that most young leaves are so classified (as young) could affect the degree and incidence of insect attack on them, but I do not believe this would alter the preceding generalizations.

It is also significant that young leaves of *Funtumia* and both young and mature leaves of *Diospyros* and *Symphonia* show little attack from either insects or monkeys. Clearly, these items are unpalatable and are probably very toxic and/or otherwise indigestible to both groups of folivores.

Factors Correlating with Selectivity

Life-style and wood hardness of trees as they relate to red colobus and insect food habits

It has been suggested that the amount of energy a tree expends in protecting its leaves against predation depends on its life-style. Colonizers are considered to develop "r" strategies and therefore are expected to invest little in their leaves, whereas noncolonizers, which are important constituents of the mature forest, are considered to develop "K" strategies and to place considerable investment into the preservation of their leaves (Cates and Orians, 1975). This dichotomy not only is a gross simplification but also becomes complicated when one considers that some colonizers are virtually evergreen and some noncolonizers are deciduous. Deciduous species presumably invest less in their leaves than evergreen trees. One also expects a greater investment by non-colonizers in their wood as part of the "K" strategy; a greater wood density is one probable feature.

If these relationships are valid, one would predict that evergreen noncolonizers have highly protected leaves that are toxic and/or indigestible to folivores, whereas deciduous colonizers would have relatively unprotected leaves. The degree of leaf predation would be expected to follow these relations. Predictions for evergreen colonizers and deciduous noncolonizers are less apparent. Species with high-density wood would be expected to have low leaf predation.

In this analysis I have considered only tree species that I have been able to characterize according to evergreen-deciduous and colonizer-noncolonizer. Using the data from Table 1, I have excluded only climbers, lianas, unidentified species, *Pinus caribaea* (an exotic), and *Ficus capensis*. These exclusions have little effect on the analysis, for it still includes 93 percent of the young leaf diet and 90 percent of the mature leaf diet. The young leaf diet from Table 1 comprises columns VIII–XII inclusive and the mature leaf diet includes columns XVII, XX, and XXI only. "Pieces of mature leaf" have been excluded as they are considered to be primarily leaf galls. The selection ratio (number of feeding observations/number of stems of species A per ha) corrects only for differences in density and not for differences in crown size of the trees.

The data (Table 6) clearly show that the majority of mature leaf blade in the red colobus diet comes from evergreen noncolonizing species. The majority of young leaf blade in the diet comes from noncolonizing deciduous and evergreen species. These results take into consideration only tree species providing leaf food for red colobus. If one considers nonfood tree species as well, the dietary selection ratios of red colobus are somewhat altered. In this analysis, the total number of feeding scores for mature leaves or young leaves (Table 6) from trees of a particular life-style was divided by the estimated density of stems of all tree species having this life-style whether fed upon or not. These density estimates were based on strip enumerations in the home range of the main study group (see Struhsaker, 1975, for these enumeration data). Of all mature leaf blade feeding scores, 77 (75.5 percent) came from evergreen trees. The density of evergreen trees at least 10 m tall was estimated at 256/ha and constituted 80.8 percent of the enumeration sample. Only 25 (24.5 percent) of mature leaf blades were eaten from deciduous trees and deciduous species accounted for only 19.2 percent (60.8/ha) of the trees enumerated. The selection ratios computed with these data indicate that red colobus tend to select mature leaves somewhat more from deciduous than evergreen species: $77/256 = 0.3008$ for evergreen and $25/60.8 = 0.4112$ for deciduous.[2] This is accounted for by the fact that red colobus did not feed on the mature leaves of 3 very common evergreen species which accounted for 45.4 percent of the trees enumerated: *Diospyros abyssinica*, *Markhamia platycalyx*, and *Uvariopsis congensis*.

Table 6.—*Colobus badius* leaf diet and life-style of food species based on 2,399 feeding observations (August 1972–March 1975)

	I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*
								Insect damage	
Species	*Wt. of wd. in* kg/m^3 *at 12% moisture content*	*Life-style*	*Density* no./ha*	*No. of scores mature leaf blade*	*Selection ratio mature leaf blade*	*No. of scores young leaf blade*	*Selection ratio young leaf blade*	*mean mature leaf damage score***	*mean young leaf damage score***
Albizia gummifera	481	D-NC	<1.0	0	0	15	≥15		
Aningeria	497	D-NC	0.7	0	0	36	51.43	1.39	0
Balanites		D-NC	1.4	0	0	7	5.0		
Bosqueia	497	E-NC	2.8	1	0.36	62	22.14		
Cassipourea		E-NC	3.5	0	0	3	0.86		
Celtis africana	657	D-NC	2.1	1	0.48	29	13.81	1.87	0.08
Celtis durandii	561	D-C	34.3	0	0	32	0.93	2.14	0.22
Chaetacme		E-NC	8.4	1	0.12	29	3.45		
Chrysophylum		E-NC	2.1	9	4.29	1	0.48		
Cordia		D-NC	1.4	0	0.0	3	2.14		
Diospyros	705	E-NC	65.7	0	0.0	0	0.0	0.40	0.23
Dombeya		D-C	4.2	12	2.86	58	13.81		
Elaeodendron		E-NC	<1.0	0	0.0	12	≥12.		
Fagara		D-NC	0.7	0	0.0	1	1.43		
Fagaropsis		D-NC	2.1	1	0.48	1	0.48		
Ficus brachylepsis		D-NC	<1.0	11	≥11	12	≥12		
Ficus natalensis		E-NC	<1.0	2	≥2	6	≥6		
Funtumia	513	E-NC	14.7	23	1.56	0	0.0	1.09	0.05
Lovoa	625	E-NC	2.8	0	0.0	34	12.14	0.68	0.07
Markhamia	513	E-C	58.0	0	0.0	12	0.21	1.98	0.44
Millettia		D-C	7.6	0	0.0	34	4.47		
Mimusops		E-NC	2.1	29	13.81	2	0.95		
Newtonia	561	E-NC	1.4	0	0.0	46	32.86		
Olea	801	E-NC	2.8	0	0.0	3	1.07		
Pancovia		E-NC	6.3	0	0.0	6	0.95		
Parinari	753	E-NC	10.5	0	0.0	34	3.24	0.66	0.04
Premna		D-C	1.4	0	0.0	6	4.29		
Sapium		E-C	<1.0	0	0.0	3	≥3		
Strombosia	769	E-NC	14.7	2	0.14	10	0.68	2.38	0.30

Table 6. *(cont.)*

I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*
Symphonia	E-NC	0.7	0	0.0	2	2.86	0.24	0.0
Teclea	E-NC	21.0	2	0.095	16	0.76	1.16	0.59
Trema	E-C	0.7	4	5.71	1	1.43		
Trichilia	E-NC	<1.0	2	≥2	8	≥8		
Xymalos	E-NC	0.7	2	2.86	3	4.29		
Total			102		527			

Selection ratio = no. scores/density
*based on enumeration of all trees ≥10 m tall
**these are mean values of 5 monthly mean scores (*see* Table 5)

D = deciduous
E = evergreen
C = colonizer
NC = non-colonizer

A similar analysis comparing the selection of mature leaf food from noncolonizing and colonizing species did not alter the previous conclusions. Of the mature leaf diet, 86 scores (84.3 percent) came from noncolonizing trees that had a density of 212.7/ha, giving a selection ratio of 0.4043. This is considerably higher than that of colonizing trees: 16/108.3 = 0.1477.[3] Selection ratios for young leaves were also somewhat modified. Deciduous species were preferred over evergreen trees: 234/60.8 = 3.8487 deciduous and 293/256 = 1.1445 evergreen.[2] Noncolonizers were still preferred over colonizing tree species: 381/212.7 = 1.7913 noncolonizer and 146/108.3 = 1.3481 colonizer.[3]

The results for mature leaves are partially consistent with the preceding predictions. Although in an absolute sense, evergreen species contribute most of the mature leaf blade to the red colobus diet, deciduous species tend to be preferred. The preference of noncolonizers over colonizers is inconsistent with the preceding hypotheses and with the results of Cates and Orians (1975) for slugs and herbs. This could be related to the greater species diversity afforded by the noncolonizers. The red colobus may be able to cope digestively only with small amounts of mature leaves from a given species within a given time period, such as might be involved in detoxification or in the digestion of high-lignin content foods (e.g., Freeland and Janzen, 1974). Consequently, small amounts taken from many evergreen species would total more than similar small amounts taken from very few colonizers. It is also important to emphasize that although some of the preceding predictions are not supported by these results, the red colubus are, in fact, not greatly dependent on mature leaf blades. The greater importance of deciduous trees in supplying young leaves versus mature leaves to the red colobus diet is seen as a logical consequence of their deciduous nature in producing more young leaves more often than evergreen species. Young leaves are clearly taken from a much greater number of species than are mature leaves and this may reflect a difference in chemical composition between the 2-leaf types which affects red colobus digestion: young leaves presumably have greater digestibility and/or lower toxicity than mature leaves. This latter point was earlier suggested by McKey (1974). A. Hladik (1978) has shown that alkaloids generally occur in greater concentrations in mature leaves than in young leaves of rain-forest trees of Gabon. Furthermore, Fitzgerald (1978) has shown that soft leaves are 30 percent more digestible than hard leaves for brush-tailed opossums and, similarly, Montgomery and Sunquist (1978) found that sloths digest young leaves more rapidly than mature leaves. These results are consistent with the general pattern for domesticated ruminants where plant digestibility decreases with the age of the tissue (Harkin, 1973).

Insect damage to leaves does not correlate well with any of the gross categories of tree life-styles (Table 6).

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[2] Includes only 97.4 percent of trees in the enumeration because of categorization problems.

[3] Includes only 97.9 percent of trees in the enumeration because of categorization problems.

There was no significant difference in mean leaf-damage score for deciduous versus evergreen trees ($t = 1.552$, $0.2 > p > 0.1$ for mature; $t = -0.863$, $0.5 > p > 0.4$ for young leaves), nor for colonizer versus noncolonizer trees ($t = 1.864$, $0.10 > p > 0.5$ for mature; $t = 1.204$, $0.4 > p > 0.2$ for young leaves). The implications of these results should be accepted with caution because of the small sample size, especially the small numbers of deciduous and colonizing species. The results suggest, however, that the whole question of leaf digestibility/palatability is more complex than can be encompassed by the simple hypotheses offered at the beginning of this section and by the equally simple categories of tree life-styles. Opler (1978), for example, has found greater insect damage in the leaves of deciduous California oaks than in evergreen oak species.

Wood hardness,[4] expressed as density (kg/m^3; see Table 6), does not appear to correlate with whether or not the mature leaves of a species are afforded with compounds protective against folivores. There was no significant correlation between wood density and insect damage to mature leaves ($r_s = -0.088$, $p > 0.05$, $N = 9$; Table 6) or between wood density and the proportion of mature leaves in the red colobus diet ($r_s = 0.177$, $p > 0.05$, $N = 13$; Table 6).

Considering all food types from 40 species which made up 94.8 percent of the 2399 feeding scores of the red colobus, it is seen that 46.7 percent came from deciduous tree species and 53.3 percent from evergreen species.[5] Colonizing tree species contributed only 22.1 percent of the red colobus foods, whereas noncolonizing species constituted 77.9 percent of the diet. The significance of these figures is best appreciated when compared to similar data provided by J. F. Oates (1977) for the black and white colobus (*Colobus guereza*) from the same part of the Kibale Forest. Fifteen tree species made up 91.9 percent of 2366 feeding scores for *C. guereza*;[5] 78.2 percent of these scores were from deciduous species and 21.8 percent from evergreens. Colonizing trees accounted for 76.1 percent of the diet and noncolonizers only 23.9 percent.

The differences between these 2 colobus monkeys are striking and clearly support our earlier conclusion that the red colobus is adapted to the relatively old and mature rain forest whereas the black and white colobus is adapted to relatively young secondary forest (Struhsaker and Oates, 1975). Furthermore, because the red colobus has a much greater dietary diversity than the black and white colobus, it can be considered more of a generalist feeder than the black and white colobus which is more of a specialist. This is inconsistent with the hypothesis proposed by Cates and Orians (1975): ". . . the herbivores feeding on early successional plants should be more generalized in their foods and foraging than species utilizing later successional plants, most of which would be host specific and have evolved physiological mechanisms for handling the defenses of their host."

I suggest that one reason the Kibale colobus do not conform to this hypothesis is because they tend to avoid toxic species and plant parts or consume toxic foods at a rate sufficiently slow to allow detoxification. None of these proposed mechanisms would involve the evolution of highly specialized physiological systems. Finally, it is pointed out that the Kibale red colobus exist in greater biomass densities in mature rather than colonizing forest and at much greater biomass densitites than black and white colobus living in any of the Kibale habitats (Struhsaker, 1975). This is at odds with Opler's (1978) conclusion that greater folivore biomass occurs in early forest stages.

Basis of dietary selectivity

From the foregoing account it is obvious that red colobus take the majority of their mature leaf blade diet from tree species that one might expect to have the greatest chemical protection against folivores: evergreen noncolonizers. Furthermore, 53.7 percent of their mature leaf blade diet comes from plant families that are widely considered to be toxic—Sapotaceae and Apocynaceae—and the greatest amount comes from *Funtumia latifolia* whose mature leaves are known to contain alkaloids (Table 1). An additional 14.9 percent comes from other so-called toxic families: Meliaceae, Sterculiaceae, and Rutaceae (Table 1).[6] The leaves and very young growth of *Elaeodendron buchananii* are reported to be highly toxic to sheep and rabbits, often resulting in fatalities (Verdcourt and Trump, 1969). Nevertheless, red colobus eat the leaf buds, young leaves, mature leaf blades, mature leaf petioles, and unripe fruits of this species without any apparent ill effect (Table 1, and Struhsaker, 1975). When one considers the entire red colobus diet, nearly half of it comes from so-called toxic families of plants.

How might the red colobus monkeys be coping with such a diet? In the absence of sufficient chemical

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[4] Wood hardness data from Tack (1969) and personal communication, Uganda Forest Department.

[5] Climbers, lianas, unidentifiable species, and species whose life-style could not be categorized were excluded from this analysis. This amounted to 5.2 percent of the total scores for red colobus and 8.1 percent for the black and white colobus.

[6] See Janzen (1974) for reference to the toxicity of these families.

analysis and experimental physiological studies, I can only offer speculation. It is clear from Table 1 that mature leaf blades comprise a relatively small portion of the red colobus diet. In contrast, the petioles of mature leaves and leaflets constitute important items in their diet. The chemical basis of this selectivity is not known, but limited analysis of *Markhamia platycalyx* suggests that lignin may be important. In this species the mature leaflets contain 15.7 percent lignin (dry weight) compared to the mature leaf petioles which contain only 8.8 percent lignin (Struhsaker, 1975).[7] *Markhamia* mature leaflets are rarely eaten and did not occur in the 1972-1975 sample, whereas the petioles of mature leaves are always an important food to red colobus and comprised 5.4 percent of the 1972-1975 diet.

Lignin not only slows the rate of digestion in small ruminants (Short, et al., 1974), but it also reduces the quantities of cellulose, hemicelluloses, and protein that are digested (Phillipson, 1970; Harkin, 1973). The significance of this has been clearly stated by Short et al. (1974); "The importance of rate of digestibility to the well-being of small ruminants relates to their relatively high basal metabolic rates per unit of body weight and relatively small rumen volumes. They must consume large quantities of readily fermentable foodstuffs and have a rapid turnover rate of ruminal contents." The 15 percent lignin content of *Markhamia* mature leaflets is high compared to most plant parts and, if the same physiological principles apply to red colobus as to small ungulate ruminants, then the basis of their pronounced selectivity between *Markhamia* petioles and leaflets may be related to lignin content.

Lignin may explain other cases of red colobus dietary selectivity such as the consumption of rotten wood (Struhsaker, 1975) which was presumably delignified by fungi and bacteria (Harkin, 1973). Lignin composition sheds little light, however, on other examples: mature leaves of *Celtis durandii* are not eaten by red colobus even though they contain only 7 percent dry weight of lignin (Struhsaker, 1975). Even if the mature leaf blades eaten by red colobus do contain toxins, the detoxification may be facilitated by the small amounts actually consumed. The fact that there is a great quantity of flowers, buds, and young leaves in the red colobus diet, combined with the fact that other monkey species of a different subfamily feed on many of the same items, suggest that most of these foods are not toxic or indigestible to red colobus. So-called toxic plant species can be exploited by animals through selection of nontoxic parts, by consumption of small amounts that can be detoxified, by feeding on other items that counteract the toxins, and, as in the case with insects, by the incorporation of the plant toxins into their own chemical defense. The red colobus diet provides simply another example of why unqualified references to "toxic" plant families are usually unjustified and erroneous. As Rothschild (1972) has succinctly pointed out: "The toxic substances within the plant host vary both in time and space, seasonally, ecologically, geographically, morphologically and chemically."

Adaptive Responses of Trees

Floral synchrony, predation, and fruit-crop size in 5 species of rain-forest trees

Since August 1970, monthly phenological checks have been made on 85 individually marked trees representing 11 species. All trees were in the main study area of compartment 30 of the Kibale Forest (0° 34′N, 30° 21′E).

In an attempt to understand better the effect of floral predation by monkeys upon the subsequent fruit crop, I have analyzed the above phenological data with respect to the correlation between the degree of floral synchrony within a tree species and the size of the subsequent fruit crop. It is reasoned that if floral predation by monkeys is sufficiently great, then they will greatly reduce, if not altogether eliminate, the subsequent fruit crop. Consequently, the greater the degree of intraspecific floral synchrony shown by a tree species, the more successful will be its fruit crop as a function of predator swamping.

The plausibility of this hypothesis in relation to the Kibale Forest trees was first suggested to me by the case of *Markhamia platycalyx*, one of the most common trees there. During the course of my first 2 years of study in compartment 30 (K30), I was impressed by the notable absence of *Markhamia* fruits. K30 has an extremely high density of primates and all of the 7 anthropoids there probably feed heavily on *Markhamia* floral buds and flowers (this has been observed in 5 of the 7 species, including the most common monkeys, red colobus and redtails). For example, within a period of about 1 hour, I observed a group of about 20 red colobus consume all of the flowers of a single *Markhamia*, which, until their arrival, was covered with flowers. Furthermore, during the same 2-year period, I had seen *Markhamia* fruits only on trees that were isolated from the forest and thereby not influenced by primate predation or in parts of the

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[7] Mature wood, regardless of species, contains about 30 percent lignin (Harkin, 1973).

forest with considerably lower densities of primates, such as in K12 which had recently been selectively timbered.

In September 1972, an unusual phenomenom occurred in K30 and the adjacent forests. There was an incredibly high degree of floral synchrony among the *Markhamia*. Standing on hilltops overlooking the forest, one had the impression of looking over a great yellow sea, so prevalent were these flowers. The following months were the first to yield *Markhamia* fruits in K30. This is the only time I have witnessed such floral synchrony in *Markhamia* and the only time their fruits were so abundant in K30 during my entire 5 years of working in this area. One particular *Markhamia* in K30 had fruits in March and May 1973, and again in March 1975. It may have borne fruits more frequently than this because my observations of it were not systematic. This specimen was distinctive in being isolated from all other trees. It could only be reached by a monkey if the monkey climbed to the ground and walked at least 15 m along the ground to the base of the tree. I attribute the regular fruiting success of this specimen to its relative inaccessibility. *Markhamia* away from the forest and monkey populations, such as in the city of Kampala and the town of Fort Portal, regularly bore flowers and fruits during this 5-year period. Huxley and Van Eck (1974) present data for a single *Markhamia*, located at Kabanyolo 17 km north of Kampala, which bore flowers and fruits for the great majority of the 5-year period it was under observation.

Unfortunately, the 10 *Markhamia* trees included in my phenological sample did not bear flowers during this period and, in fact, have borne very few during the entire study. This I attribute to heavy predation on their floral buds. Consequently, I have been unable to quantitatively test the hypothesis relating floral synchrony and fruit success in this species.

There were, however, 5 other tree species in my phenological sample which met the criteria necessary for testing this hypothesis. These criteria are: (1) the floral buds and flowers must be readily eaten by 2 or more primate species or at least by the most abundant species (red colobus); (2) the individual tree must have the potential for autogamy, having either hermaphroditic flowers or male and female flowers simultaneously; and (3) the tree must show varying degrees of intraspecific floral synchrony. Aside from *Markhamia*, the only other species in my sample of 11 which met these criteria were: *Aningeria altissima, Strombosia scheffleri, Symphonia globulifera, Celtis africana,* and *Celtis durandii. Celtis durandii* was eliminated from the analysis because the phenological data for the 10 specimens of this species usually failed to show a period of flowers or floral buds prior to the fruit crop! I have seen other specimens of this species in which virtually all leaves had been dropped and the tree was literally covered with floral buds and flowers. However, only 1 of the 10 trees in my sample demonstrated this extreme. This means that either the sampling interval of 1 month was too long and that the floral bud and flower stages began and ended during the interval between samples, or alternatively, that these specimens may be continually producing very few inconspicuous flowers. These could be easily missed in the analysis if they were concealed among mature leaves. If this is, in fact, the case, then *Celtis durandii* is a species exhibiting at least 2 life-styles in the same area; i.e., some individuals have most of their flowers at one time and other individuals produce very few flowers more or less continuously.

The 5 *Symphonia* trees demonstrated extreme inter-individual variation in the sample of 50 months considered in this analysis. One of them had floral buds and/or flowers in 80 percent of the samples; 1 had them in 64 percent; 1 in 46 percent; 1 in 32 percent; and 1 in only 30 percent of the months samples. The analysis was affected by the difficulty of determining which flowering periods produced the fruit crops and thereby made difficult the correlation analysis of floral synchrony and fruit-crop size. For example, 3 of the 5 trees often bore floral buds and/or flowers simultaneously with fruits. Not knowing the real interval between the time of floral fertilization and the appearance of fruit, combined with the prolonged flowering periods, weakened the entire analysis of the species. If, however, one assumes an interval of 2–4 months between flowering and fruiting, one can back date from the first appearance of fruits and deduce the approximate time of fertilization. Examination of the phenological data for the 5 *Symphonia* between October 1970 and December 1974 and including 50 monthly samples reveals 16 "periods" of flowering. Correlating the degree of synchrony (number of trees having the phytophase of floral buds and/or flowers) in these periods with the subsequent fruit-crop size revealed no significant correlation ($r_s = -0.24$, Table 7*a*).

Five *Celtis africana* were analyzed for the same period of time. This species had a very short flowering period, usually of less than 1 month. Consequently, flowers were rarely seen on a given tree for 2 or more consecutive monthly samples. This short period of flowering was apparently missed in only 1 cycle, i.e., there was only 1 fruit crop on 1 tree that was not preceded by flowers. Fruit typically appeared within 2–4

Table 7a.—Phenological summary of 5 *Symphonia globulifera*

	Tree number & scores *(1)*			*(2)*			*(3)*			*(4)*			*(5)*		
Date	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*
25–26 Aug 1970	4			4	?		4			1					
26 Sept	4	2		3	?1		4	3	3	3			3		
26 Oct	4			4	3		4		3	2			4		
27 Nov	4	2		4	2		4	3	4	4			4	?	
27 Dec	2			2			4		4	2			3		
27 Jan 1971				3			4		4	1					
27 Feb	1			2			3		4	1		1			
26 Mar	2			4			2		4	1			?		
21 Apr	1			2			2		3	1			2		
27 May	2		1	2			2		2	1			1		
June	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
* 27 July															
* 28 Aug							?		1						?2
27 Sept							4			1					
25 Oct	1						4						1		
29 Nov							4								
27 Dec				2			4			1					
29 Jan 1972				1			4	4		1					
27 Feb	4			2			3		2						
23 Mar	2						3		2						
* 27,29 Apr	3								1						
* 29–30 May	3	2		1					1			1		1	1
* 28–29 June			1						1				2	1	
* 29–30 July															1
30 Aug	1						4		1						
28 Sept							3		1						
29–30 Oct				2			4		3						
17 Nov							4		1				1		
* 29–30 Dec			1	1			3	1					?		
28 Jan 1973				1			3		2				1		
27 Feb			1				4								
27–28 Mar	2			3			4								
28 Apr	3			3			4	1	1				1		
30–31 May	3	3		3	?		4	?					1		
29–30 June	1			2			2	2	1	1			1		
31 July				1			3		1						
* 31 Aug									1						
* 30 Sept				1			-	-	-						
1 Nov				1			3		2						
29 Nov							1		2						
28–29 Dec						1	1		2						
26–27 Jan 1974				1			1	1	2						
* 28 Feb				1			2		2						
30–31 Mar	3			3					2						
1 May	4			4			1		1						
26–27 May	3			4			1		1				1		
* 29–30 June		1			1	1	?		2						
* 26 July				1			3								
* Aug			1	1			3								
* 28–29 Sept	2		2	?		2	0 ↔ 31						2		
2–3 Nov			1	1		1	4	1	1	2					
29–30 Nov	1		4	2		2	4		1	2					
28–29 Dec			3			2	4		1	2					2

* Data collected by other observers
FLB: flower buds
FL: flowers
FR: fruits

4-many
3-some
2-few
1-very few
0-none

months of the last sample in which the tree had flowers and/or floral buds. During the 50 samples, there were 12 periods of flowering. There was no significant correlation between the degree of floral synchrony and subsequent fruit-crop size for these 5 *Celtis africana* ($r_s = 0.375$, Table 7*b*).

Strombosia scheffleri has discrete flowering periods lasting only 1-2 months with fruits following within 2-3 months. Ten flowering periods occurred during the 50 monthly samples. There was a significant positive correlation between the number of trees in floral synchrony and the relative size of their subsequent fruit crop ($r_s = 0.67$, $0.05 > p > 0.01$, Table 7C). The floral bud and flower stages of *Aningeria altissima* last up to 5 months, but are usually of about 3 months' duration. Fruits typically appear within 2 months of the last sample showing flowers and/or floral buds. In the 5 specimens sampled, there was a significant positive correlation between the number of trees in floral synchrony and the resulting fruit-crop size ($r_S = 0.602$, $0.050 > p > 0.01$, Table 7d.

There are 3 obvious hypotheses accounting for the positive correlation between intraspecific floral synchrony and the resultant fruit-crop size.

Swamping of floral predators.

In this hypothesis it is suggested that floral synchrony between members of the same species leads to larger fruit crops as a consequence of swamping or exceeding the predatory capacity of its floral predators. Floral predation by the 5 most common primates in K30 is summarized in Table 8. Interpretation of these data should include the fact that the total numbers and biomass of red colobus greatly exceed those of all 4 other species combined. Consequently, predation by them is proportionally far more important than that of any other single species. This is consistent with the correlation analysis supporting the predator swamping hypothesis for *Strombosia* and *Aningeria*. It is not apparent to me why the correlation between floral synchrony and fruit-crop size—and thus this hypothesis—fails to hold for *Celtis africana*. Possibly the very short duration of the floral bud and flower stages is sufficient to reduce effectively the impact of floral predators. *Symphonia globulifera* is not exposed to the same degree of floral predation as are the other 3 species. This lower pressure combined with the prolonged periods of floral production by individual trees is probably enough to counteract the effects of floral predation. Consequently, predator swamping through interindividual synchrony is relatively unimportant.

Xenogamy

Some or all of the 4 tree species may be dependent on cross pollination between individual trees before fruit is produced. Even facultative cross pollination would result in greater fruit production when more trees were in floral synchrony. In the absence of detailed and experimental studies of pollination, one cannot make definitive statements about the importance of cross pollination. However, analysis of the phenology of neighboring conspecifics does allow one to make reasonable conclusions concerning the probable importance of xenogamy. Examination of spatial parameters lead to the rejection of the xenogamy hypothesis for *Aningeria*. Two of the 5 trees in the *Aningeria* sample were only about 25 m apart (numbers 3 and 4). In the 4 flowering cycles of these 2 trees, they were always in synchrony (Table 7D). There was only 1 cycle in which neither of them bore fruit and in this cycle none of the other 3 *Aningeria* was in floral synchrony with them. In 2 cycles they both bore fruit; in 1 of these, 2 other trees were in synchrony with them and in the other case 1 other of the five sampled trees was in synchrony with them. In the fourth cycle, when only 1 of these 2 close-neighbor trees bore fruit, there was a third tree in floral synchrony with them. Thus, although these 2 trees were only 25 m apart and were the closet conspecific neighbors of one another, and further were always in floral synchrony and the most likely candidates for xenogamy, the only time either one of them bore fruits was when at least one other of the marked *Aningeria* was also in floral synchrony with them.

Of the 10 *Strombosia* sampled, there were 3 different pairs of trees whose crowns were contiguous. If xenogamy is important to this species for fruit production, then it is within these 3 pairs that one would expect to see the closest correspondence between floral synchrony and fruit-crop size. The first pair consisted of trees number 1 and 2. Between these 2 trees there were 8 cycles (Table 7c). They were in floral synchrony during 4 of these cycles, but 1 or both of them bore fruit as a consequence in only 3 of these 4 cycles. During these 3 fruitful cycles, they were in floral synchrony with 7, 8, and 8 of the other sampled *Strombosia*, respectively. The 1 cycle in which trees 1 and 2 were in synchrony, but did not bear fruit as a consequence, was that in which no other trees flowered. In the 4 cycles when trees 1 and 2 were not in synchrony, neither of them bore fruit. In 3 of these cycles, there was only 1 or no other *Strombosia* in floral synchrony with it. Once tree number 1 was in synchrony with 7 other trees, but did not bear fruit. This pair of trees did not appear

Table 7b.—Phenological summary of *Celtis africana*

Abbreviations and sample dates same as Table 7a.

Tree number and scores

	(1)			*(2)*			*(3)*			*(4)*			*(5)*		
Date	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*
Aug 1970			4			3									
Sept			4			2	3	4	4			4			
Oct	2		3			3			4			2			1
Nov			3			2			3			3			
Dec			3			1			3			2			
Jan 1971			3	?					3			2			
Feb			2			1			3			2			
Mar			3			3			2			1	4		
Apr	4		2			1	4	4		4	4				
May			3						3			1			
June	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
* July			4			2			4			4			
* Aug			4			1			4			4			
Sept	?		3	?	?	1			2			3			
Oct			2			1			2			3			
Nov			1						2			1			
Dec			2			1			2			2			
Jan 1972			1			1	?					2			
Feb			1			1			1			2			
Mar						1			1			1			
* Apr									2			3			
* May			3												
* June			2			1									
* July			3			2			1						
Aug			4	3		1						3			
Sept			4	3	4	4	2	3	3	?		4	?		
Oct			4			3			3			4			
Nov			4			4	1	1	2			4			
* Dec			2			2			1			3			1
Jan 1973			2			3			2			4			
Feb			3			4			3			4			
Mar			3			3			3			4	1		
Apr			1			2			1			1			
May	3	1		2	1		2	1		4					
June			2		2	1		4	1			2			
July			2			2						2	4		
* Aug			2			1			1			1			
* Sept						3			1			2			
1 Nov			2			2			1			2			
29 Nov			2			2			1			2			
Dec			1			1			2			1			
Jan 1974		4		1					1	3	2	2			1
* Feb			1						1			2			
Mar			2		2			4				1			
1 May			3			1			1	1		2	4		
26-27 May			3			2			1			2			
* June						?						?			
* July						1						1			
* Aug						2						1			1
* Sept	2	4			2						1	4			
2-3 Nov			4			1			1			3			
29-30 Nov			3				1					3			
Dec			3	3	3		4					3			

to be dependent upon one another for pollination.

The second pair of *Strombosia* with contiguous crowns consisted of trees number 4 and 5. They, too, underwent 8 cycles, but 1 or both bore fruit during only 3 of them (Table 7c). In 2 of these cycles, trees number 4 and 5 were in floral synchrony with one another as well as with 7 and 8 other trees, respectively. In a third case, tree number 5 bore fruit after flowering in synchrony with 7 others, but not with tree number 4. Interpretation of these results is less clear than for the previous pair, but does tend to support the conclusion that xenogamy is not important.

The third and final pair of *Strombosia* with contiguous crowns consisted of trees number 9 and 10. They were in floral synchrony in 4 of their 5 cycles (Table 7c). In 2 of these synchronized cycles, only 1 of them bore fruit; in 1 both did so; and in 1 neither did. Fruit was produced by these 2 trees only when they were in floral synchrony with 6 or 8 other trees. Tree number 9 failed to produce fruit when it was in synchrony with 8 other trees, but not synchronized with tree number 10. Again, these data support the conclusion that xenogamy is unimportant to *Strombosia*.

Only 1 pair of the 5 sampled *Celtis africana* had contiguous crowns. They were in floral synchrony during only 2 of their 8 cycles. Tree number 4 bore fruit after all 6 of its floral cycles, 4 of which were unsynchronized with its contiguous neighbor, tree 5. Tree 5 had fruit only twice in its 4 cycles. Both of these were synchronized with tree 4. Xenogamy seems unimportant for significant fruit production in *Celtis africana*.

The 5 *Symphonia* sampled were too widely separated from one another to permit reasonable conclusions based on an analysis of the sort done for the preceding 3 species.

Optimal climatic conditions

The positive correlation between floral synchrony and subsequent fruit-crop size within a population of a particular species may be in response to optimal climatic conditions and appropriate environmental cues. Unless the environmental cues are extremely exact, consistently complete synchronization in flowering within the population of a species is not expected. Inherent biological variability and local environmental variation would account for the fact that some individuals flower in response to suboptimal climatic conditions. When the cues that trigger flowering are optimal, one would expect greater floral synchrony and a more successful fruit crop.

The data on flowering and fruit-crop size for *Strombosia* and *Aningeria* clearly show that these phytophases are not regular calendar events.[8] Rainfall is the most obvious climatic factor demonstrating intermonthly and interyearly variability and the one for which reliable and extensive data are available. Plotting monthly rainfall against the mean fruit-crop size of the 10 *Strombosia* trees and similarly for the 5 *Aningeria* for the period of October 1970 through December 1974 suggested a direct correlation between fruit-crop size and the amount of rainfall in the preceding 1-2 months.

In the first analysis, consideration was given to the relation of rainfall peaks and fruit-crop peaks. Months with rainfall peaks were those having at least 135 mm of rainfall. This definition is based on 52 years of data from Fort Portal where the 6 rainy months have a mean value greater than 135 mm and the 6 dry months have a mean value less than 135 mm. The actual rainfall data used in this analysis were, however, collected at the Kanyawara Forest Station next to the study area. Months with fruit-crop peaks were those in which the mean fruit-crop score was at least 0.4. For *Strombosia* this represents about 29 percent of the maximum mean fruit-crop score (1.4), and for *Aningeria* it represents 40 percent of the maximum mean score. These data can be analyzed in two ways. First, it can be asked in how many months did a fruit-crop peak occur within 1-2 months after a month with a rainfall peak *versus* in how many months did a fruit-crop peak occur within 1-2 months after a month without a rainfall peak? Eleven fruit-crop peaks were scored for *Strombosia* and all occurred in months that followed rainfall peaks within 1-2 months. This distribution was tested with an χ^2 test and found to be highly significant ($\chi^2 = 11$, $p < 0.001$). An identical analysis of 12 *Aningeria* fruit-crop peaks showed that 9 followed within 1-2 months of rainfall-peak months and 3 did not. This distribution was not significantly different from that expected by chance ($\chi^2 = 3.00$, $0.10 > p > 0.05$).

The second analysis asked how many rainfall-peak months were followed within 1-2 months by fruit-peak months *versus* how many rainfall-peak months were not followed within 1-2 months by fruit-peak months? There was a total of 23 rainfall-peak months. Ten of them were followed by *Strombosia* fruit-peak months and 13 were not. This difference is not significant

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[8] The other 3 species (*Celtis africana, Symphonia,* and *Celtis durandii*) are not considered in this hypothesis because they do not show a significant positive correlation between floral synchrony and subsequent fruit-crop size, and therefore could not possibly fit this hypothesis.

Table 7c.—Phenological summary of 10 *Strombosia scheffleri*

Tree number and scores

Date	*(1)*			*(2)*			*(3)*			*(4)*			*(5)*		
	FLB	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*
Aug 1970															
Sept															
Oct															1
Nov				?2									1		1
Dec															
Jan 1971												1			
Feb				1									2		
Mar	?												1	1	
Apr	?1			2											
May															
June															
* July									1						
* Aug															
Sept															
Oct				1									1		
Nov															
Dec															
Jan 1972															
Feb															
Mar				2?											
* Apr															
* May															
* June															
* July															
Aug		2			3			1			2			2	
Sept															
Oct															2
Nov						1									1
* Dec															
Jan 1973													1		
Feb															
Mar															
Apr															
May															
June															
July	3	1		3	4		4	3		1	1		3	3	
* Aug															
* Sept			1			2			2						
1 Nov			2			1			2						
29 Nov			2			1			1						
Dec	1														
Jan 1974	2	2					1	1					1	1	
* Feb													1		
Mar															
1 May						1									1
26–27 May															
* June															
* July															
* Aug															
* Sept	0↔4		0↔3			0↔3				?	?		0↔2		
2–3 Nov			2			3			1			1			1
29–30 Nov						3			2						1
Dec			1			1			1						

Table 7c. Phenological summary of 10 *Strombosia scheffleri* *(Cont.)*

Tree number and scores

	(6)			*(7)*			*(8)*			*(9)*			*(10)*		
Date	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*	*FLB*	*FL*	*FR*
Aug '70															
Sept						?1			2			?			?
Oct	?2			?3					2						
Nov			1												
Dec															
Jan 1971															
Feb															
Mar							1								
Apr															
May															
June	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
* July															
* Aug															
Sept															
Oct															
Nov															
Dec															
Jan 1972								1							
Feb															
Mar															
* Apr															
* May															
* June															
* July															
Aug		4				2		2		2			?	?	
Sept															
Oct						4			1						
Nov			2			3			3						1
* Dec															
Jan 1973	1			2			3			1			1		
Feb															
Mar															
Apr			2						2						
May			1						2						
June															
July	3	3		4	2		3	3		2	1		2		
* Aug															
* Sept						1			1						
1 Nov									1						1
29 Nov			1						1						
Dec															
Jan 1974		2		3	2		2	3		1			3		
* Feb				1											
Mar						1			2						
1 May						1			2						1
26–27 May	1					1			2						1
* June			1												
* July								1							
* Aug															
* Sept	0↔2			0↔2			0↔3			0↔3			0↔1		
2–3 Nov			1			1									1
29–30 Nov			3			2			2			1			
Dec			1			1			2						1

Table 7d.—Phenological summary of 5 *Aningeria altissima*

Date	*(1) FLB*	*(1) FL*	*(1) FR*	*(2) FLB*	*(2) FL*	*(2) FR*	*(3) FLB*	*(3) FL*	*(3) FR*	*(4) FLB*	*(4) FL*	*(4) FR*	*(5) FLB*	*(5) FL*	*(5) FR*
Aug 1970	4			4			4			1					
Sept		?													
Oct															
Nov															
Dec					4										
Jan 1971				?3	3										
Feb							?3								
Mar							3			4					
Apr							?			3					
May										1					
June															
* July	4	4											4		
* Aug												?1			
Sept															
Oct				?1											
Nov				4											
Dec				4	4		4	4							
Jan 1972				2	3			4		4	4				
Feb						1	1			3					
Mar						1			2	2					
* Apr			1			1			1						
* May															
* June															
* July															
Aug		3			2									2	
Sept			1											3	?
Oct				4	?								?		?
Nov					4										
* Dec				2			3								1
Jan 1973				2		2	3			4					
Feb				2						3	3				
Mar						1				?					
Apr	1			1		2			1						
May	1					1			1			1			
June						1									
July	3								1						
* Aug	2												1	2	
* Sept													2		
1 Nov			1												
29 Nov															3
Dec	1									1					2
Jan 1974	1	1		4	1		3	2		4	1				1
* Feb	?			1			3			3					?
Mar	1								1			2			?
1 May						1			2			1			1
26-27 May	2					1			1			2			1
29-30 June	?														
* July															1
* Aug		1													1
* Sept													3↔3		
2-3 Nov												?1		?1	
29-30 Nov		1													
Dec				4	2		4	2		4	2			1	

Tree number and score

($\chi^2 = 0.39$, $p > 0.50$). Nine of these rainy months were followed by *Aningeria* fruit-peak months and 14 were not, also insignificant ($\chi^2 = 1.08$, $p \simeq 0.30$). These analyses suggest that there is some positive relation between the size of *Strombosia* fruit crop and rainfall, but not so for *Aningeria*.

The result of this floral predation is, presumably, to select in favor of floral synchrony as a means of swamping the predators. The cues triggering flowering in these 2 species must be somewhat broad, otherwise one would expect close synchrony of flowering at all times. The importance of floral predation is demonstrated and additional support is given to the preceding analysis by our extensive data on the food habits of the monkeys in the Kibale Forest, as schematically summarized in Table 8. *Aningeria*, the 1 species (of these 4) whose floral buds and flowers are most heavily preyed upon by the monkeys is the only one of the 4 for whom the predator-swamping hypothesis seems paramount. Determinants of fruit-crop size in *Symphonia* and *Celtis africana* are not strongly dependent on floral synchrony and, therefore, presumably not very much affected by floral predation or by broad climatic factors.

Floral predation has previously received little attention and most of that has been concerned with economic plant species and insects (Le Pelly, 1932; Mani, 1964; Janzen, 1971; Schuster, 1974). Hypotheses regarding the ecological implications of interspecific and intraspecific synchrony or asynchrony in flowering have been concerned with pollination, seed dispersal, and seed predation (Janzen, 1967, 1971; Snow, 1965). The results presented here stress the importance of additional studies on the impact of floral predation by mammals, especially the primates. An improvement over the present study method would involve direct observations of floral predation on individual trees to test the relation between the extent of floral predation, the number of neighboring conspecifics in phenological synchrony, and fruiting success.

Discussion and Summary

The ecological stability exhibited by the red colobus in terms of food habits and ranging patterns combined with the stability of their mature rain-forest habitat constitutes the kind of situation where one expects to find examples of co-evolution between plants and animals. The dietary diversity of red colobus qualifies it as a rain-forest polyphagous herbivore or a generalist herbivore. As with most dietary generalists, there are no striking or highly specialized co-evolutionary patterns between the red colobus and their food trees.

The final analysis consisted of a linear regression of total rainfall in the preceding 2 months *versus* mean fruit-crop size, considering rainfall to be the independent variable and fruit-crop size the dependent variable. For *Strombosia* the regression coefficient was 0.00103 ($N = 50$), which, when testing for significance using the t-test (Sokal and Rohlf, 1969), was a highly significant positive regression ($t_s = 2.76$, $0.01 > p > 0.001$, $df = 48$). A similar analysis for *Aningeria* gave a regression coefficient of 0.00019, which was not significant ($t_s = 0.61$, $p > 0.50$, $df = 48$). I conclude from this that fruit-crop size in *Strombosia* is directly dependent on the amount of rainfall in the preceding 2 months (or some other directly related but unknown parameter), whereas *Aningeria* is not.

This study clearly demonstrates the variability in the reproductive biology of tropical rain-forest trees. Those species which within 1 population demonstrate phenological synchrony at some times and phenological asynchrony at others pose some of the more intriguing problems. Of the 4 species having this variation and for which suitable data are available, 2 (*Strombosia* and *Aningeria*) demonstrated a positive correlation between floral synchrony and subsequent fruit-crop size. This correlation appears to be independent of xenogamy. Optimal climatic conditions in the form of, or closely tied to, rainfall in the 2 months preceding fruiting appear to be important in determining fruit-crop size in *Strombosia,* but not in *Aningeria.* The effect of floral predators (mostly monkeys) seems to be the strongest selective pressure leading to floral synchrony and the positive relation between such synchrony and fruit-crop size for *Aningeria*. This same pressure may also be important to *Strombosia* in addition to the effect of rainfall.

Table 8.—Floral predation by the 5 most common primates in the Kibale Forest.

Predator species	*Celtis africana*	*Symphonia globulifera*	*Strombosia scheffleri*	*Aningeria altissima*
Colobus badius	+ + +	—	+	+ + +
Colobus guereza	—	—	—	—
Cercopithecus ascanius	+	+ +	—	+ +
Cercopithecus mitis	+	+ +	—	+ +
Cercocebus albigena	—	+ +	—	+

The apparent unpalatability of mature leaf blades to red colobus could be the result of browsing pressure by herbivorous insects having selected for mature leaves of low nutritional value, low digestibility, and/or high toxicity and not the result of the browsing pressure of red colobus in particular. The longer association between insects and trees in evolutionary time also makes this more tenable. In addition, the greater array of insect species correspondingly exerts a greater array of selective pressure on the leaves. The importance of mature leaf petioles in the red colobus diet would seem to constitute sufficient selective pressure for the evolution of petiolar defenses. In fact, such defenses may exist for most of the food trees.

Examination of Table 1 reveals that, with the exception of *Markhamia*, no single tree species contributes many mature leaf petioles to the diet of red colobus. The petioles of any given species may be lacking in 1 or more important nutrients or they may be sufficiently undigestible or toxic to restrict the amount that can be consumed by the red colobus at any one time. There may be some interspecific complementarity among the tree species and, as a consequence, the feeding pressure exerted by red colobus on mature leaf petioles is distributed among many species. *Markhamia* is a notable exception, but it should be pointed out that this is a colonizing species of very high density in the study area (58/ha). The high density of this species probably results in relatively low browsing pressure on any one individual. Relevant to this issue is the apparent fact that a red colobus group travels more than is necessary to acquire its requisite *quantity* of food. It is likely that some of this movement is dependent on qualititative dietary requirements. Thus, for example, after feeding on *Markhamia* mature leaf petioles for 30 minutes the group may move 50 to 100 meters away and feed on another species. An hour or so later and after the "latency period" for *Markhamia* petioles has passed they again feed on them, but because they have moved since the last such feeding they now feed on different *Markhamia* individuals, thereby reducing the browsing pressure on any one individual. In any case, it is apparent that mature leaf petioles are less well protected against browsing by red colobus than are the mature leaf blades, in spite of the fact that the 2 types of feeding are equally detrimental to the tree through defoliation.

The short life of buds, flowers, and young leaves may constitute their major defense against predation by red colobus. Any degree of intraspecific synchrony or, in the case of 2 or more highly palatable species, interspecific synchrony in these phytophases would add to their defense through the process of predator swamping. The importance of floral feeding by red colobus and its influence on floral synchrony may constitute the major class of coevolution between them and their food trees. It is probable that this floral feeding exerts strong selection for intraspecific phenological synchrony. The degree to which this is achieved must be limited to some extent by environmental and intrinsic factors, but the importance of this pressure on the reproductive success of the individual will determine to what extent synchrony is ultimately achieved in the population. The floral buds and flowers of *Teclea* are readily consumed by red colobus (Struhsaker, 1975), but the high degree of intraspecific synchrony and the short duration of this phytophase means that the pressure on any individual tree is relatively low. *Aningeria* and *Strombosia* would appear to be other tree species upon which similar selection pressure is exerted but which, for some reason, have not achieved the same degree of synchrony nor the same degree of protection as has *Teclea*.

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Soils, Vegetation, and Seed-eating by Black Colobus Monkeys

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Introduction

In April 1973 I began a study of the ecology and behavior of the black colobus monkey (*Colobus satanas*) in the Douala-Edea Reserve, a 160,000-ha tract of coastal rain forest in southern Cameroun

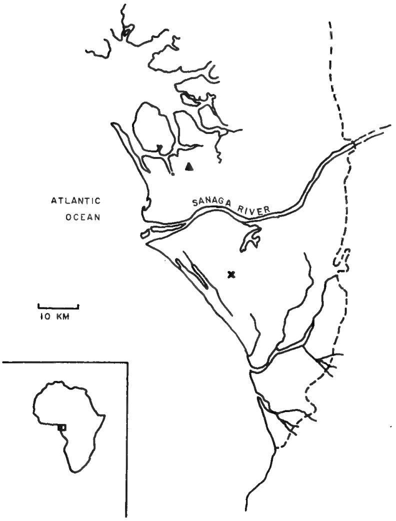

Figure 1. Location of the study area. Dashed line indicates approximate limits of Tertiary and Quaternary marine sediments. Small black triangle marks location of Elf-Serepca core sample cited in text. "X" marks location of study site. Sanaga River is northern limit of *C. satanas* distribution in this region.

(Figure 1) at the northern edge of this monkey's range (Dorst and Dandelot, 1970). Here I will summarize briefly some of my preliminary findings on the feeding behavior of this monkey and point out some striking differences in its feeding behavior from that of 2 *Colobus* species studied in another African rain forest, Kibale Forest in western Uganda (Struhsaker and Oates, 1975). The two Ugandan species are the black and white colobus, *C. guereza,* and the red colobus, *C. badius.* The discussion centers on hypotheses designed to answer the following questions:

Why do black colobus spend much less of their feeding time eating leaves than do either of the Ugandan *Colobus*?

Why do black colobus avoid the leaves of almost all the common trees of the study area, although they spend about 35 percent of their feeding time eating leaves?

Why do black colobus feed heavily, in all months, on seeds?

My working hypothesis is that differences in the overall levels of toxic secondary compounds in the vegetation of these 2 sites have led to (1) differences in the degree to which these monkeys feed on leaves, (2) other differences in feeding and ranging behavior, and (3) differences in population density of *Colobus* between the 2 sites. Differences between sites in toxic-compound content of the vegetation seem to be ultimately related to gross differences in soil quality between the 2 sites (cf. Janzen, 1974).

General Features of Feeding and Ranging Behavior

Methods

My methods of gathering quantified information on feeding and ranging behavior closely followed those used by Struhsaker (1975). Most of this information was gathered from my main study group during systematic samples of 5 consecutive full days usually in the second and third weeks of each month. The size of this group varied from 11 to 16 animals during the course of the study, most changes being additions from new births. Systematic samples were begun in October 1973; the monkeys were considered well habituated to my presence by April 1974. Even prior to full habituation it was possible to remain in fairly close visual contact with the group throughout the day without their being much disturbed.

It proved impossible to follow individual monkeys continuously, to estimate the amount of food eaten during a feeding bout, and to record the time spent feeding by an individual monkey on a specific item. Quantitative estimation of diet composition was thus based on a frequency criterion: when a monkey was first seen feeding on an item, this was scored as 1 record. If the same monkey fed on the same item at least 1 hour after the previous record, it was scored again for this item. Thus the feeding records are estimates of the amount of time spent feeding on different items. In the 16 systematic samples from October 1973 through March 1975, which provided the bulk of the information to be discussed here, 3178 feeding records were gathered.

Daily field maps were made plotting the monkeys' movements relative to my trail system, which divided the group's range into a grid of quadrats 50 m on a side. The path of the group's movements during the day was recorded, as were the number of minutes each quadrat was occupied by at least 1 monkey and the number of quadrats entered during the day. These monthly systematic samples were supplemented by additional full-day samples of the main group and by opportunistic observation of this and other groups in the study area.

Feeding

The most striking features of black colobus feeding

Table 1.—Approximate percentages of major item classes in diets of *Colobus guereza*, *C. badius*, and *C. satanas*. Data for *C. guereza* and *C. badius* from Oates (1974 and in press) and Struhsaker (1975).

— = infrequently fed upon.

	Mature leaves	*Petioles of mature leaves*	*Young leaves*	*Leaf and floral buds*	*Fruits*	*Seeds*
guereza	12	—	58	5	14	1
badius	4–5	13–19	33	16–20	—	—
satanas	19	0	18	5	—	58

behavior are the low proportion of leaves in the diet, the relatively high proportion of mature leaves among the leaf records, and the very high proportion of seeds when compared to the 2 Ugandan *Colobus* (Table 1). The 2 species at Kibale rarely fed on seeds, but seeds were the class of item most frequently eaten by black colobus. The mean monthly proportion of seeds in the diet, for all months of the study, is 57.6 percent. It must be noted that these monkeys are destroying and digesting seeds. I have found only 1 kind of seed (the small hard seeds of *Discoglypremna caloneura* [Euphorbiaceae]) occasionally intact in feces. That these monkeys feed on many seeds which are not accompanied by a fleshy fruit, and that they sometimes (e.g., when feeding on *Trichilia zenkeri* [Meliaceae]) discard fleshy fruits and eat only the seeds, suggest strongly that seeds, and not fleshy fruits, are the principal items being selected.

A large number of seed types from a great variety of plant families are eaten (Table 2). Black colobus crack woody capsules such as those of *Mareya* sp. (Euphorbiaceae) and eat the dry seeds inside. They open legume pods such as those of *Didelotia brevipaniculata* and *Erythrophleum ivorense*. They eat wind-dispersed seeds such as those of *Hippocratea* sp. (Hippocrateaceae) and *Lophira alata* (Ochnaceae), discarding the wings. They also eat drupes—seed, pericarp, and all—such as the fruits of *Rhaphiostylis* sp. (Icacinaceae) and *Strombosia pustulata* (Olacaceae). They also feed on arillate seeds such as those of *Staudtia* and other Myristicaceae and several species of Connaraceae.

Table 2.—Some seed items heavily used by black colobus in the Douala-Edea Reserve.

Family	*Species*	*Months of heavy use*
Anacardiaceae	*Sorindeia* sp.	June–August '74
Connaraceae	undetermined	August '74
Euphorbiaceae	*Discoglypremna caloneura*	June–July '74
	Macaranga sp.	August '74
	Mareya longifolia	July '74
	Protomegabaria stapfiana	October '73–January '74 September–November '74
Hippocrateaceae	*Hippocratea* sp.	October '73, October '74, December '74
Icacinaceae	*Rhaphiostylis* sp.	October '73, December '74
Leguminosae	*Didelotia brevipaniculata*	August '74
	Erythrophleum ivorense	December '73–May '74
Loganiaceae	*Strychnos* spp. (3 species used)	June–July '74
Meliaceae	*Trichilia zenkeri*	November–December '73 August–September '74
Myristicaceae	?*Coelocaryon* sp.	September '74
Ochnaceae	*Lophira alata*	January–March '74, January–March '75
Olacaceae	*Strombosia pustulata*	April–May '74
	Strombosiopsis tetrandra	June–July '74

Leaves make up less than 40 percent of the feeding records obtained. As with seeds, a great variety of leaves is eaten. These monkeys eat leaf blades, and have not been observed to feed on petioles and discard blades, as red colobus often do (Struhsaker, 1978). Young leaves are preferred,[1] but mature leaves are very heavily fed upon at certain times of the year. Mature leaves comprise a much greater proportion of the leaf-feeding records than for either of the Ugandan *Colobus*. The mean monthly proportion of mature leaves in the diet records is 19 percent, that of young leaves 18 percent; mature leaves account for just over half of the leaf records. For both the species studied in Kibale Forest, mature leaves accounted for much less than half of the total number of leaf records (Table 1).

Floral buds, flowers, young stems, and other items are irregularly eaten by black colobus and account for about 5 percent of the records. No activity resembling foraging for animals has ever been recorded, in contrast to red colobus in Kibale forest (Struhsaker, 1978).

The monkeys spent most of their feeding time in the middle and upper levels of the forest, but in some months they frequently entered small patches of very low-statured second growth to feed on leaves of semi-herbaceous vines and tree saplings. During these bouts of "treefall-foraging," the monkeys sometimes came to the ground. Leaves of *Cissus* sp. (Vitaceae) were the item most regularly eaten during the bouts of treefall-foraging, but a great variety of leaves from other vines and from some tree saplings were eaten as well.

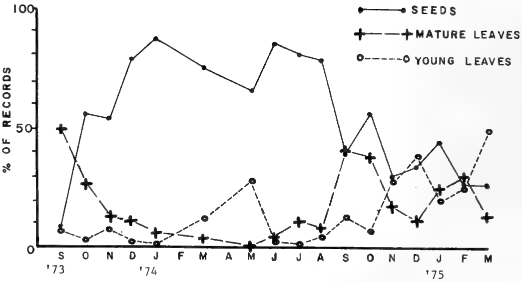

Figure 2. Proportions of 3 major item classes in feeding records of monthly systematic samples (except September 1973, which represents opportunistic sample consisting of all food records obtained during month).

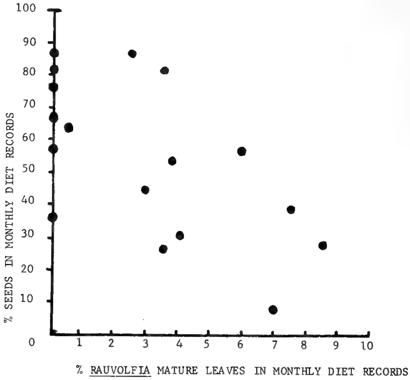

Figure 3. Variation in extent of use of *Rauvolfia vomitoria* mature leaves with variation in percentage of seeds in diet records of monthly systematic samples. Spearman's rank-order correlation coefficient is 0.62, which is significant at the 1 percent level (n = 17).

As would be expected from the monkeys' dependence on seeds, which are usually produced at long intervals, there is great intermonthly variation in the composition of the diet (Table 2). Most of the seed items are each present only 1 to 3 months of the year. There is also striking variation in the proportions of major diet item classes, and in diet diversity, between months. In many months, seeds dominated the feeding records, accounting for up to 89 percent of records in some (Figure 2). In other months, the diet was a mixture of seeds and young and mature leaves. However, seeds always accounted for at least 27 percent of the records. Mature leaves formed a large part of the diet in September and October (height of the rains) in both years. At this time, seeds and young leaves appear to be rare. Typical of all the regularly used mature-leaf items is the pattern of use shown for the mature leaves of *Rauvolfia vomitoria* (Figure 3). This item, present in the same quantities throughout the year except for a 2- to 3-week period in December and January when the leaves are shed and replaced, is heavily used only when acceptable seeds are scarce.

In months when a particular seed item is abundant, it often accounts for 30 percent or more of the records. For example, in the March 1974 sample, seeds of *Erythrophleum* and of *Strombosia,* and

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[1] The statement that young leaves are preferred is based on 2 facts: (1) The monkeys eat young leaves of many trees whose mature leaves are not eaten. (2) When both young and mature leaves of a tree species are eaten, young leaves are much more heavily used than are mature leaves. For example, young leaves of *Berlinia bracteosa* comprised up to 27.5 percent of these monthly records, but mature leaves of this species never accounted for more than 13.4 percent of the records for any month.

young leaves of *Berlinia bracteosa* (Caesalpiniaceae), together accounted for 87.0 percent of all records, and the monkeys were recorded feeding on only 10 different items in the 5-day period. On the other hand, when these seeds and a few highly favored young-leaf items are scarce, the diet is a very diverse collection of seeds, young leaves, and mature leaves, with up to 46 different items being fed on in a 5-day sample.

Ranging

The study group ranged over an area of about 60 ha, though some spaces enclosed within this area were not entered. Ranges of other groups in the study area were of similar size. There was considerable overlap with the range of 1 other group, but the relatively heavily used central part of the range, about 13 ha, was seen to be entered only twice by other *Colobus* groups during the study.

Daily ranges have not yet been computed. Figures are available on the number of 50-m-square grid quadrats entered each full day and each 5-day sample. Both these parameters showed extreme variation between months. For example, in May 1974 the group entered an average of 6.23 quadrats per day and in October 1974, 23.8 quadrats per day. These months also present the extremes in the total number of quadrats entered during a 5-day sample, 23 in May and 105 in October. Thus, in October the monkeys entered more quadrats each day than they did in 5 consecutive days in May.

Soils, Vegetation, and *Colobus* Feeding Strategies

Why do black colobus feed so heavily on seeds, and so much less on young leaves, then do either of the Ugandan species? Why do they avoid young and mature leaves of almost all the abundant trees in the study area? I propose that because the soils of the Douala-Edea study area are extremely deficient in plant nutrients, there has been selection for exceptional chemical defense in the vegetation of this site, since the replacement of a leaf eaten by a herbivore entails a greater cost to the plant than if the plant were growing in a site richer in nutrients (Janzen, 1974). There are even suggestions that nutrient content of leaves in such sites may be lower than that of leaves of trees in nutrient-rich sites (Janzen, 1974). A mammalian herbivore in such a forest should respond in several ways to the lower food quality of leaves. Before considering these possible responses I wish to summarize available information on soils and vegetation of the 2 areas.

Soils

Soils of the Kanyawara study area in North Kibale Forest, Uganda, are dark gray to red sandy clay loams or sandy clays underlain by strongly folded and metamorphosed sedimentary rocks (Lockwood Consultants, 1973). Their fine texture and the presence of weatherable schists and gneisses near the surface along the slopes probably account for the "fair" to "favorable" and "good" (Lockwood Consultants, 1973) fertility of these soils. The rolling terrain of Kibale Forest Reserve is covered by 3 main types of soils, developing on different parts of the slopes. Buruli soils are shallow loamy soils developed on old laterite caps on the hilltops. These grade into Kazo soils, stony, coarse-textured soils built usually on quartzite hills and ridges. These in turn merge with the Kiamara soils, deep, sandy clay loams or sandy clays occurring on middle and lower slopes. Valley bottoms have waterlogged silty soils overlain by a peaty layer.

Soils of the Douala-Edea Reserve contrast very dramatically with those of the Kibale study site in their origin and composition. These are extremely sandy soils developed on beach sand deposited by south-to-north longshore currents of the Atlantic Ocean. Since the area has been receiving such deposits since the end of the Cretaceous, the sandy sediments are extensive in area and are deep. A core drilled several km north of the Sanaga River and about 13 km from the present shoreline (see map, Figure 1) revealed about 400 m of unconsolidated marine sediments, primarily beach sand (P. Mandengue, chief geologist, Elf-Serepca, personal communication).

Soil samples have been gathered from my study area and analyzed in the pedology laboratory of the Ecole Nationale Supérieure Agronome in Yaoundé, Cameroun. I have compared the results of these analyses with those published for soils of the northern Kibale Forest Reserve by Lockwood Consultants (1973). The Ugandan soils were taken not from forest, but from the anthropogenic grasslands scattered through the forests on hilltops. These grassy hilltops were covered by forest around the turn of the century, when they began to be cleared, burned, and cultivated (Lockwood Consultants, 1973). At least before their forest cover was cleared, these soils probably did not greatly differ from the soils which currently support forest and colobus monkeys. I have collected soils from Struhsaker's study site, but results of the analyses are not yet available.

Figure 4 compares the textural composition and contents of some major plant nutrients in soils of the 2 sites. Values presented are means of the values from

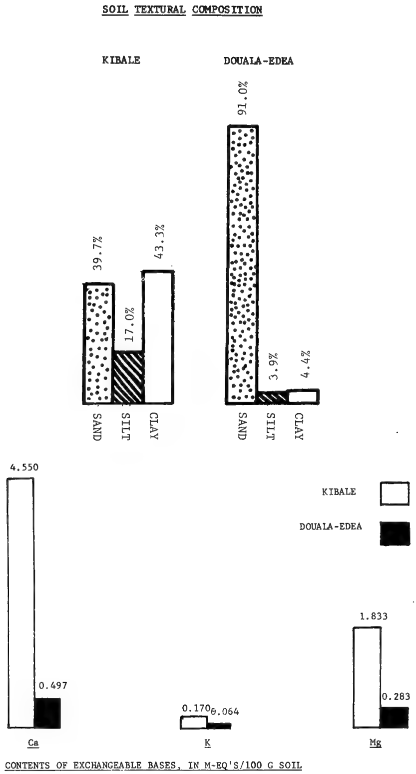

Figure 4. Comparison of Kibale and Douala-Edea soils. A, textural composition; B. contents of exchangeable calcium, magnesium, and potassium.

the upper B horizon of 3 samples (1 from each of the major soil types) from Kibale and means of 7 samples from the Douala-Edea site taken at comparable depths (just below the A horizon, about 10 cm-20 cm beneath the surface). As shown in the figure, the Douala-Edea soils have very small amounts of silt and clay, and average about 91 percent sand. Not surprisingly, given their low content of anything but sand, the contents of exchangeable bases in these soils are much lower than in the Kibale soils, up to 10 times lower in the case of calcium. The beach sands on which these soils are built were probably deficient in nutrients to begin with. The intensive leaching that should occur when heavy rainfall (about 4 m annually) percolates through a material with such a high percentage of sand and very poor ion retention properties has doubtless led to a further reduction in the amounts of nutrients available to plants. Other features of this soil appear inimical to plant growth. Preliminary results for an extensive series of soil profiles collected by J. S. Gartlan reveal that surface pH values can be as low as 2.7 (Gartlan, personal communication).

Vegetation

In a habitat such as the Douala-Edea study area, where the availability of nutrients for plants is very low but the physical environment is favorable to animals, there should be selection for increased investment in the chemical defense of leaves, since it costs the plant more to replace a leaf eaten by a herbivore (Janzen, 1974). There should also be strong selection for the plant to construct a leaf which is very resistant to leaching of minerals by rainfall, possibly by investing it with greater concentrations of fiber and cuticular wax. Leaves in such sites may also be lower in nutrient content (Janzen, 1974). Collections are being made so that contents of secondary compounds, lignin, waxes, and nutrients can be compared between the 2 sites, but this information is not yet available. There is some circumstantial evidence, however, which supports the hypothesis that concentrations of toxic secondary compounds are higher in most plants of the Douala-Edea site than in most of those of the Kibale site.

(1) Insect damage to leaves of most Douala-Edea tree species is exceptionally low, as are the population densities of foliage-dwelling arthropods. An 800-sweep sample of understory vegetation in July (early rainy season) yielded only 24 individual beetles. This is about one-fifth the number of beetles collected in a daytime, wet-season sample in the understory of a Costa Rican rain forest built on lateritic soil (Janzen, 1973).

(2) Dense stands of tree species which appear to be well defended are common in the study area. In an area adjacent to the study group's range, the forest is dominated by 2 species of *Garcinia* (Guttiferae) and *Strombosia pustulata* (Olacaceae). In an enumeration of all trees at least 25 cm in girth at chest height in a strip 400 m by 5 m (0.2 ha) through this area, these 3 species made up almost 60 percent of the stand. Both species of *Garcinia* produce a copious yellow resinous latex. The latex of 3 Asian species of this genus furnishes well-known drugs (Hegnauer, 1966). The fourth most common species in this enumeration was *Dichostemma* sp. (Euphorbiaceae), a species which produces an irritant milky latex. The shrub layer in this area is usually domi-

nated by a species of *Glossocalyx* (Monimiaceae), which has very pungent leaves that are sometimes used as a household insecticide (S. Ekondo, personal communication).

In a 1.45 ha (2900 m by 5 m) enumeration through the main group's range, another Euphorbiaceae, tentatively identified as *Mareya* sp. by the staff of the Cameroun National Herbarium, accounted for 42.7 percent of all individuals over 50 cm circumference at chest height. Dalziel (1937) cites 2 different sources which state that the leaves of *Mareya spicata* are a powerful drastic purgative and have been responsible for many deaths. The second most abundant species in this enumeration, *Sorindeia* sp. (Anacardiaceae: 5.0 percent of all individuals) contains resinous latex. Many species of this family are notable producers of tannins and other phenolics (Hegnauer, 1964).

The dominance of tree species which appear to be well defended is especially marked in the understory. In the enumeration of the main group's range I also recorded trees of 25 cm-50 cm girth at chest height. This size class (in which 527 individuals were recorded) was dominated by Euphorbiaceae (39.6 percent, 7 species), Guttiferae (17.6 percent, 3 species), and the genus *Diospyros* (Ebenaceae) (13.7 percent, 4 species). Naphthaquinone derivatives are widely found in the genus *Diospyros* and are ichthyotoxic, anthelminthic, insecticidal, repellent to termites, and irritating to skin (Hegnauer, 1966).

In the absence of quantitative information of the toxic-compound contents in the plants of the 2 forests under consideration (in both of which probably *all* tree species contain some toxic secondary compounds), my estimation of the differences is necessarily subjective. It is clear, however, that in Kibale Forest there is no tendency for species with visually conspicuous defenses, such as resinous latex, to dominate the stand. I have noted several cases of such a tendency in the Douala-Edea site. It must be emphasized that there is no substitute for chemical examination of material from these 2 sites in evaluating this point. Subjective evaluations of the degree of investment in defense in various plant families are not a good prediction of what colobus monkeys eat and avoid (Struhsaker, 1978). Investigations of secondary compound content of leaves from these 2 sites are in progress.

(3) Deciduous trees make up a much smaller proportion of the vegetation than at Kibale. In the enumeration mentioned previously through the main group's range, I recorded 377 trees, representing 52 species, of greater then 50 cm girth at chest height. Only 11.5 percent of the species and 7.2 percent of the individuals are deciduous [compared to approximately 33-36 percent of species and 19 percent of individuals in Struhsaker's (1975) enumeration]. The low proportion of deciduous trees is significant in that it reflects selection for long-lived leaves in a site where nutrients lost in shed leaves are very difficult to replace. In the humid tropics, if a leaf is to remain productive throughout a long life, it must be adequately defended. Deciduous trees, to the extent that they replace their leaves more rapidly than do evergreen species, should invest their leaves with smaller amounts of toxins, since their leaves have less time in which to accumulate damage before they are shed and replaced (Janzen, 1974). Thus, higher density of deciduous trees may mean higher density of trees whose leaves have relatively low concentrations of toxic secondary compounds (Stanton, 1975).

(4) Water in streams draining the study area is tea-brown in color, indicating high contents of humic acids, derived from phenolic constituents of the vegetation. The brown color of the water indicates that large amounts of phenolic compounds are present in the litter leachate.

Expected Features of Feeding and Ranging Behavior

If Douala-Edea vegetation does have generally higher concentrations of toxic secondary compounds and substances such as waxes which prevent mineral leaching, while still containing the relatively low nutrient levels generally characteristic of leaves, this should greatly lower its quality as food for herbivores. In such a site, a leaf-eating mammal may be expected to respond over evolutionary time in the following ways. (1) It may largely switch from leaves to other items with a more favorable combination of nutrients and toxins. (2) When feeding on leaves, it may require accessory nutrients to subsidize processing of the toxins, cellulose, waxes, etc., they contain. (3) When it does feed on leaves, it should be extremely selective.

Dietary switch from leaves to seeds

Toxic secondary compounds should be expected to be difficult to break down. Also, their presence may decrease the rate at which other components of the food are made available to the animal, both by generally decreasing the processing rate of food in which they are mixed, and by specifically inhibiting the activity of microfloral elements which digest other components of the food (see Freeland and Janzen, 1974, and references therein). Leaves, particularly mature leaves, usually contain relatively low concentrations of easily available nutrients and high contents of fiber. If a mammalian herbivore can find leaves or pieces of leaves with low contents of toxins, it may be able to subsist largely on leaves. But if the content of secondary compounds in the leaves confronting a herbivore is very high, the animal may not be able to assimilate energy quickly enough to meet its needs by feeding on leaves alone. High toxin concentration lowers the quality of items which may already be marginal food at best. However, the same toxin concentration which makes a leaf item unprofitable might be tolerated in seed items, because their greater concentrations of easily processed nutrients may provide greater return for the initial cost of processing similar contents of toxins. Seeds generally have high concentrations of fats and/or easily digestible carbohydrates (Baker, 1972; Janzen, 1971; Levin, 1973). It is important to note that the nutrients in seeds are largely storage nutrients, of lower diversity and perhaps more easily digested than the structural lipids, carbohydrates, and proteins found in leaves (cf. Wolff and Kwolek, 1971, on legumes).

Additional nutrients can offset the costs of processing high toxin concentrations in several ways. In a ruminantlike herbivore such as black colobus, greater nutrient concentration in the food may increase the activity rate of the microbes which digest toxins (Freeland and Janzen, 1974) and other difficult components of the food, so that more food can be processed per unit time. In ruminants, increased dietary nitrogen, for example, leads to an increase in rumen bacterial populations and in the rate of cellulose digestion, and to decreased food retention time in the rumen and increased food intake (Moir and Harris, 1962; Balch and Campling, 1965). Extra nutrients may also provide a greater pool of materials available for conjugation of toxin molecules by microsomal enzymes (Freeland and Janzen, 1974). Some classes of toxins may impose an additional kind of requirement for certain nutrients by binding to them in the digestive tract and preventing their absorption. Tannins, for example, form insoluble complexes with proteins, and it could be that many of the proteins ingested by the animal are going neither to the microflora nor to the animal, but are in effect being fed directly to tannins. Presence of tannic acid in the diet leads to excretion of high levels of nitrogen in the feces of rats (Tamir and Alumot, 1970). The availability of these nutrients to the microflora and to the animal may depend in part on the degree to which the herbivore has already eaten enough proteins to saturate the tannins. Feeding supplemental protein greatly reduces the effects of tannic acid (Singleton and Kratzer, 1973). Binding to nutrients within the digestive tract is not restricted to tannins. Gossypol binds with dietary iron (Singleton and Kratzer, 1973) as well as with protein (Reiser and Fu, 1962). Supplementation of the diet with iron salts greatly decreases gossypol toxicity (Singleton and Kratzer, 1973).

These and other kinds of interactions between the nutrient status of the animal and the effect of ingested toxic compounds appear to be of widespread importance. Starvation leads to lowered detoxification rate of drugs in rat liver (Marselos and Laitinen, 1975), and to prolonged and elevated blood concentrations of orally administered sulphanilimide in sheep (Clark and Wessels, 1952). Animals on rich diets are less susceptible to nitrate poisoning than animals on poor diets (Kingsbury, 1964). Increased protein value can delay the onset and reduce the effects of *Lathyrus* poisoning (Morcos, 1970). Toxicity of cyanogenic glycosides is reduced by supplementation of the diet with sulphur-containing amino acids, which are used as sulphur donors in the detoxification of cyanide to thiocyanate (Maner and Gomez, 1973).

If the leaves confronting black colobus do in fact contain generally high concentrations of toxic secondary compounds, these animals should feed heavily on nutrient-rich items such as seeds when acceptable seed items are present. They do so, in fact, spending more than 80 percent of their feeding time eating seeds (Figure 2) in several months.

It should be emphasized that probably most of the seeds eaten by black colobus contain secondary compounds. Seeds of *Erythrophleum ivorense* contribute up to 60 percent of the feeding records for a 5-day sample. These seeds contain major concentrations of alkaloids (E. A. Bell, personal communication). Seeds of some species of *Strychnos*, 3 species of which are used, are well known to contain strychnine and other highly toxic indole alkaloids (Bisset, 1971). Seeds of *Lophira alata,* another heavily used item, are unsuitable for cattle food because of their bitterness and astringency and are used in some areas as a hair unguent and lice remedy (Dalziel, 1937). The high nutrient contents (Table 3) of these and other seed items may be an important factor in the acceptability of such toxin-containing items to these monkeys.

Not all seeds will be exploitable by the monkeys. In fact, black colobus use only a very small proportion of the kinds of seeds present. Of the 15 most abundant trees in the study area (Table 4) seeds of only 3 are used. Of 52 species appearing in the enumeration of the study group's range, seeds of only 10 are used.

Table 3.—Available information on nutrient content of some seed items used by black colobus.

Seed item	*Remarks on nutrient content*	*References*
Lophira alata	40%-50% fat dry weight	Dalziel, 1937; Voorhoeve, 1965
Staudtia stipitata	over 30% fat; seeds of African Myristicaceae generally oil-rich and free of starch	Dalziel, 1937
Euphorbiaceae (4 species used by black colobus)	typically oil-rich and starch-free	Hegnauer, 1966
Leguminosae (2 species heavily used by black colobus)	usually contain much protein	Jones and Earle, 1966

Table 4.—Use of most abundant trees, and density of some heavily used items. X = never observed; 1 = less than 10 records for entire study; 2 = always less than 5 percent of records for a sample; 3 = accounted for at least 5 percent of records for 1 or more samples; 4 = accounted for at least 20 percent of records for 1 or more samples.

	Use of % of total stand	*Mature leaves*	*Young leaves*	*Seeds*
Most abundant trees				
1. *Protomegabaria stapfiana*	42.7	X	X	4
2. *Sorindeia mildbraedii*	5.0	X	X	4
3. *Anthonotha macrophylla*	3.7	X	2	X
4. *Uapaca staudtii*	3.2	X	X	X
5. *Coula edulis*	2.9	X	X	X
6. *Garcinia mannii*	2.9	X	X	X
7. *Leptaulus* sp.	2.9	1	1	X
8. *Lophira alata*	2.7	1	1	4
9. Unidentified 4-B	2.4	X	X	1
10. *Anthocleista* sp.	2.1	X	X	X
11. *Dichostemma glaucescens*	2.1	X	X	X
12. *Pachypodanthium* sp.	1.9	X	X	X
13. *Librevillea klainei*	1.9	X	1	1
14. *Pausinystalia* sp.	1.9	X	X	X
15. *Berlinia auriculata*	1.9	1	3	X
Heavily used items				
Strombosia pustulata	1.06	1	3	4
Erythrophleum ivorense	0.52	1	2	4
Berlinia bracteosa	0.26	3	4	X
Discoglypremna caloneura	0.26	2	3	4
?*Coelocaryon* sp.	0.26	3	3	2
Trichilia zenkeri	<0.26	1	2	4
Rauvolfia vomitoria	<0.26	3	1	X

Table 5.—Indications of secondary-compound content of some seeds avoided by black colobus. *Anthocleista* sp. is one of most common trees in study site; other species occur at densities comparable to heavily used species such as *Erythrophleum* and *Discogylpremna*. No feeding has been observed on seeds of any of these species.

Seed item	*Remarks on secondary-compound content* seeds used as purge, but in small amounts because regarded as toxic	*References*
Anthocleista sp.	seeds used as purge, but in small amounts because regarded as toxic	Dalziel, 1937
Xylopia aethiopica	contain a reberoside and resin rich in essential oils; oily extract of seeds used medicinally	Cousteix, 1961; Dalziel, 1937
Xylopia quintasii	extract of fruits used medicinally	Dalziel, 1937
Anthostema aubryanum	seeds provide a drastic purgative	Raponda-Walker and Sillans, 1961

Some seeds may contain toxins which the monkeys cannot degrade, others may contain toxins which are degradable but occur in too high concentration relative to the nutritive value of the seed. Some of the seeds avoided by black colobus are known to contain secondary compounds (Table 5), but it is not yet known whether there are consistent qualitative or quantitative differences in toxin content between these seeds and those the monkeys eat. Harvesting of some seeds may be unprofitable because of small size or extreme dispersion. Also, 3 species (*Coula edulis* Olacaceae, *Sacoglottis gabonensis* Humiriaceae, and *Klainedoxa gabonensis* Irvingiaceae) produce seeds which appear to be highly edible to man (Dalziel, 1937; Hegnauer, 1969; Raponda-Walker and Sillans, 1961; personal experience) and chimpanzees (*Coula edulis*: Struhsaker, personal communication) but which are enclosed in thick bony endocarps. All of these are heavily attacked by rodents and pigs, but it is doubtful that they could be cracked by a *Colobus*.

Seeds as an accessory nutrient source for subsidizing leaf digestion

When suitable seeds are scarce, the monkeys may be forced to feed to a greater extent on leaves. At these times, if most of the leaves present are in fact rich in toxic secondary compounds, it may be important for the monkeys to find accessory nutrients to subsidize digestion of the high-toxin, low-nutrient leaf portion of their diet. Seeds could serve as a source of such accessory nutrients. The function of seeds in the seed-leaf mix might be that of a nutrient concentrate, which enables the monkey to obtain the rest of its diet from lower quality, but more easily found, items which would not meet the animal's requirements if they alone were used. The mix of seeds and leaves must contain enough nutrients to offset the costs of toxin processing, and to maintain the rate of food processing at a level that enables the animal to meet its needs. What factors would determine the most suitable composition of the mix? High-quality items will often be rare, so that the greater cost of harvesting them, in terms of foraging effort required, may sometimes make it advantageous for the monkeys to accept lower quality items. Availability of suitable seeds would be expected to affect the composition of the mixture: the cost of accepting a higher proportion of leaves must be weighed against the feasibility of finding a higher proportion of seeds. Likewise, the quality of the leaves available may determine how important it is that the monkeys include a given proportion of seeds in the mix. For example, if suitable young leaves are abundant, the animal may require only a very low proportion of seeds. But if mature leaves must be heavily used, then the animal may require a greater proportion of seeds, to subsidize the processing of the higher contents of toxins and cellulose in mature leaves. If the monkeys are confronted with extreme scarcity of both seeds and young leaves, then they should be extremely selective in their choice of mature leaves.

Several features of black colobus feeding and ranging behavior suggest that seeds are being exploited as sources of accessory nutrients for the processing of the leaf portion of the diet, and that their leaf-feeding behavior varies with the abundance of suitable seeds in the manner expected.

(1) In none of the systematic samples did the proportion of seed records fall below 27 percent (Figure 2). This indicates that it may be important for the monkeys to maintain a substantial proportion of seeds in the diet at all times.

(2) Whenever the proportion of seeds has been

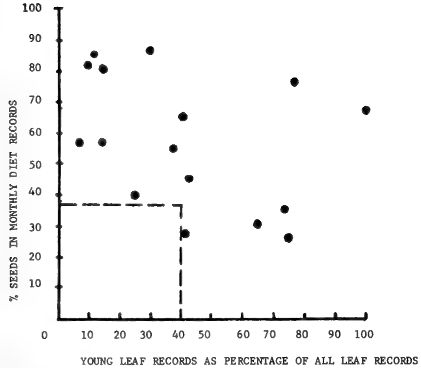

Figure 5. Variation in the proportion of young leaves in the leaf fraction of the diet, with variation in percentage of seeds in diet records, for all monthly samples.

below 40 percent, young leaves have always accounted for at least 40 percent of the leaf fraction. When young leaves have comprised less than 25 percent of the leaf fraction of the diet, seeds have always made up at least 57 percent of the total and usually at least 80 percent (Figure 5). This suggests that it may be very important for the monkeys to find young leaves when seeds are scarce, and to find seeds when young leaves are scarce.

(3) The frequency of bouts of "treefall-foraging" (see the introductory section on feeding and ranging behavior) is positively correlated with the proportion of mature leaves in the diet records (Figure 6). This suggests that as the proportion of higher quality foods such as seeds and young leaves decreases, the monkeys must be more selective in their mature-leaf feeding, obtaining a larger part of their diet from the leaves of those plants which colonize openings in the forest. Such plants may be expected to have lower concentrations of secondary compounds in their leaves than do plants of later successional stages (Cates and Orians, 1975; Janzen, 1974). Though the time sampled and the number of feeding records obtained are both very small, the information for September 1973 is very interesting. In this month neither *Trichilia zenkeri* nor *Mareya* sp., which provided the bulk of the seed records in September 1974, had begun fruiting. Of 43 records gathered, only 3 (7.2 percent) were seeds, only 4 (9.5 percent) were young leaves, and 21 (50 percent) were mature leaves. The proportion of seeds is much lower than for any of the samples in all months afterward, and the proportion of young leaves is much lower than the mean. The frequency of treefall-foraging is the highest of any month in the study. Confronted with extreme scarcity of both seeds and young leaves, the monkeys were obtaining a large portion of their mature-leaf diet from small scattered patches of second-growth vegetation.

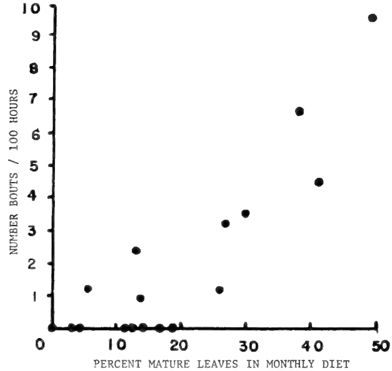

Figure 6. Frequency of bouts of "treefall-foraging" with variation in the extent of use of mature leaves in monthly systematic samples.

As noted in the general description of feeding behavior, mature leaves comprise a greater proportion of the leaf fraction in the diet of black colobus than is true for either of the Ugandan species. I suspect this might be a consequence partially of lower rates of young leaf production by individual trees in the Douala-Edea site, due to lower nutrient availability and to lower rates of young leaf replacement, but more particularly a result of the much lower density of trees producing suitable young leaves, especially deciduous trees. In addition, young leaf availability in Kibale Forest may be less seasonal than in the Douala-Edea site. The deciduous trees whose young leaves are heavily used by black colobus all produce young leaves at about the same time, the middle and late dry season. Whatever the reason for it, the greater dependence of black colobus on mature leaves may contribute to the requirement for nutrient-rich items to subsidize processing of the leaf part of its diet.

Greater selectivity in leaf-feeding

All 3 of the *Colobus* studied avoid the leaves of some of the most abundant trees in their habitat, but this pattern is even more striking for the black colobus than for the Ugandan species. Guereza feed heavily on the young leaves of 2 of the 3 most common trees in the Kanyawara site (*Celtis durandii* and *Markhamia platycalyx*) and feed heavily on mature leaves of *C. durandii* when its young leaves are scarce (Oates, 1974 and in press). Red colobus likewise eat young leaves of some of the most common trees, e.g., *C. durandii, Markhamia* and *Millettia dura,* all among the 10 most abundant trees in the site. In addition, they use the mature leaf blades of *Funtumia latifolia,* also among the 10 most common trees. In contrast, black colobus strongly avoid the mature leaves of *all* of the 15 most common trees in the Douala-Edea study area (Table 4). For 12 of these, I have not a single observation of mature-leaf eating after almost 2 years of study. The other 3 have provided less than 10 records each. Somewhat more surprisingly, the *young* leaves of almost all of these are also strongly avoided. For 10 of these 15 trees, I have never observed black colobus eating young leaves. Three others have provided fewer than 10 records each. (For 1 of these, *Lophira alata,* all the records of young-leaf eating were on saplings, never adult trees.) The young leaves of only 2 of these 15 species are regularly used when present, and only 1 ever accounted for more than 5 percent of the records for a sample.

Black colobus spend about 35 percent of their feeding time eating leaves. As striking as their avoidance of the abundant trees in the habitat is their disproportionately heavy use of often rare elements of the vegetation whose leaves may be expected to contain relatively low concentrations of toxic secondary compounds.

(1) Though deciduous trees account for only 7.2 percent of the individual trees in the main group's range, most of the few tree species whose leaves are heavily used by the monkeys are deciduous. Of the 4 tree species whose mature leaves have comprised more than 5 percent of the records in at least one 5-day sample, 3 are deciduous trees. Of the 9 species whose young leaves have attained this criterion of heavy use, 5 are deciduous trees.

(2) The leaves of vines comprise a much larger part of the leaf fraction of the diet of black colobus than for either of the Kibale *Colobus.* Vine-leaf records account for 22.5 percent of all leaf-feeding records obtained in the systematic samples, and for about 8 percent of all records in the samples. Vines (mostly vine leaves) account for 3 percent of all records obtained by Oates (1974, 1977) for guereza. Since leaves and leaf parts account for about 77 percent of guereza's diet, vine leaves then comprise about 4-5 percent of the leaf records. Red colobus use vine leaves even less than do guereza (Struhsaker, personal communication). "The success of the vine life form clearly depends on its ability to grow rapidly in length at the expense of other portions of its resource budget" (Janzen, 1974). A possible implication of this statement is that vine leaves may generally be invested with lower concentrations of defense chemicals than are leaves of primary forest trees. Information is not yet available on comparative vine abundance in the 2 sites, so we do not know whether black colobus select vine leaves to a greater degree than do Ugandan *Colobus.* It is clear, however, considering only the Douala-Edea site, that black colobus prefer vine leaves to the leaves of the most abundant trees.

(3) The previously described behavior of "treefall-foraging," in which black colobus descend into small patches of second growth and feed on leaves of colonizing plants, occurred at frequencies up to about 0.8 per day when the monkeys were feeding heavily on mature leaves (more frequently than once per day in the small opportunistically gathered sample of September 1973). This foraging behavior has been observed in *C. guereza* in Kibale Forest, (Oates, in press), but not in *C. badius.*

An important aspect of the black colobus' greater selectivity in leaf-feeding is that when they feed heavily on leaves, they often move much greater distances each day than do the Ugandan species. When black colobus are feeding primarily on seeds, they are often very sedentary, sometimes obtaining a very large part of their food from 4 or 5 individuals of 1 species. For example, in the May 1974 sample, the main group entered an average of 6.2 50 m quadrats each day, and only 23 quadrats during the 5 consecutive days. But in October 1974, when they were feeding heavily on mature leaves, they used 23.8 quadrats per day and 105 quadrats in 5 days. This is many more quadrats per day and per 5-day sample than are used by the primarily leaf-feeding Ugandan *Colobus.* Guereza enter an average of 9 quadrats per day and 29 (range 14-44) in 5 days; red colobus enter 12 (range 4-24) quadrats per day and 45 (range 27-65) in 5-day periods (Struhsaker and Oates, 1975). The largest number of quadrats entered by red colobus during a 5-day period (65) is much lower than the 2 largest values (85 and 105) for this parameter in black colobus. I suspect that the longer distances moved by black colobus when feeding heavily on leaves are due to 2 factors: first, suitable leaf items are rarer in their habitat; second, heavy use of leaves requires them to find a minimal portion of seeds to subsidize processing of toxins. Since they feed heavily on leaves primarily when suitable seeds are rare, they may have to move long distances to find this minimal portion of seeds.

Population Density

I have explored the hypothesis that black colobus are forced to find a minimal proportion of nutrient-rich items such as seeds, in order to increase the rate of processing of the leaf portion of the diet to a point where the monkey is processing and assimilating food fast enough to stay alive. If this is so, then the seed portion, even (especially) when it constitutes only a low proportion of the feeding records, is extremely important to them. Regardless of how many leaves are present, the monkeys cannot get a living from them unless they find a minimal proportion of nutrient-rich items to mix with the leaves. I have also proposed that the Kibale *Colobus* are not under this constraint because it is easier for them to find leaves or bits of leaves with relatively low concentrations of toxic secondary compounds.

It seems that the limiting portion of the black colobus resource base in the Douala-Edea Reserve is a set of items which are often rare, local, and seasonal. When it is noted, in addition, that the seeds of most of the abundant trees are not used by black colobus, and that most of the accepted leaf items are likewise provided by relatively rare trees, the small size of resource base for these monkeys in this site becomes especially dramatic. Their resource base may be smaller than for *Colobus* which live in sites where they can subsist largely on leaves, without having to find seeds to mix with them, and which can eat the leaves of a number of the most common tree species. We can expect the population density of black colobus to be much lower than that of colobus in Kibale Forest.

In fact, the density of black colobus in Douala-Edea (approximately 30 animals per km^2) is about one-tenth that of red colobus (about 300 per km^2) in Struhsaker's study area, and about one-third that of guereza (about 100 per km^2) in Oates's study area. (Guereza density in Struhsaker's site, however, is much lower than in Oates's site, though the 2 areas are only several hundred meters distant. Oates's site is closer to the disturbed forest in which guereza does best [Struhsaker and Oates, in press].) All the estimates are based on repeated censuses of monkeys along a set 4-km census route during a set time block (approximately 0730 hours–1230 hours).[2]

The proposed explanation for the low density of this population of black colobus is the same as that put forward for another herbivorous mammal, the opossum *Trichosurus vulpecula*, by Freeland and Winter (1975): The chemical defenses of the leaf supply force the animals to find nutrient-rich items to subsidize processing of the leaves, and the rarity of these items limits the population. In effect, the population density is indirectly limited by the chemical defenses of the plant community. To this it may be added that (1) only an extremely small fraction of the leaves present are acceptable even when their processing can be subsidized by nutrients from seeds; (2) only a small fraction of the seeds present are edible and thus available for subsidizing leaf processing.

This proposal has a weakness which is probably universal to explanations of population density of large tropical mammals: the activities of man obscure our understanding of their "natural" population densities. In my study area, black colobus were subject to some hunting up to the time of my arrival, though there are indications that shooting of *Colobus* in the immediate area was just commencing and that hunting activity had been only spottily distributed. Recensuses after some years of the protection this population is expected to receive from now on should help clarify our understanding of the way in which their numbers are limited.

Further Questions

The 3 species of *Colobus* under consideration here are very different animals in many ways. The evolution of a feeding strategy in a colobine confronting a forest whose leaves are exceptionally well defended might differ depending on the type of colobine. Struhsaker and Oates (1975) have demonstrated how different may be the feeding behavior and population densities of 2 *Colobus* species surviving in the same forest. If red colobus were present in the Douala-Edea site, would they also supplement leaf items with nutrient-rich items, or could they subsist primarily on leaves by being very selective of the *parts* of leaves they eat—e.g., feeding on petioles of leaves or pieces of leaf blade, as they do at Kibale? Such questions are unapproachable without information on the chemical composition of these parts of leaves between the 2 sites. Red colobus (*C. badius preussi*) do exist in coastal rain forest in the Korup Reserve, near the Nigerian border, and at least part of this forest seems to be built on sandy soils, perhaps similar to those of

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[2] On these census walks, the number of groups seen and their distance from the observer and from the census line were noted. Density estimates were constructed from knowledge of mean group sizes and from estimates of the area that was accurately censused. Discussion of the census methods can be found in Struhsaker's (1975) monograph. While methods of determining the area censused varied between sites (McKey, in preparation; Oates, 1974 and 1977; Struhsaker, 1975), all 3 observers arrived at similar estimates, i.e., 45 m–50 m on either side of the census line.

the Douala-Edea Reserve. A study of the feeding behavior of these animals might tell us much about how red colobus and black colobus differ in their exploitation of similar forest.

In conclusion, I wish to emphasize that the feeding behavior of black colobus in the Douala-Edea Reserve may point to the real significance of foregut fermentation in the ruminantlike stomach of colobines. I believe that this feature of colobine digestion is to be viewed not primarily as a device for processing diets with high contents of fiber, but rather as an adaptation for dealing with food containing toxic secondary compounds. Leaves and seeds are interchangeable in this respect, and thus it is not anomalous that this "leaf-eater" feeds so heavily on seeds.

Summary

Feeding behavior of black colobus (*C. satanas*) in the Douala-Edea Reserve in southern Cameroun differs in several ways from that of other species of *Colobus*. Seeds are by far the most frequently utilized class of food item, comprising on average 57.6 percent of monthly food records and over 80 percent of records in some months. Leaves account for less than 40 percent of records. *Colobus guereza* and *C. badius* in Kibale Forest, Uganda, are predominantly leaf-eaters and eat very few seeds. It is proposed that these differences in feeding behavior between the 2 sites may be ultimately related to gross differences in the amount of plant nutrients in the soils of the 2 study areas. Since the soils of the Cameroun site have much lower contents of plant nutrients, there has been selection for greater investment in chemical defense in the vegetation of this site, because the loss of a leaf entails a greater cost to the plant than if it were growing in a site richer in nutrients. The resultant lower quality of leaves in this site as food for herbivores may have led evolutionarily to the black colobus' dependence on seeds rather than on leaves, and to the observed greater selectivity in leaf-feeding by black colobus.

NOTE: The abundant ephorbiaceous tree in the Cameroun study area, tentatively referred to above as *Mareya* sp. has since been determined as *Protomegabaria stapfiana*.

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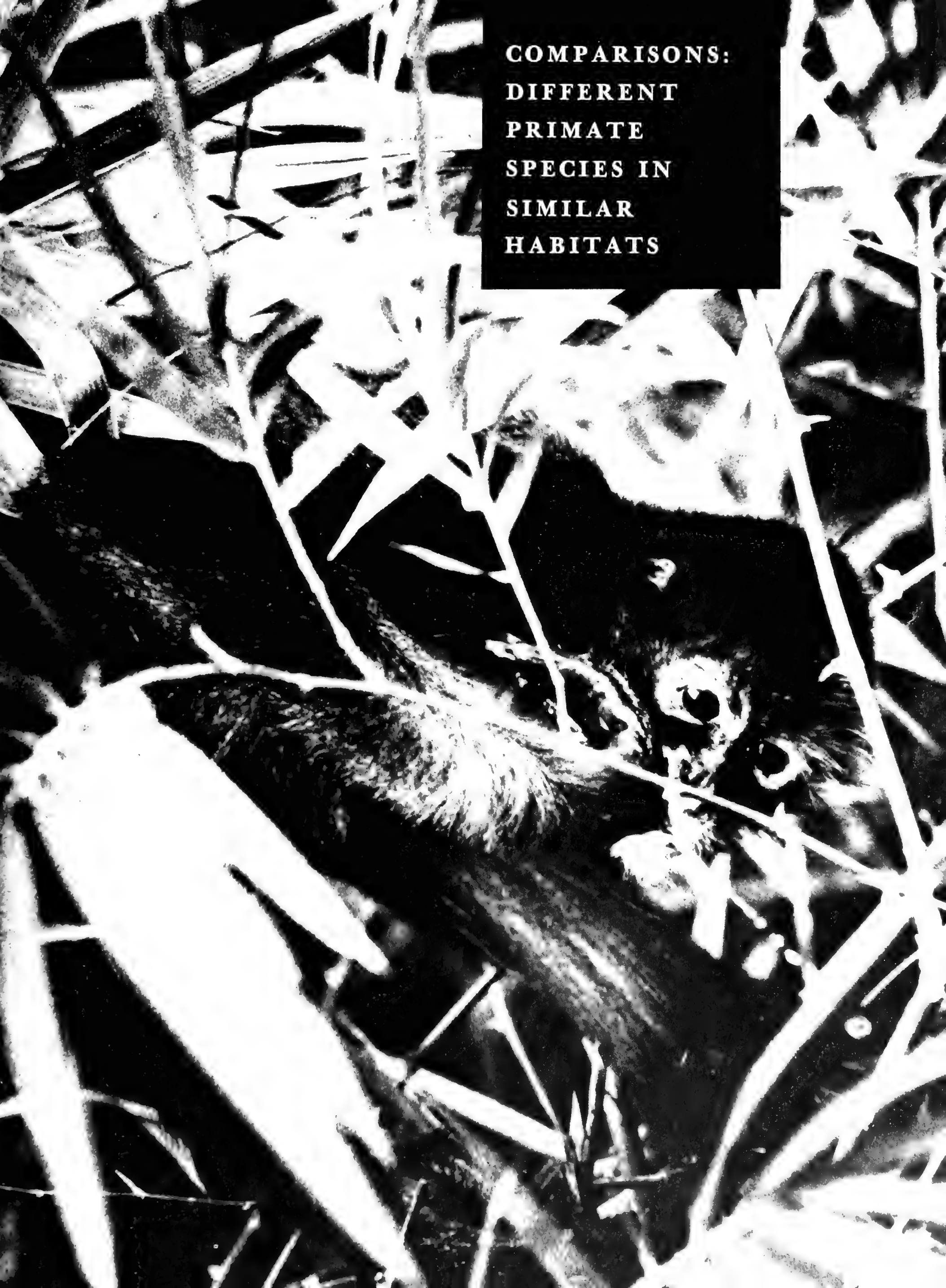
Ateles geoffroyi, the spider monkey is a partial folivore and occurs in sympatry with four other primate species on Barro Colorado Island. (Photo by C. M. Hladik)

COMPARISONS: DIFFERENT PRIMATE SPECIES IN SIMILAR HABITATS



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Leaf-eating Primates of Peninsular Malaysia: the Siamang and the Dusky Leaf-Monkey

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Introduction

Systematic field studies of nonhuman primates, which were first undertaken during the 1930s (Carpenter, 1934; 1940) and then resumed after World War II, have for the most part concentrated on species which spend much if not most of the day on the ground, such as baboons (DeVore, 1962; Altmann and Altmann, 1970; Kummer, 1968), macaques (Southwick et al., 1965; Frisch, 1968; Deag, 1973), and the common Indian langur (Jay, 1965; Sugiyama, 1965). The availability of sites characterized by favorable observation conditions and tolerance of observers by the animals have been important considerations in the choice of target species. Within the last decade a growing number of investigators have turned their attention to the more difficult to observe arboreal primates (Struhsaker, 1969; Marler, 1969; Aldrich-Blake, 1970; Klein, 1971, 1972; MacKinnon, 1971; Clutton-Brock, 1972; Rodman, 1973; Ellefson, 1974). Most of the folivorous members of this group, especially those inhabiting dense rain-forest habitats, are still largely unstudied.

The primates of Krau Game Reserve, Pahang, Malaysia have been the subjects of a series of field studies since 1968. It is hoped to obtain eventually a detailed picture of the synecology of primate species in this area. Observations covering periods of 1 year or longer have been made on the siamang, *Hylobates syndactylus* (Chivers, 1971a, 1971b, 1972, 1973, 1974), dusky leaf-monkeys, *Presbytis obscura*, and banded leaf-monkeys, *P. melalophos* (Curtin, 1976, 1977), and the white-handed gibbon, *H. lar*. Studies of shorter duration have been completed on siamang (Aldrich-Blake and Chivers, 1973; Chivers, et al., 1975) and on comparative habitat utilization by hylobatids, leaf-monkeys, and macaques (MacKinnon and MacKinnon, 1973; Fleagle, 1978). A study of long-tailed macaques, *Macaca fascicularis*, is in progress (Aldrich-Blake, personal communication) and future work is planned on the pig-tailed macaque, *M. nemestrina*.

The Krau Game Reserve includes more than 500 square kilometers of mostly undisturbed forest between elevations of 30 and 2,100 meters. The Kuala Lompat study area at the confluence of the Lompat and Krau rivers on the southeast corner of the Reserve is lowland evergreen rain forest of the Dipterocarp type (Wyatt-Smith, 1953). The forest contains a high percentage of trees and lianas of the family Leguminosae (Chivers, 1974). Especially notable components of the floral community are the emergents *Koompassia excelsa* and *K. malaccensis*, which tower above other trees in the upper canopy and may reach heights of more than 80 meters. Other common leguminous trees are *Intsia palembanica, Parkia javanica, and Dialium playtsepalum*. Climbing and strangling members of the genus *Ficus* are also abundant.

Although the huge trees of the upper canopy are the most striking feature of the forest, most of the vegetation is borne in the middle story[1] and the greatest density of animal life is found there. This region varies between 25 and 35 meters (D.J.C.'s area) and 15 and 30 meters (S.H.C.'s area) depending on local floral composition and proximity to rivers.

Seasons are not as pronounced in the humid tropics as in temperate areas but seasonal variations in temperature and rainfall do exist. A major feature of the Malayan climate is the northeast monsoon during the last 2 to 3 months of the calendar year, producing heavy rainfall and often serious flooding. The months from January to April are characterized by high temperatures and low rainfall. At other periods of the year weather patterns are less predictable, although a second wet season caused by the southwest monsoon often occurs in May and June (Chivers, 1974).

Some forest trees at Kuala Lompat renew their leaves more or less continuously throughout the year, but many others show pronounced cycles of complete defoliation followed by leaf flush. Dominant species of the upper canopy exhibiting this pattern include the leguminous genera *Koompassia, Parkia,* and *Intsia*. Defoliation and flush cycles in these species are synchronous (as are those of *Dillenia* but not *Sindora*), occurring during the dry season months from January to March; they produce a dramatic change in the general aspect of the forest. Another period of phenological synchrony occurs from July to September, when many different trees come into fruit simultaneously (Medway, 1972). Some fruit is always available during other times of the year but not in the quantity that characterizes this period. Many species of the genus *Ficus* bear fruit outside the main fruiting season, either once or as many as 3 or 4 times a year.

Methods

The aim of this paper is to describe and compare the feeding behavior and social organization of 2 Malaysian primate folivores, the siamang and the dusky leaf-monkey, and to contrast their feeding strategies

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[1] Dividing the forest into vertical levels proved convenient during the fieldwork. However, the reality of such levels has recently been questioned by a number of authors. See A. Hladik, 1978.

with those of other members of this large primate community.

Siamang of 1 group were studied by D.J.C. for 14 months in 1969–1970. The group of 5 animals (adult pair and 3 immature offspring) was followed from dawn to dusk on a minimum of 10 consecutive days per month for a total of 148 days and 1707 hours of observation. Individual behavior, group activity, daily ranging, calling, inter-animal spacing, and social interactions were recorded. The siamang group habituated to the observer after approximately 40 hours and could thereafter be observed continuously from distances as close as 10 meters without disturbing normal activity patterns.

Dusky leaf-monkeys and banded leaf-monkeys were studied simultaneously for 12 months in 1970–1971 by S.H.C. Observations of dusky leaf-monkeys totalled 356 hours and of banded leaf-monkeys 485 hours. Data were collected on social interactions, group activity patterns, ranging, intergroup relations, calling, and interspecific relations. The main study group of dusky leaf-monkeys numbered 17 animals in September 1971 and included 2 adult males, 7 adult females, 2 subadult females, 4 juveniles, and 2 infants. After 2 months of work, contact could be maintained with members of the group almost indefinitely, but throughout the study, certain individuals and sometimes the entire group occasionally were startled and hid. Observations were made for periods of 2 to 4 days, alternating with similar periods spent following banded leaf-monkey groups that ranged over the same area of forest.

Food trees of siamang and dusky leaf-monkeys were tagged, mapped, described, and identified when possible. Description of dusky leaf-monkey food trees included location, height, branching pattern, number of lianas, size and appearance of leaves, flowers, and fruit. At the conclusion of the 1969–1970 study 450 trees had been tagged and 545 mapped. The 1970–1971 study contributed an additional 438 trees tagged and mapped, representing 98 percent of all observed feeding occasions. Other investigators working at Kuala Lompat since 1971 have made significant additions to the tree inventory.

Feeding activity was recorded in terms of time of day, tree identity, article consumed, number of visits, and duration of feeding. A visit constituted a discrete occasion on which the animals fed upon resources in a particular tree. D.J.C. has calculated the representation of different categories of food items in the diet of the siamang using 3 separate measures: (1) the number of food trees, (2) the number of feeding visits, and (3) feeding time. Proportions for the main categories did not change significantly according to the different measure, with the exception of fig trees (Chivers, 1974). None of these measures are as useful as measures of food intake by weight or composition (C. M. Hladik, 1978).

Results and Discussion

Categories of food items

Primates of the family Hylobatidae have generally been considered frugivorous (Carpenter, 1940; Ellefson, 1974). The Malayan siamang, however, is primarily folivorous (Chivers, 1974) and recent work indicates that the white-handed gibbon is less frugivorous than described previously (Jeremy Raemaekers, personal communication). A similar traditional characterization of the subfamily Colobinae as folivorous (Napier and Napier, 1967) also has notable exceptions (Curtin, 1977).

Like the diet of the siamang, that of the dusky leaf-monkey contains a high percentage of leafy material. Proportions of food types in the diets of the 2 species shows a close agreement (Table 1). Principal differences are: (a) the presence of insects in the diet of the siamang and their apparent absence in the diet of the other species, and (b) state of maturity of leaves eaten. The first difference is probably attributable to differences in observation conditions. On a number of occasions dusky leaf-monkeys examined bark surfaces and probed cavities with their hands or mouths, and in one instance strips of bark were systematically torn off and discarded; the nature of the food substance if any was not determined. The second difference, that of leaf maturity, is of more significance. Siamang only very rarely fed on fully mature leaves, while dusky leaf-monkeys did so regularly (Table 2). On over half the occasions on which mature leaves were consumed by dusky leaf-monkeys, the monkeys showed selectivity in the portion of leaf taken, either by eating the leaf tip (especially in *Ficus* spp.) or the petiole.

Table 1.—Proportions of different food types eaten by siamang and dusky leaf-monkeys.

Food	*Siamang* *% visits (N = 1835)*	*Dusky leaf-monkey* *% visits (N = 238)*
Leaves	59	58
Fruit	31	35
Flowers	8	7
Insects	3	0

Table 2.—Selective feeding on mature leaves by siamang and dusky leaf-monkey.

	Siamang number of visits	*Dusky leaf-monkey number of visits*
Entire leaf		24
Leaf petiole		15
Leaf tip		14
Total visits	11	53
Number of all leaf-eating visits	1083	138
% of all leaf-eating visits for mature leaves	1%	39%

If the high proportion of structural compounds in mature leaves is to be used as a food source, the cellulose-containing substances must be converted into volatile short-chain fatty acids through bacterial fermentation. The anatomical and physiological features underlying this semiruminant type of digestion are unusual in the higher primates, and form the basis for the separation of the subfamily Colobinae. Specializations of the Asian branch of the colobines include a complex sacculated stomach and the presence in at least 2 species (*P. entellus* and *P. cristata*) of high numbers of cellulose-digesting bacteria in the gastric contents (Bauchop, 1971; Bauchop and Martucci, 1968). It is probable that the dusky leaf- monkey also depends on bacterial fermentation during digestion, although the appropriate studies have not yet been made on this species. Evidence from rearing captive dusky leaf-monkeys points to a critical period in development, between 2 and 4 months of age, during which the stomach bacteria are acquired either from the mother or another member of the social group[2] (Curtin, personal observation).

If fermentation occurs in the siamang's gastro-intestinal tract it would probably occur in the colon, which is large relative to that of most other Old World primates. The poorly digested state of leafy material in their feces, however, suggests that the siamang is less capable of digesting cellulose than the leaf-monkeys.

Seasonality of diets

Seasonal variation in the diets of siamang and dusky leaf-monkey occurred, but was not as marked as might have been expected (Table 3). In the diet of the dusky leaf-monkey the prevalence of leaves and flowers and the relative scarcity of fruit in the dry season were reflected in high scores for the former categories (77 percent of the overall total); fruit became increasingly important during the intermediate season (comparative data are not available for the rainy season at the end of the year).

The siamang data, however, did not show the

Table 3.—Seasonal variation in food type proportions of siamang and dusky-leaf monkey.

Siamang	*"Season"*	
	Dry: Jan. to Apr.	*Intermediate: May to Aug.*
Food	*% visits (N=637)*	*% visits (N=526)*
Leaves, young	58	60
Fruit	31	25
Flowers	6	14
Insects	6	1
Dusky leaf-monkey		
Food	*% visits (N=78)*	*% visits (N=147)*
Leaves, young and mature	65	57
Fruit	23	39
Flowers	12	4

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[2] Of three infants acquired from aborigines outside the Reserve and maintained in captivity during S.H.C.'s field study, two died at the age of five months of a bloat syndrome culminating in fatal pneumonia. Both had previously been in excellent health and had been fed on a diet closely approximating that of their wild conspecifics. A third infant survived. Several points are suggestive: (1) the first two infants were captured at the age of about two months while the third infant was captured at the age of four to five months; (2) the deaths occurred at a time when solid food intake was rising sharply; (3) all three infants had been cared for in an identical manner; and (4) the two that died showed very similar symptoms, and the course of development of the illness was the same in both cases. Apparently the infants that died had been removed from contact with conspecifics before the bacterial symbionts had been acquired, and although they flourished in captivity for several months, they finally succumbed when their diet was shifting from liquid to solid foods. An infantile behavior pattern of persistently nuzzling and licking adult females' mouths might provide the means by which the bacteria are acquired.

Table 4.—Pattern of use of main food tree species by siamang.

Tree species	*% of 525 food trees*	*% of 1912 feeding visits*	*% of 14 months*	*Height class*
Ficus spp. (13 +)	12.2	20.0	100	M
Sloetia elongata	11.4	13.4	100	U
Endospermum malaccense	5.9	2.2	29	U
Randia scortechinii	2.5	1.6	50	U
Koompassia excelsa	1.9	2.2	57	E
Nauclea sp.	1.9	0.8	14	U
?*Wiedelandia* sp.	1.5	2.0	43	U
Carallia brachiata	1.5	1.5	43	M
Sarcotheca griffithi and *S. monophylla*	1.5	3.2	43	M
Gnetum macrostachys and *Gnetum* sp.	1.3	1.3	43	M
Xylopia caudata and X. malayana	1.1	1.3	64	U
Knema laurina	1.1	0.8	29	U
Eugenia sp.	0.8	0.7	14	M
Aglaia sp.	0.8	1.2	43	M
Parinari oblongifolia	0.8	0.8	43	M
Maranthes corymbosa	0.6	0.8	21	M
Calophyllum sp.	0.6	0.4	14	M
Diospyros sp.	0.6	0.3	14	M
Bouea oppositifolia	0.6	0.6	14	M
Total Ficus + 21 spp.	48.7	56.4		
Other identified trees	14.9	15.2		
Unidentified trees	36.6	28.4		

E = emergent (36 + m). M = middle (24-36 m). U = understory (<24 m).

same pattern; if anything they seemed to contradict it. The siamang maintained considerable stability of dietary composition, despite fluctuations in available resources produced by seasonality in the forest vegetation. Fruit and leaf consumption hardly varied at all by feeding visits; the only significant differences were in the fewer visits to feed on flowers and insects. The intermediate season covers the flowering and start of the fruiting season, hence more flowers are consumed at this time; insects are more abundant periodically, in this case during the 1970 dry season.

The siamang achieved consistency in its diet throughout the year by exploiting different plant species with different seasonal cycles, in such a way that the proportions of each dietic category remained more or less constant. This strategy requires considerable species diversity in the diet (Table 4). In addition to at least 13 species of climbing or strangling fig, *Ficus* spp., there were 21 species in 18 other genera that were repeatedly exploited by the siamang. Particular tree species differ in importance in 4 main ways: (1) numerous individuals of the species were used; (2) only 1 or 2 individuals were used; within either of these categories (3) the trees were used intensively at only certain seasons, or (4) they were less intensively used over longer periods (Chivers, 1974).

Diversity of diets

The numerous species of *Ficus* were the most important single group of food trees for siamang, providing a continuous supply of new leaves and fruit throughout the year. The fig trees were particularly favorable food sources for a number of reasons : (a) their abundance in the Malayan flora exceeds that of any other native genus (Corner, 1952); (b) they are typically of large size, particularly the strangling figs; (c) they show a diverse set of leaf-flushing strategies; (d) the genus is characterized by a great diversity of fruiting cycles, some species fruiting 2 or 3 times a year, others at long irregular intervals, so there is a high probability that one or more trees will be in fruit at any one time, even within as small an area as the siamang territory; and (e) they produce an exceptionally large quantity of fruit compared to most other forest trees.

Second to the *Ficus* species in importance were *Sloetia elongata* trees, from which siamang ate new leaves during the period August to April, and fed intensively on flowers between March and July. Other notable food sources included new leaves of *Koompassia excelsa, Parinari oblongifolia,* and *Xylopia* spp., produced during the main period of leaf flush during the dry season; fruits of *Randia scortechinii* and *Maranthes corymbosa,* available during the months of the main fruiting season; and fruits and new leaves of a number of lianas such as *Gnetum, Connarus,* and *Combretum.* Owing to special difficulties in obtaining specimens and making specific identifications, the lianas are under-represented, and are probably of greater importance to the siamang than this analysis would indicate.

A minimum of 25 species of trees and lianas were eaten 3 times or more by dusky leaf-monkeys (Table 5). The true number is somewhat higher, since many lianas, including climbing figs, could only be identified as to genus. As with the siamang, species of *Ficus* figure prominently in the diet. New leaves and

Table 5.—Important food species of dusky-leaf monkey.

Species	*Percent of 200 food trees*	*Percent of 233 feeding visits*	*Height class*
Maranthes corymbosa	4.5	7.7	E
Pentaspadon velutinum	6.0	6.0	E
Ficus spp. (1)	5.5	5.2	E
Intsia palembanica	5.5	5.2	E
Parkia javanica	3.0	3.4	E
Spatholobus spp. (1)	3.0	2.6	E
Ficus spp.	2.0	2.1	E
Koompassia malaccensis	2.0	2.1	E
Koompassia excelsa	2.0	1.7	E
Connarus spp. (1)	2.0	1.7	E
Ventilago spp. (1)	2.0	1.7	E
Vitis spp. (1)	2.0	1.7	E
Xylopia malayana	0.5	1.7	E
Alstonia angustiloba	1.5	1.3	E
Dillenia reticulata	1.5	1.3	E
Dillenia sp.	0.5	1.3	E
Eugenia spp.	1.0	1.3	E
Combretum spp. (1)	1.0	1.3	E
Hibiscus floccosus	1.5	1.3	E
Indorouchera griffithi (1)	1.0	1.3	E
Palaquium hispidum	1.5	1.3	E
Rourea spp. (1)	1.5	1.3	E
Xanthophyllum excelsum	1.5	1.3	M
Xanthophyllum scortechinii	1.0	1.3	E
Xylopia magna	0.5	1.3	E
Total 25 spp.	54.0	58.4	
Other identified trees	42.0	36.9	
Unidentified trees	4.0	4.7	

(1) = liana. E = emergent (30 + m). M = middle (15-30 m).

fruit were consumed at all times of the year. A large strangling fig in fruit might be used several days in succession, but usually each tree was visited only once. On 4 occasions the monkeys spent long periods of 2 hours or more feeding on petioles of fully mature fig leaves.

In addition to *Ficus*, 3 species of emergent trees were especially important in the dusky leaf-monkey diet. New leaves of *Intsia palembanica* were intensively used throughout the dry season and were a principle source of food during this period of relative food scarcity. Mature leaf tips of *Pentaspadon velutinum* were fed on repeatedly during the dry season, and later new leaves then fruit were eaten. During the height of the main fruiting season *Maranthes corymbosa* was the most frequently visited tree species. Unlike the majority of Malayan forest trees, *Maranthes corymbosa* typically occurs in clumps of several individuals. One such clump in the core area (Kaufmann, 1962) of the main study group was visited repeatedly in July and August, and was also used by banded leaf-monkeys, long-tailed macaques, and rhinoceros hornbills (*Buceros rhinoceros*).

The diversity of the diets of both siamang and dusky leaf-monkeys is indicated in Figure 1. More than one-third of siamang food trees were visited only once, while nearly 80 percent were visited 5 times or less. Most of the 7 percent of food trees which accounted for 30 percent of the visits were *Ficus* species or *Sloetia elongata*, each tree containing several species of lianas. Major siamang food trees were thus characterized by providing a diversity of plant species (host tree and lianas) and of food categories. Over 80 percent of all food trees of dusky leaf-monkeys were visited only once and only 10 percent of the remainder were visited twice (Figure 1). Trees visited 3 times or more shared 2 characteristics: (a) almost all were emergents, and many were trees 45 meters or more tall, and (b) most trees contained 1 or more lianas. It thus appears that size of tree and diversity of food sources in it are crucial determinants of repeated use by dusky leaf-monkeys (for comparison see Montgomery and Sunquist, 1978).

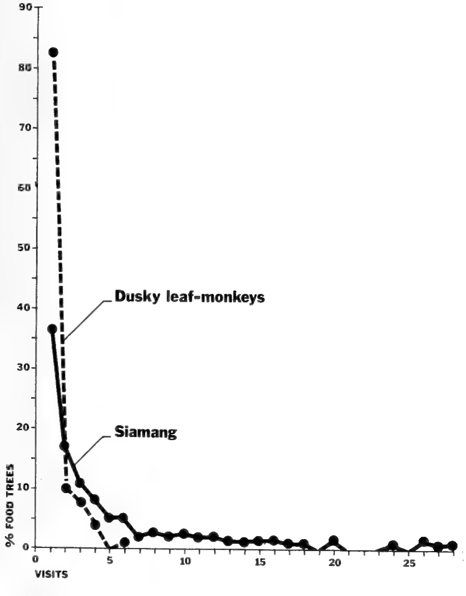

Figure 1. Number of visits to each food tree by siamang and dusky leaf-monkeys.

Food species and plant secondary compounds

The role of plant secondary compounds in influencing the food preferences of mammalian herbivores has received growing attention of late (Eberhard, 1978; Glander, 1978; Janzen, 1978; McKey, 1978; Freeland and Janzen, 1974; Janzen, 1970, 1974; Willson, 1973). Although the chemical composition and prevalence of plant secondary compounds are not completely known for any one tropical habitat, there is suggestive evidence that such substances are widespread and common in the tropics. Tropical forest on extremely nutrient-poor soils drained by "blackwater" rivers may consist almost exclusively of plant families especially rich in defensive chemicals (Janzen, 1974; McKey, 1978). Forest on comparatively nutrient-rich lateritic soil may also show a high percentage of defended plant species (A. Hladik, 1978).

A majority of feeding tree visits by both siamang and dusky leaf-monkeys were to trees belonging to families known to be rich in secondary compounds (Table 6). Families listed by Janzen (1974) as having wood and roots containing large amounts of latex, resins, essential oils, tannins, terpenols and phenols and utilized for food by one or both of these primate species include the following: Anacardiaceae, Apocyanaceae, Burseraceae, Chrysobalanaceae, Dipterocarpaceae, Ebenaceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae, Rubiaceae, Sapindaceae, Sapotaceae, Sterculiaceae, and Xanthophyllaceae. Other families known to contain mildly or highly poisonous trees and lianas are the Linaceae and Combretaceae (both rich in tannins), Strychnaceae, Rhizophoraceae, Urticaceae (stinging-nettle family) and Verbenaceae (Corner, 1952; Foxworthy, 1927; Willis, 1973). Feeding visits by siamang to trees be-

Table 6.—Food plants and food items of (a) siamang and (b) dusky leaf-monkey.

	SIAMANG (observed for 1707 hours)			*DUSKY LEAF-MONKEY (observed for 356 hours)*		
Family and species	*Parts consumed*	*Number of trees*	*Number of visits*	*Parts consumed*	*Number of trees*	*Number of visits*
Anacardiaceae						
Bouea oppositifolia	nl,F	3	4			
Dracontomelum mangifera	F	1	1	mlt	1	1
Mangifera indica	F,b	2	2			
Melanorrhea malayana				F	1	1
Pentaspadon velutinum	nl, b	1	5	nl,nlp,mlt,F	12	14
Annonaceae						
Cyathocalyx pruniferus				F	1	1
**Desmos* sp.				nl	1	1
Oxymitra filipes	?	1	?	F	1	1
Polyalthia sp.				F	1	1
Xylopia caudata	nl,nlp,f	6	12			
Xylopia ferrugina				ml	1	1
Xylopia magna				f	1	3
Xylopia malayana	nl	1	1	nl,F	1	4
Apocyanaceae						
Alstonia angustiloba	nl	2	3	nl,f	3	3
Alstonia sp.				nl	1	1
Dyera costulata				nl	1	1
Kibatalia maingayi				f	1	1
**Parameria* sp.				nl	1	1
Teysmanniodendron sp.	nl	1	2			
Willughbea sp.	nl	1	2	F	1	1
Bignonaceae						
Stereospermum fimbriatum				nl	1	1
Bombaceae						
Durio lowianus				f	1	1
Durio zibethinus				f	1	1
Burseraceae						
Canarium littorale				F?	1	1
Canarium megalanthum	b	1	1	nl	1	1
Celastraceae						
Salacia flavescens				nl	1	1
Salacia sp.				nl	1	1
Chrysobalaurceae						
Maranthes corymbosa	F	3	15	mlt,F	9	18
Parinarioblongifolia	nl	4	13	nl	1	1
Combretaceae						
**Connarus* sp.	nl	2	4	ml,F	4	4
**Rourea* sp.				ml,F	3	3
Convulvulaceae						

Table 6.—Food plants and food items of (a) siamang and (b) dusky leaf-monkey.

	SIAMANG (observed for 1707 hours)			*DUSKY LEAF-MONKEY (observed for 356 hours)*		
Family and species	*Parts consumed*	*Number of trees*	*Number of visits*	*Parts consumed*	*Number of trees*	*Number of visits*
Covulvulaceae						
**Merremia* sp.	nl	1	4	nl	1	1
Dilleniaceae						
Dillenia reticulata	b	1	1	nl,F,f	3	3
Dillenia sp.				ml,F	1	3
**Tetracera* sp.	nl	2	12			
Dioscoreaceae						
*?*Dioscorea* sp.				nl	1	1
Dipterocarpaceae						
Hopea sp.	nl	1	1			
Dipterocarpus baudii				mlt,F?,b?	2	2
Shorea bracteolata				ml?	1	1
Shorea leprosula	nlp	3	11			
Shorea sumatrana	nl	1	1			
Ebenaceae						
Diospyros cf. *pendula*	nl,F	5	7			
Euphorbiaceae						
Blumeodendron kurzii				F	1	1
Elateriospermum tapos				F	1	1
Endospermum malaccense	F,i	27	43			
Mallotus muticus				nl	1	1
Mallotus sp.				nl	1	1
Sapium baccatum	nl,F	2	3			
Fagaceae						
Lithocarpus lucidus	F	1	1			
Flacourtiaceae						
Paropsia veraciformis				F	1	1
Gnetaceae						
**Gnetum macrostachyum*	nl,F	7	10			
Gnetum sp.	nl,F	2	5			
Guttiferae						
Calophyllum sp.	nl,F	2	3			
Cratoxylum formosum				nl	1	1
Garcinia sp.	F	1	1			
Ixonanthaceae						
Irvingia malayana				nl?	1	1
Ixonanthes icosandra				F	1	2
Lauraceae						
Dehaasia sp.				F	1	1
Endiandra sp.				F	1	1
Nothphoebe umbelliflora				nl,F	1	1
Linaceae						
**Indorouchera griffithi*	nl	1	4	nl	2	3

Table 6.—Food plants and food items of (a) siamang and (b) dusky leaf-monkey.

	SIAMANG (observed for 1707 hours)			*DUSKY LEAF-MONKEY (observed for 356 hours)*		
Family and species	*Parts consumed*	*Number of trees*	*Number of visits*	*Parts consumed*	*Number of trees*	*Number of visits*
Leguminosae						
**Acacia pennata*				ml	1	1
Cassia nodosa	nlp	1	5			
Cynometra inaequifolia	nl	1	5	nl,ml	2	2
**Derris* sp.	nl	4	6	nl,F	2	2
Dialium patens				nl,ml,F	1	1
Dialium platysepalum	nl	4	5			
Koompassia excelsa	nlp,F,f	11	23	nl,ml	4	4
Koompassia malaccensis				nl	4	5
Intsia palembanica				nl,ml,F	11	12
Microtropis sp.				nlp	1	1
Parkia javanica				nl,ml,mlt,F	6	8
Parkia speciosa				F	2	2
Peltophorum pterocarpum				nl	1	1
**Spatholobus* sp.				mlp,nl,F,f	6	6
**Spatholobus* sp.	nl	1	5	F	1	1
Lythraceae						
Lagerstroemia flos-reginae				nl	1	1
Malvaceae						
Hibiscus floccosus				nl,mlp	3	3
Meliaceae						
Aglaia sp.	nl,F,f	5	11			
Chisocheton erythrocarpus				F	1	1
Dysoxylum costulatum				F	1	1
Dysoxylum sp.				nlp,F	2	2
Sandoricum sp.	nl,F	1	3			
Walsura neuroides	nl,F	1	3	nl	1	1
Moraceae						
Ficus annulata	nl,F	2	6			
Ficus bracteata	F	1	1			
Ficus consociata	nl,F	2	7			
Ficus heteropleura	F,nlt	3	10			
Ficus kerkhovenii	nlp	3	14			
Ficus pellucido-punctata	F	5	8			
**Ficus auriantacea*	F	6	21			
Ficus stupenda	F,nl	5	21			
Ficus subutata	nl	4	8			
Ficus sumatrana	F	3	7			
Ficus virens	F,nl	6	15			
Ficus spp.	F	2	5	ml,mlp,F	4	5
**Ficus* spp.	F,nl	5	46	nl,ml,mlp,F	11	12
Sloetia elongata	nl,F,f,b,	61	147			
Myristicaceae						
Horsfieldia irya	nl,b	1	4	nl	1	1
Knema laurina	F	6	9			
Myristica inera				F	1	1
Myrsinaceae						
Ardisia sp.	F	2	3			

Table 6.—Food plants and food items of (a) siamang and (b) dusky leaf-monkey.

	SIAMANG (observed for 1707 hours)			*DUSKY LEAF-MONKEY (observed for 356 hours)*		
Family and species	*Parts consumed*	*Number of trees*	*Number of visits*	*Parts consumed*	*Number of trees*	*Number of visits*
Myrtaceae						
Eugenia sp.	nl,F	5	5	nl,ml	2	3
Rhodamnia trinerva	b	1	1			
Olacaceae						
Ochanostachys amentacea				?	1	1
Strombosia javanica				ml,f	1	1
Oxalidaceae						
Sarcotheca griffithi	f,F,nl	8	15			
Sarcotheca monophylla	nl,F	1	3			
Potaliaceae						
**Fagraea auriculata*				f	1	1
Polypodiaceae						
Platycerium sp.				l	1	1
Rhamnaceae						
* *Ventilago* sp.				nl	4	4
Rhizophoraceae						
Carallia brachiata	b,F,nl	9	12			
Rosaceae						
Maranthes corymbosa	F	3	15	mlt,F	9	18
Parinari oblongifolia	nl	4	13	nl	1	1
Rubiaceae						
Canthium sp.				nl	1	1
Nauclea sp.	F	4	4			
Randia scortechinii	F	13	24			
Randia anisophylla				F	1	1
**Uncaria* sp.	nl	4	16			
?*Wiedelandia*	F	8	18			
Sapindaceae						
Xerospermum muricatum				nl,F	2	2
Sapotaceae						
Palaquium hispidum				mlp,F	3	3
Payena lucida				F	1	1
Sterculiaceae						
Sterculia parviflora				mlp	1	1
Stilaginaceae						
Antidesma coriacea	F,nl	2	17			
Strychnaceae						
* *Strychnos* sp.	F	1	1			
Theaceae						
Adinandra sp.	F,f,nl	2	3			
Gordonia concentricatrix				F?	1	1
Tiliaceae						
Grewia blattaefolia	nl	1	1			
Grewia laurifolia				F	2	2
Pentace triptera				f	1	1
Ulmaceae						
Celtis sp.				mlp	1	1
Gironniera subaqualis	nl	1	1			

Table 6.—Food plants and food items of (a) siamang and (b) dusky leaf-monkey.

	SIAMANG (observed for 1707 hours)			*DUSKY LEAF-MONKEY (observed for 356 hours)*		
Family and species	*Parts consumed*	*Number of trees*	*Number of visits*	*Parts consumed*	*Number of trees*	*Number of visits*
Urticaceae						
**Poikilospermum* sp.				mlp	1	1
Villebrunea sp.				nl,F	2	2
Verbenaceae						
Vitex trifoliata	nl	1	10			
Vitaceae						
* *Vitis* sp.				mlp,mlt	4	4
Xanthophyllaceae						
Xanthophyllum excelsum				F,f	3	3
Xanthophyllum scortechinii				mlt,F	2	3

* = liana

ml = mature leaf
mlp = mature leaf petiole
mlt = mature leaf tip
nl = new leaf
nlp = new leaf petiole
nlt = new leaf tip

F = fruit
f = flower
b = bud
i = insect

More species identified and leaf parts consumed recorded more precisely by S.H.C.

N = 139 spp.

No. of species eaten by both species = 22 (16%)
No. of species eaten by siamang only = 49 (35%)
No. of species eaten by dusky leaf-monkey only = 68 (49%)

Sources of scientific names: Willis (1973) and Corner (1952). Whitmore (1975) places some genera in different families:

Chrysobalanaceae	*Maranthes* and *Parinari* placed in Rosaceae
Ixonanthaceae	*Irvingia* placed in Simaroubaceae *Ixonanthes* placed in Linaceae
Leguminosae	*Microtropis* placed in Celastraceae
Potaliaceae	*Fagraea* placed in Loganiaceae
Stilaginaceae	*Antidesma* placed in Euphorbiaceae
Strychnaceae	*Strychnos* placed in Loganiaceae

longing to 19 of these families (70 percent of total families fed upon) made up 89 percent of all visits in which the tree or liana was identified to genus. Visits by dusky leaf-monkeys to 22 of these families (57 percent of total families) comprised 76 percent of all visits in which the food species was identified.[3,4]

One strategy for an herbivore faced with such a daunting array of food substances is to selectively consume the least toxic plant parts (Glander, 1978), which would most often be immature leaves (Freeland and Janzen, 1974; McKey, 1974). The feeding behavior of the siamang seems to conform to this strategy (Tables 1 and 6). Major food species such as *Sloetia elongata* (Moraceae), *Endospermum malaccense* (Euphorbiaceae) and *Ficus* spp. (Moraceae) were harvested for their leaves and fruit but not for

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[3] This analysis has been made in terms of families rather than individual species because, with some notable exceptions (e.g. Strychnaceae spp.) most species in the diets of these two primates have not been analyzed from a chemical standpoint. It would be desirable to know the average intra-familial variability in amount and type of secondary compounds, in preference to a general characterization such as "rich in secondary compounds". To our knowledge this information is not available.

[4] On a sample plot 20 meters by 200 meters in S.H.C.'s study area, all trees over 36 cm. girth breast height were measured and identified when possible. Of the 21 families listed above, 16 occurred in the sample plot and made up 64 percent of all families recorded there, and 78 percent of all identified individuals. Although more and larger sample plots are needed to obtain a fuller picture of species composition and representation in this forest (Wyatt-Smith, 1953), it would appear from this data that the occurrence of families rich in secondary compounds in the diet of the dusky leaf-monkey parallels the occurrence of these families in the forest as a whole.

mature leaves. Only the new leaves of *Alstonia* (toxic latex) were eaten and then only rarely. The fruits of *Strychnos* (Strychnaceae) were only sampled once. The greatest contribution of the family Moraceae to the siamang diet was in the form of new leaves and fruit (preferred food items on 80 percent of all visits to trees of this family).

Dusky leaf-monkeys exhibited a similar preference for new leaves when feeding on trees belonging to particularly virulent families. Of 8 visits to members of the family Apocyanaceae, new leaves were consumed 5 times, flowers twice, and fruit once (Table 6). On both occasions on which they fed on *Antiaris toxicaria* ("upas," the arrow poison tree, Moraceae), new leaves were the preferred food item. A similar pattern was shown for Euphorbiaceae (new leaves twice, fruit twice), Rubiaceae (new leaves and fruit), and Sapindaceae (new leaves and fruit). Only the new leaves of *Indorouchera griffithii* (Linaceae) were eaten. Fruit was fed on 3 times in members of the family Lauraceae, and new leaves once.

The selectivity with which dusky leaf-monkeys fed on mature leaves (Table 2) was especially in evidence when the food source belonged to a family rich in secondary compounds. For example, of 16 visits to trees of the family Anacardiaceae, 12 involved highly selective feeding in terms of the leaf part consumed (mature leaf tips 9 times, new leaf petioles twice, new leaf tips once). On the one occasion on which the monkeys fed on *Sterculia parviflora* (Sterculiaceae), mature leaf petioles were the food item. Selective leaf-eating was less evident for the Moraceae, and not evident for the Leguminoseae: both these families are characterized by lower levels of secondary compounds.

Although selective feeding has, of course, other advantages beyond avoidance of high concentrations of secondary compounds (e.g., high protein and water content and low cellulose content of new leaves, A. Hladik, 1978), it would appear that such avoidance is at least a strong possiblity in the case of both these primate species. The siamang avoids toxic compounds by eating primarily new leaves.

The dusky leaf-monkey is a selective feeder not only by choosing only or primarily new leaves from food sources rich in secondary compounds, but also by consuming certain leaf parts (petioles, leaf tips) more often than others (entire mature leaf blades). Presumably the symbiotic bacteria contained in the stomach and lower digestive tract of this semiruminant play a role not only in digesting foods with a high cellulose content, but also in the detoxification of plant secondary compounds (Freeland and Janzen, 1974).

Social organization

Siamang The typical siamang social group includes a mated pair with their immature offspring. The study group at Kuala Lompat (Figure 2) included an adult male, an adult female, a subadult male, a juvenile male, and a male infant. The ages of the Kuala Lompat adults were estimated to be at least 17 or 18 years in 1968. Once the pair-bond between a male and a female has been established, the relationship apparently endures for the lifetime of the partners. Infants up to the age of 10–14 months are dependent on the female for nourishment and transport. Older siamang infants, however, unlike those of the white-handed gibbon (Ellefson, 1974), are carried by the male throughout the day at the start of their second year. By their third year they only needed help over difficult crossings during daily travel and only returned to the female at night. The female was thus free of this responsibility for her previous offspring at least 1 year before her next infant was born, after a birth interval of 3 years.

Relations among the members of the group showed a high degree of cohesion; the young follow the female without straying far from the male (Chivers, 1974). Aggressive interactions were rare and were mostly confined to brief threats and chases directed by the adult male toward the subadult male. Positive interactions such as social grooming and play form the basis for strong affectional bonds between individual members of the group. Communication between individuals is rarely overt, consisting for the most part of visual monitoring of other animals and their activities (Chivers, 1976). Visual monitoring appears to be an adequate means of ensuring group cohesion and synchronization of individual activities. The monogamous type of social organization, typical of hylobatids, ensures that adults of a social group know each other well through their long association; this allows a high degree of predictability of another group member's actions, perhaps making more complex communication superfluous.

The maintenance of a monogamous social unit requires that young animals be separated from the group as they approach sexual and physical maturity. The early stages of this process occurred toward the end of the study when the adult male became increasingly more aggressive toward the subadult male, effectively preventing him from close spatial association with other members of the group. These aggressive interactions were most common when the siamang were all feeding within the same tree. The adult male's intolerance of the young male's proximity while feeding resulted in the subadult becoming increasingly peripheralized. At the end of the study

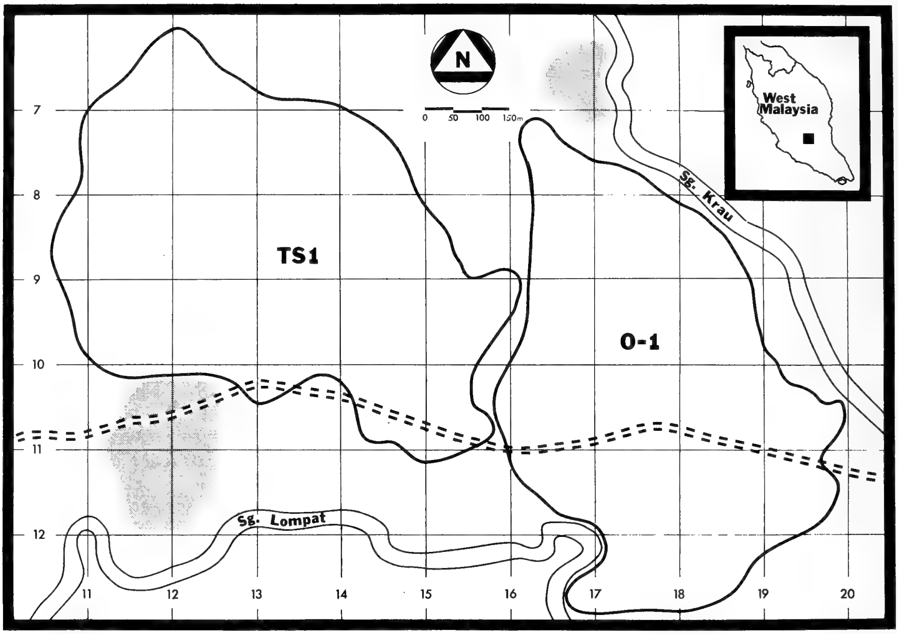

Figure 2. Location of main study groups of siamang (TS1) and dusky leaf-monkeys (0–1) at Kuala Lompat.

he lagged far behind the other siamang during their daily round of activities. Four months later he had left the group and established a territory adjacent to that of his natal group. He was joined by a young female and subsequently by a fully mature female siamang. When the latter animal became sexually receptive they mated and the subadult female left or was expelled from the group. By 1974 the group had disintegrated; this confirms the expectation that it is not a simple process to find a suitable partner for life. Further details of the formation of this group and a comparison of its ranging and other activities with those of the main siamang group may be found elsewhere (Aldrich-Blake and Chivers, 1973; Chivers et al., 1975).

Relations between siamang groups were characterized by mutual avoidance and, when encounters occurred, hostile interaction between the adult males. Spacing was maintained by the distinctive booming and barking calls given in concert by all members of the group except infants. Calling sessions occurred every 3 to 4 days on the average at Kuala Lompat but were more frequent in other study areas where the siamang population density was higher (Chivers, 1974). The siamang appears to differ from the white-handed gibbon, which shows a much higher level of intergroup confrontation and display on shared territorial boundaries (Ellefson, 1974).

Dusky leaf-monkey In contrast to the siamang, dusky leaf-monkey social groups are multimale and multifemale. With the exception of 1 small group of 5 animals, all groups whose composition was reasonably well known by S.H.C. contained more than 1 adult male. Solitary males were observed on 2 occasions: 1 in rubber plantation and secondary forest 2 miles outside the southeast boundary of the Reserve, and 1 within the core area of the main study group. In both cases the absence of conspecifics was confirmed by repeated searches of the surrounding forest. In the second case the male was a member of

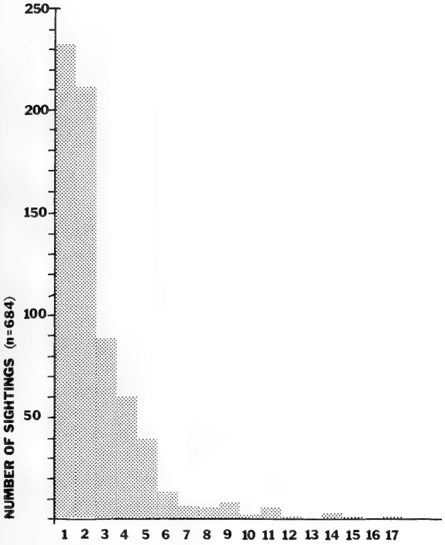

Figure 3. Frequencies of dusky leaf-monkey subgroups sizes.

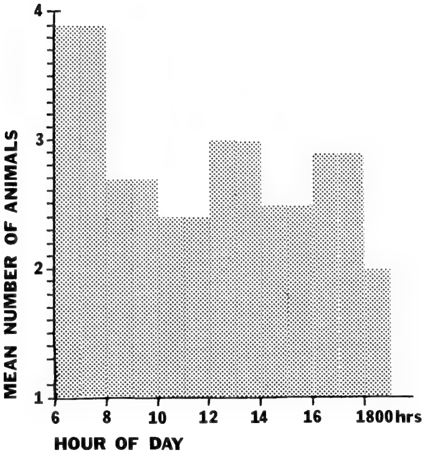

Figure 4. Diurnal variation in size of dusky leaf-monkey subgroups.

the main study group, which he rejoined within 1 day. The unequal sex ratio in groups of this species (1 adult male to 3-plus adult females) and the fact that no all-male groups were encountered, raise the question of the fate of the extra males. A combination of solitary males (probably more common than the present study would indicate) and greater vulnerability of males than females to predation would appear to be the most likely explanation for their low frequency in social groups.

Dusky leaf-monkey social organization shows loose overall group structure combined with small cohesive subgroups (Figure 3). A "subgroup" was defined as that portion of a group visible to the observer at one time, when no other conspecifics were known to be in the vicinity. Mean subgroup size for the main study group of 17 animals was 2.6. Temporal variation in subgroup size (Figure 4) shows larger groupings occurring mainly early in the day.[5] Typically the monkeys traveled in relatively large groups in early morning, and fed in smaller groups during midmorning and midafternoon. The transition from a large group to small feeding and resting subgroups was gradual. No special signals or events were seen to precede group fission; the animals simply drifted away from each other. When subgroups rejoined, the meetings were frequently marked by the exchange of greetings in the form of embraces followed by grooming.

This pattern of daily group fission and fusion requires that different subgroups have some means of locating each other and joining again. Surprisingly, dusky leaf-monkeys do not use contact vocalizations, in sharp contrast to the more vocal banded leaf-monkeys and long-tailed macaques. The means of regaining contact seems to be partially visual and partially through shared knowledge of traditional daily routes and arboreal pathways. While traveling and feeding mainly in the upper levels of the forest in large emergent trees, dusky leaf-monkeys had a relatively unimpeded line of sight. There were occasions when 2 subgroups which had previously been separated by as much as 500 meters rejoined each other. They may have used the ability of members of a subgroup to predict the movements of other group members. Group members used the same pathways, often the identical branches, at the end of the study as they did at the beginning. The small size of the group territory (Figure 2) and the conservative nature of ranging patterns and territory use would make such predictions possible.

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[5] Discrepancies between mean subgroup sizes for the hours of dawn and dusk are explained by the fact that this species was often active until nightfall. Presumably subgroups coalesced when they were no longer visible to an observer on the forest floor.

A typical subgroup consisted of 1 to 2 adult females and their immature offspring. The basis for associations between adult females was possibly genealogical, although long-term observation is needed to demonstrate the truth of this hypothesis. Young dusky leaf-monkeys appear to have a very long period of association with and dependence on the mother. Juveniles joined together in play groups but typically rested in close contact with an adult female and were frequently carried over difficult passages during travel. On one occasion an adult female attempted to carry a subadult female fully two-thirds of her own body size.

Interactions between adult females and immature animals were characterized by a high degree of body contact typified by embraces and huddling (Rosenblum et al., 1964). Maternal behavior in this species included behavior patterns analagous to "aunting" (Rowell, 1972). It consisted of an adult female (not necessarily the same female from one day to the next) attending to and physically following the movements of a playing group of juveniles while other adults in the vicinity rested or fed. With external disturbance, juveniles clustered tightly around the adult female, rather than seeking their own mothers. Such an arrangement frees the other adults in the group while ensuring a measure of protection for immature animals.

The role of the adult male in dusky leaf-monkey society is less central to the daily life of the group. Although he may lead travel on occasion, he does not do so on a regular basis. In 2 kinds of situations adult males came into prominence. On 2 occasions when a potential predator, either a big cat or a python, was in the vicinity of the group other members of the group hid in heavy cover while 1 male mobbed the predator, uttering continuous alarm calls. The same distinctive call, a two- or three-phase honk that gives this species its local name of "chengkong," was voiced in a second kind of situation: (a) when the group was on the edge of its territory, abutting on the territory of an adjacent group or sometimes on unoccupied forest, or (b) when 2 groups met. Calling in the first case was spontaneous, elicited by no apparent stimulus other than the group's general location. Its effect was sometimes to bring the other animals closely around the calling male, but at other times they appeared to ignore him entirely.

Intergroup encounters were rare during this study (1 observation) but previously D.J.C. observed 2 chases as a new group of 5 animals tried to establish its territory between a group of 12 and a group of 15-plus, and MacKinnon and MacKinnon (1973) have reported "fierce clashes including fighting and calling." A possible means of intergroup spacing are the honk vocalizations occasionally heard in the early morning hours (Figure 5). They occur too infrequently, however, to constitute the sole means of intergroup avoidance.

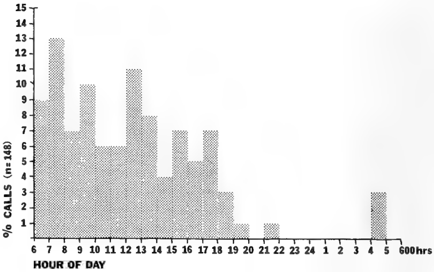

Figure 5. Diurnal variation in calling by dusky leaf-monkeys.

Ecological aspects of social organization

Despite their apparent dissimilarity in social structure, siamang and dusky leaf-monkeys forage in similarly sized groups. The adaptiveness of particular social organizations relative to species ecology has been explored by a number of investigators (Klein, 1972; Kummer, 1971; MacKinnon, personal communication; Orians, 1961; Smith, 1968). For the nonhuman primates these hypotheses have generally been phrased in terms of arboreal frugivores (Klein, 1972; MacKinnon, 1971) or terrestrial omnivores (DeVore and Hall, 1965; Kummer, 1971), while tropical arboreal folivores have received little attention (but see C. M. Hladik, 1978). The question arises whether small foraging groups can be considered adaptive for primate arboreal folivores.

As far as is known all the members of the family Hylobatidae possess the same type of social organization, the monogamous family unit. This appears to be a phylogenetic trait (Kummer, 1971) of the hylobatids, and is perhaps associated with an ancient and distinctive adaptive complex (Ellefson, 1974). The social organization of dusky leaf-monkeys at Kuala Lompat, however, differs considerably from that of its 2 congeneric species in peninsular Malaysia, the silver leaf-monkey (*P. cristata*) and the banded leaf-monkey, which do not form subgroups (Bernstein, 1968; Fleagle, personal communication; Curtin, 1977).

There is a growing body of evidence suggesting that, despite their apparent abundance, food sources for arboreal tropical mammals may instead be limited (Ellefson, 1967; Janzen, 1978; McKey, 1978; Glander, 1978), especially when there is a high density of closely related primate species (Chivers, 1973; 1974). The pattern of wide dispersion between individuals of one plant species, the variability of leaf-flushing cycles, and the prevalence of plant secondary compounds all contribute to the contraction of available food sources for arboreal tropical mammals.

It is suggested that the small foraging subgroups of dusky leaf-monkeys may be adaptive for feeding on a limited and dispersed food supply. Edible new and mature leaves are both likely to be dispersed but in different ways. Widely dispersed individuals of deciduous tree species may flush synchronously (*Koompassia, Parkia, Intsia, Dillenia*) or asynchronously (*Sindora*, many *Ficus* spp.). Other species may renew their leaves gradually (e.g., *Pentaspadon*). Mature leaves appear widespread and abundant in tropical forest but edible mature leaves may not be. The leaf-monkey pattern of selective feeding on mature leaves suggests that the food value and/or palatability of different leaf parts varies. The small amounts of food taken (petioles, leaf tips) and the necessity for frequent position shifts while feeding, reduce the number of animals that can feed in one tree at one time. The age of the mature leaf in tree species that renew their leaves gradually is an additional consideration. All these factors contribute to a reduction in the available supply of new and mature leaves, and may act together to favor small feeding groups in this species.

Relations between species

POPULATION SIZE AND DISTRIBUTION The 2 study areas cover an area of 140 hectares between the Krau and Lompat rivers. Between 1969 and 1971 inclusive they contained 2 groups of siamang, 1 group of white-handed gibbons (with 2 others adjacent to the north and west) and at least 1 solitary animal in the east, 5 groups of dusky and 7 groups of banded leaf-monkeys, and 2 groups of long-tailed macaques near the rivers. A small group of pig-tailed macaques occasionally visited the area; their core area seemed to be in the higher land to the west.

Determination of the size and composition of each primate group within the 140-hectare study area, and knowledge of the home range size of each, permits calculations of biomass (Table 7). In 1970–1971 there were about 10 kg of primate per hectare; more than half of this total for 5 species was accounted for by the 2 species of leaf-monkey. In terms of home range, and therefore of habitat utilization, the biomass of primates per unit area was somewhat higher (0.18 cf. 0.48 kg/ha for siamang; 4.81 cf. 2.93 kg/ha for dusky-leaf-monkeys).

With white-handed gibbons being half the size of siamang, and living in territories twice the size, the biomass of the smaller hylobatid is one-quarter that of siamang, at least with regard to home range. Similarly, although there is close similarity in body size and biomass within the home ranges of the 2 leaf-monkey species, the calculations show that banded leaf-monkeys are more numerous in, and more widely distributed through the study area (Table 7).

These 2 measures of biomass confirm other data that suggest that activity of primate social groups is not only localized within the home range, but also within the habitat, and that the degree of localization of activity within the habitat varies markedly between species in ways that correspond to differences in feeding and ranging strategies. Data collected by MacKinnon (personal communication) in 1973 by different techniques provided similar results (Table 7).

INTERSPECIFIC ENCOUNTERS The ranges of conspecific groups at Kuala Lompat usually did not overlap extensively, separation being maintained by hostile encounters at territorial boundaries (the white-handed gibbon and, to a lesser extent, the siamang), calling (both hylobatids, the banded leaf-monkey, and, to a lesser extent, the dusky leaf-monkey), mutual avoidance (the long-tailed macaque) or a combination of these factors. Groups of different species, however, occupied partially or wholly coincident ranges. Typically they appeared to ignore each other's presence, the main exception being the 2 hylobatids.

Interspecific encounters may be classified into 4 main types: (1) groups were in visual and auditory contact on adjacent arboreal pathways, separated by 30–100 meters; (2) groups traveled along the same pathway, one behind the other; (3) one group was stationary, either feeding or inactive, while another moved through the same tree(s); and (4) both groups were stationary within the same tree(s), either feeding or inactive. Overt interactions almost never occurred in encounters of the first 2 types and were comparatively rare in the last 2. Aggressive interactions occurred mainly when groups of different species were feeding in the same tree. If white-handed gibbons were feeding in a fruiting *Ficus* when the siamang arrived, they would be chased out; similarly, they were driven out if they tried to enter while the siamang were feeding there. Presumably, the large body size of the siamang (twice that of the white-handed gibbon) plays a crucial role in the maintenance of interspecific dominance.

Siamang were much more tolerant, however, of

Table 7.—Population structure and biomass of the primates at Kuala Lompat (1969–1971).

										Biomas (kg/ha)		
		Group size									*Kg/ha*	
Species	*Group*	*M*	*F*	*SA*	*J*	*I*	*Total*	*Home range (ha)*	*Ad/imm*	*Total wt. (kg)*	*Home range*	*Total area (140 ha)*
Hylobates lar	G2	1	1	1	1	1	5	60	5.2/2.5	20.6	0.34	
	G2A		1				1			5.2		
							6	60		25.8		0.18
H. syndactylus	S1	1	1	1	1	1	5	35	11.5/5.0	44.5	1.27	
	S1A	1	1				2	21		23.0	1.09	
							7	56		67.5		0.48
Presbytis obscura	D1	1	4	2	2	3	12	10	7.2/3.6	68.4	6.84	
	D2	1	6	4	3	4	18	12		104.4	8.70	
	D3A	1	2		1	1	5	5		28.8	5.80	
	D3/03	3	6	2	3	5	19	25		108.0	4.32	
	0-1	2	7	2	4	2	17	33		100.8	3.05	
							71	85		410.4		2.93
P. melalophos	B1	10	ad,	5 imm.			15	13	6.8/3.4	85.0	6.53	
	B2	10	ad,	5 imm.			15	17		85.0	5.00	
	M-1	1	5	1	3	1	11	9		61.2	6.80	
	M-2	2	8	2	4	2	18	21		102.0	4.86	
	B3/M4	4	6	2	4	3	19	20		105.4	5.27	
	M-5	2	4	2	3	1	12	19		68.0	3.58	
	RH-m	3		1			4	12		27.2	2.27	
							94	111		533.8		4.81
Macaca fascicularis		3	7	5	5	4	24		4.8/3.2			

*Species**	*Number of groups**	*Number of primates**	*Total wt. (kg.)**	*Kg/ha total area**
H. lar	2	7	29	0.21
H. syndactylus	2	5	45	0.32
P. obscura	4	56	324	2.31
P. melalophos	8	67	381	2.72
M. fascicularis	4	49	—	—

* Mackinnon and Mackinnon (1973).

other species (Table 8). Siamang and dusky leaf-monkeys were frequently observed traveling together over the same pathways, and sometimes feeding in the same or adjacent trees. Relations were peaceful with little observable interaction. Associations between siamang and dusky leaf-monkeys (observed within the same or adjacent trees) were most frequent at dawn and dusk when the latter were most active (Figure 6). Discrepancies between association scores for the last and first hours of the day are explained by the siamang settling in their night positions 1 to 2 hours before dusk, and the leaf-monkeys foraging away from them before returning to sleep nearby as night came. The time of greatest association was at night.

ECOLOGICAL SEPARATION Both hylobatid species spend the major part of the day in the middle levels of the forest: about two-thirds of the total time for

Table 8.—Interspecific association at Kuala Lompat.

Species pair	*n*	%
Dusky leaf-monkey/ Banded leaf-monkey	53	26
Banded leaf-monkey/ Long-tailed macaque	51	25
Siamang/Banded leaf-monkey	29	14
Siamang/Dusky leaf-monkey	28	14
Dusky leaf-monkey/ Long-tailed macaque	18	9
Other associations	24	12
Total	203	100

siamang and three-quarters for the gibbon (Chivers, 1973). The 2 leaf-monkey species were found at all levels of the forest. Dusky leaf-monkeys, however, were found more frequently in the upper and middle canopy, and banded leaf-monkeys in the middle and lower levels, among the saplings (1-6 meters) or on the ground. The long-tailed macaque was most frequently encountered along the margins of streams and rivers; within the forest proper they mainly inhabited the middle and lower levels. The pig-tailed macaque was usually encountered on the ground or in the sapling level; they are the only species to run away from the observer on the ground rather than in the trees.

This general picture of vertical stratification reveals substantial overlap between species. If feeding activity is examined, however, rather than the mere presence or absence of animals at different levels, some distinctions emerge (Figure 7). Eighty-four percent of dusky leaf-monkey food trees were between 25 and 50 meters, and none was less than 9 meters in height. The food trees of banded leaf-monkeys, in contrast, were more variable in height, ranging from emergents down to the ground with the emphasis on the lower levels. Nevertheless, the most favored trees were approximately evenly divided between the emergent and middle levels (Table 9). In contrast, 96 percent of the food trees used 3 times or more by dusky leaf-monkeys were emergents (Table 5).

Similarly, whereas the siamang spent 25 percent of the day in the emergents, 61 percent in the middle level and 14 percent in the understory, never going

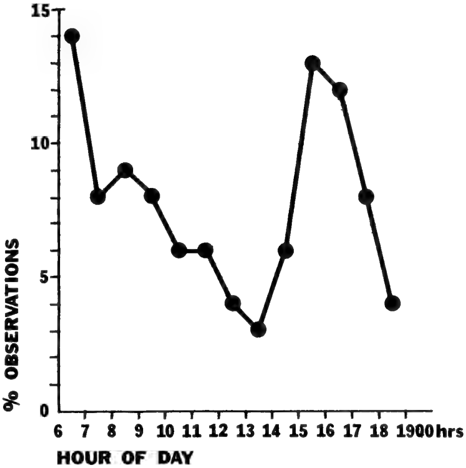

Figure 6. Daily pattern of association of dusky leaf-monkeys and siamang.

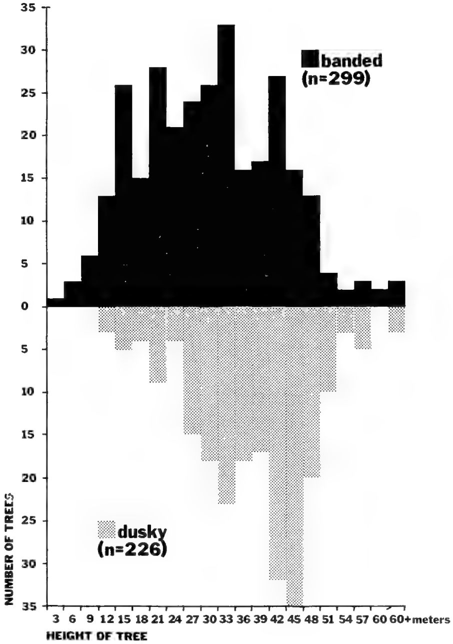

Figure 7. Heights of dusky and banded leaf-monkey food trees.

Table 9.—Important food species of banded leaf-monkey.

Species	*Number of visits*	*Number of trees*	*Height class*
Intsia palembanica	18	14	E
Parkia javanica	10	3	E
Pentaspadon velutinum	10	10	E
Xanthophyllum excelsum	9	8	M
Paropsia veraciformis	8	5	M
Xanthophyllum scortechinii	7	1	E
Derris sp. (1)	7	7	E
Payena lucida	6	5	U
Elateriospermum tapos	5	4	M
Ficus spp.	5	4	E
Nephelium eriopetalum	5	2	M
Combretum sp. (1)	5	5	E
Beilschmiedia sp.	4	2	M
Cynometra inaequifolia	4	3	E
Eugenia sp.	4	4	M
Gnetum sp. (1)	4	4	M
Strychnos sp. (1)	4	4	M
Ventilago sp. (1)	4	4	M
Acacia pennata (1)	3	3	M
Aquilaria malaccensis	3	3	M
Dialium platysepalum	3	2	E
Dysoxylon costulatum	3	3	M
Entada scandens (1)	3	3	M
Gnetum globosum (1)	3	2	E
Hibiscus floccosus	3	3	M
Maranthes corymbosa	3	3	M
Millettia atropurpurea	3	3	M
Pimeleodendron griffithanum	3	3	M
Poikilospermum sp. (1)	3	2	E
Polyalthia sp.	3	3	U
Strombosia javanica	3	3	E
Xerospermum muricatum	3	2	M
Total 33 species	164	130	
Other identified trees	129	126	
Unidentified trees	5	5	

l = Liana. E = Emergent (30 + m). M = Middle (15–30 m).
U = Understory (<15 m.)

below 10 meters in height, they fed for one-quarter of the time that they were in the emergents, for more than half the time they were in the middle level, and for three-quarters of the time that they were in the understory. This confirms that they spend most of their feeding time in the main level (67 percent) and that they go into the understory mostly to feed (21 percent). The emergents mainly provide resting places, during day and night. Although the 2 studies were conducted at different times in different parts of the forest, the finding that only 16 percent of the 139 tree species are common to the diets of siamang and dusky-leaf monkey (Table 6) indicates the degree of their dietary separation.

In addition to preferences for diet and forest level, rates of movement is a third factor contributing to niche differentiation between these closely related species. Some species are more sedentary, e.g., siamang and dusky leaf-monkeys, while others are more mobile, e.g., white-handed gibbons and banded leaf-monkeys. Rates of movement (the relationship between day range length and time spent traveling or feeding) is reflected in feeding situations with the sedentary type typically feeding while stationary (or almost so), and the mobile type feeding and traveling simultaneously (equivalent to the foraging of Ellefson, 1974).

The siamang and dusky leaf-monkey, both sedentary folivores (the former a behavioral folivore, the latter an anatomical folivore, Milton, 1978) are separated both by preferences in forest level and diet. The banded leaf-monkey is a mobile frugivore (Curtin, 1976, 1977). The 2 hylobatids appear to be separated mainly by this rate of movement factor rather than by differences in forest level or dietary preferences. The more mobile white-handed gibbon can still be labeled a frugivore, even though the difference in proportions of feeding time for fruit and leaves is not so different from the more sedentary and folivorous siamang as thought previously (Raemaekers, personal communication). These are fairly crude measures of dietary preferences, however, and MacKinnon (personal communication) suggests that analysis food item by food item and tree species by tree species will show much greater differences, corresponding with the differences in size and mobility.

For tropical arboreal frugivores high mobility confers the advantage of greater territorial coverage. Many tree species like *Ficus* spp. fruit at unpredictable intervals and in many others fruiting is not synchronized among individuals of each species. Given the added consideration that in equatorial rain forests trees of the same species are more commonly dispersed than clumped in distribution, there is an obvious premium for the frugivore on frequent, broad sampling of the vegetation. The lower activity rates of the siamang and dusky leaf-monkey may reflect: (1) the poorer nutritional quality of leaves compared to other types of food, and/or (2) the energetic costs of detoxifying foods rich in secondary compounds (McNab, 1978). Differences in activity rates of sympatric species, probably linked to dietary differences, will produce different patterns of habitat utilization and, thus, of ecological separation.

Summary

Data are presented on the feeding behavior and social organization of the siamang (*Hylobates syndactylus*) and dusky leaf-monkey (*Presbytis obscura*), with discussion of the relations between them and with other species of diurnal arboreal primates in the Krau Game Reserve, Peninsular Malaysia.

Both species have almost identical diets in terms of the frequency of visits to trees of each dietic category (three-fifths leaves, one-third fruit, and less than one-tenth flowers). Only the siamang obviously consume insects, however, and while their diet contains only traces of mature leaves, more than one-third of the dusky leaf-monkey's leaf intake involves parts of mature leaves.

The contrasts between their respective diets are even more marked in terms of the tree species concerned; only 16 percent of the 139 species so far identified are common to the diets of both primates. The dusky leaf-monkey showed more fluctuations in the intake of each dietic category with seasonal variations in food, whereas the siamang seemed to be trying to stabilize its intake of fruit and leaves, in particular, over time.

A majority of feeding visits by both primates were to trees belonging to families known to be rich in secondary compounds, but both appeared to consume selectively the least toxic parts of the trees.

Although the siamang is organized socially into very cohesive monogamous family groups and the dusky leaf-monkey into larger loosely organized multi-male groups, the tendency of the latter to break down into subgroups during feeding results in foraging units of similar size for both species.

Comparison of these relatively sedentary folivores with other species suggests, in both cases, that their congeners are more mobile and more frugivorous. Where species have similar diets, they differ in their preferences of forest level and/or in their rates of movement about the forest.

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Diets, Densities, and Distributions of Bornean Primates

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Introduction

From May 1, 1970, to July 31, 1971, and from July 1 to August 24, 1975, I collected observations of several primate species in a 3 km^2 area of forest in East Kalimantan, Indonesia. The object of this research was description of niches of primate species sympatric with orang utans, and the work was supported as part of a study of the behavior and ecology of orang utans (Rodman, 1973a, and 1978; Horr, 1972). While analyzing patterns of distribution of the primate species, I have been intrigued by the following hypothesis proposed by MacArthur and Levins (1964): " . . . species which specialize on a particular *proportion* of mixture of two or more particular resources will be found only where their favored proportion is found, and will be replaced by other species in other habitats where the proportion of the mixture changes to one on which the new species are more effective (p. 1207)" It has been found in this study and in studies by the Hladiks (Hladik and Hladik, 1969, 1972; see also Chivers, 1973, and various papers in Montgomery, editor, 1978), that sympatric, forest-dwelling primate species differ in their dietary proportions of food types (e.g., fruit, leaves, buds, insects, etc.). The diets of species with larger body size are composed primarily of plant foods, and each species is characterized by a proportion of mixture of various plant parts.

In this paper I will examine the extent to which the spatial distributions of several sympatric primate taxa are related to the distribution of their dietary proportions in the same area. The components of the diet to be considered are leaves and fruit in a first attempt to perceive and explain some order in the patterns of distribution.

Background

Location and characteristics of the study area

The study area lies in what was then the northeast corner of the Kutai Nature Reserve on the south bank of the Sengata River (Figure 1); the eastern boundary of the reserve has since been moved to the sea. The study area consists of approximately 3 km² of forest bounded in the north by the Sengata River and on other sides by arbitrary boundaries (Figure 2). Its irregular shape results from an attempt to equalize riverine area and "deep forest."

PHYSICAL CHARACTERISTICS. As shown by the topographic map (Figure 2), the highest point in the study area is slightly more than 300 m above the base camp, located near the southern boundary on one of two major ridges running from northeast to southwest through the study area. The major ridge along the eastern boundary has a very steep western face dropping to a small river (Mentoko) that runs parallel to the ridges through the study area. The bed of the small river and parts of the steep face of the eastern ridge are often rocky and inhospitable to forest. Other parts of the study area are covered by a thin layer of soil that ranges from clay to light sand and that supports forest vegetation of variable structure and com-

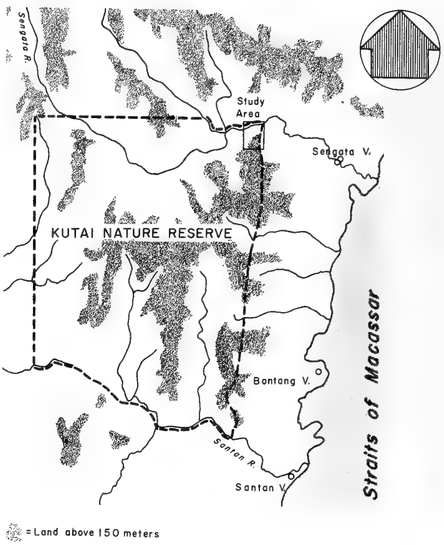


Figure 1. The Kutai Nature Reserve. The area within the boundaries is approximately 200 km². Boundaries are shown as they were in 1970. Since then the eastern boundary has been moved to the sea, and the southern boundary has been moved approximately 15 km north.

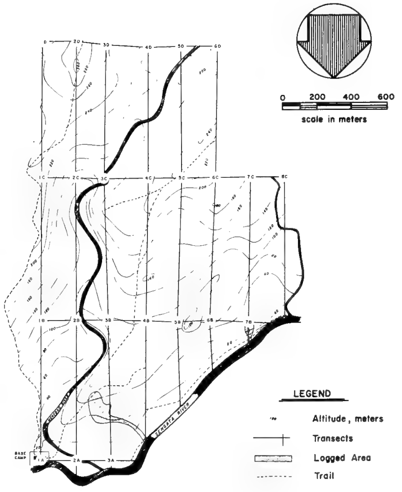


Figure 2. The study area. Transects are numbered 1 to 8 from East to West and A to D from North to South. The area within the boundaries is 2.74 km².

position. It is significant to the later discussion that there are major rapids on the Sengata River adjacent to points 6B and 7B on the map (Figure 2) because the transition from river edge to forest is quite abrupt here compared with the transition in the broader, flatter region adjacent to points 2A and 3A. In the latter area, flooding occurs periodically, while in the former area—and in the rest of the study area—the forest floor is not flooded. In the ensuing discussion, flooding will be presumed to have a major effect on predominant reproductive strategies of trees, and, therefore, on the mix of fruit and leaves.

GENERAL VEGETATION. The forest of the study area may be called "mixed rain forest" and more specifically "lowland dipterocarp forest" after Richards (1952). Stands of true mixed dipterocarp forest occur on the gentler slopes, interspersed with occasional clumps of single species. The most conspicuous clumps from my point of view are those of species fed upon by orang utans and other primates (e.g., *Dillenia borneensis, Dracontomelum mangiferum,* and *Koordersiodendron pinnatum*). The Sengata River is bordered by a band of vegetation disturbed by variations in river level, and the rate of transition from this naturally disturbed region to deep forest vegetation depends upon the immediate topography. Thus the slope to the river along transect 2 (Figure 2) is very gradual and there is a broad zone of transition to deep forest. The slope to the river at transects 5, 6, and 7 is steep, and the riverine band is narrow with an abrupt transition to forest as described above.

GENERAL FAUNA. Giant squirrels (*Ratufa affinis*) are the most obvious arboreal mammals in the study area aside from the various primates, although there are occasional flying squirrels (*Petaurista petaurista*) and many species of bats. Wild pigs (*Sus barbatus*) are the most commonly encountered terrestrial mammals, followed by mouse deer (*Tragulus kanchil*) and barking deer (*Muntiacus muntjak*). Several species of viverrids are probably common (e.g., *Viverra tangalunga*), but they are rarely encountered during the day. Clouded leopards (*Felis nebulosa*) are present, but rare, as are several smaller carnivores. Among the reptiles the monitor lizard (*Varanus salvator*) is interesting because, given its large size (up to 2 meters, nose to tail) and occasional arboreal habits, it is certainly a potential predator of primates. The python (*Python reticulatus*), a second potential reptilian predator of primates, is seldom seen in the study area, probably because the study area lacks swamps. There is a diverse avian fauna, and Pearson (1975) has identified 142 species of birds in 38 families in a study area several kilometers down river from this one. Of these, only the eagles (*Spizeatus* sp.; *Ictinaetus malayensis*) are possible predators of primates, but their prey are smaller rodents, birds, and reptiles (Smythies, 1968). The insect fauna has yet to be described in this region of Kalimantan.

Table 1.—Primate Species Sighted

Prosimii	
Tarsiidae	*Tarsius bancanus*
Anthropoidea	
Cercopithecidae	
Cercopithecinae	*Macaca nemestrina*
	M. fascicularis
Colobinae	*Presbytis aygula*
	P. frontata
	P. rubicunda
	Nasalis larvatus
Hylobatidae	*Hylobates muelleri*
Pongidae	*Pongo pygmaeus*

Primate species present in the study area.

Primate species sighted at least once in the study area are listed in Table 1. This study was limited to the Anthropoidea, who are all diurnal, and of these only the 5 species described below were sighted consistently within the study area:

Macaca fascicularis, the crab-eating macaque, or "kra": These animals are small and gracile compared with other species of the genus. The species inhabits forests from southern Thailand, Burma, and Cochin China south through the Malay Peninsula to Java, Sumatra, and Borneo, and populations occur outside Wallace's Line on Timor and the Philippine Islands. Fittinghoff (1975) and Kurland (1973) have each completed studies of *M. fascicularis* on the Sengata River.

Macaca nemestrina, the pig-tailed macaque, or "brok": Pig-tailed macaques are heavy, robust macaques who inhabit forests of Thailand, Malaya, Sumatra, Java, and Borneo. They are, thus, frequently sympatric with *M. fascicularis.* In the forest it is easy to distinguish *nemestrina* from *fascicularis* by body shape and by tail length; tails of *nemestrina* are one-third to one-half the body length, and tails of *fascicularis* are as long as the body or longer.

Presbytis aygula, the Sunda Island leaf-monkey, or "berangat": The common leaf-monkey of the study area is medium grey on the back with a white ventral surface extending to the chin and inside the arms and legs. The hands, feet, and upper face are black, and the tail is darker grey than the back. This description fits that of *P. hosei* given by Pocock (1935), but the true status of the taxon *hosei* with respect to the *aygula-melalophus* group of leaf-monkeys is unclear (Medway, 1970). I have chosen the conservative classification given by Napier and Napier (1967). In the forest these leaf-monkeys are easily distinguished from other leaf-monkeys by their distinctive markings, and from macaques by their long, heavy tails and their "triangular" heads.

Hylobates muelleri, the Bornean gibbon, or "kaliawat": Bornean gibbons are closely allied to the "*lar*" group of species of Southeast Asia (Groves, 1968). They are grey animals with dark faces. Although they are similar in size and coloration to the monkeys described above, they are easily recognized in the forest by the lack of a tail and by their characteristic brachiating mode of locomotion.

Pongo pygameus, the orang utan: These large, red apes are the easiest of all the primate species to identify and to follow in the forest because their size and coloration make them quite conspicuous while moving. Orang utans are limited in distribution to northern Sumatra and Kalimantan (including Sarawak and Sabah).

The 3 additional anthropoid species sighted in the study area were *Nasalis larvatus, Presbytis rubicunda,* and *P. frontata;* all are leaf-eating species and are of great interest to this conference. Unfortunately, my observations of these species were rare and not amenable to the analysis presented here.

Methods

Data presented here were gathered according to two procedures: (1) a repeated systematic census of the study area; and (2) tracking of individuals or groups of individuals of a "target" species. During a census, 4 or more observers walked predetermined itineraries along the transects, each observer following a different route. Four observers could cover all transects in approximately 6 hours, and by varying the itineraries and the starting times, it was possible to equalize coverage of the different sections of the transects during different quarters of the day. While walking, each observer recorded the following data at each contact with a primate: time; species; location (in coordinates); height in the canopy (estimated in meters); activity of the first animal sighted when first sighted; food type if feeding; direction of travel or escape; and number of animals sighted. In the tracking mode, observers searched some section of the transects for an assigned target species and followed that species for as long as possible if contact was made. This type of observation yielded identical data to that of the census for contacts with other species prior to contact with the target species and for the initial contact with the target species. Subsequent to contact with the target species observers recorded the same data if other primates were contacted while tracking the target animals.

Thus, there are 3 comparable sets of data on "first contacts": contacts with species during the census; initial contacts with target species; and contacts made with other primates while tracking a target species. Since the data recorded are observations of the states of the animals at first contact, the 3 kinds of data comprise a sample of instantaneous observations of the states. Such a sample should give an unbiased estimate of the proportion of time spent by species in various states as long as contacts with animals who were clearly reacting to the observer are excluded. It may be necessary to exclude the data gathered while tracking from some analyses since such data are biased toward observation of traveling animals, but for the present analysis of diets and distributions, all 3 sets of data are included. Each initial contact provides an unbiased observation of the location of individuals of a species, and since there is no apparent reason to exclude an observation of food-type under any circumstances, it seems reasonable to me to combine all 3 sorts of data.

During the summer of 1975, methods were modified because I worked with only one assistant and covered only two-thirds of the study area (Sengata River south to Transect C). Consequently, data on distribution of the animals are not strictly comparable, although there were no striking differences in the pattern. But feeding observations made in 1975 are comparable, and they are included in this analysis.

Results

Diets of the 5 species

As stated above, at each contact with a feeding primate the observer attempted to record the type of food eaten. The food-types observed were primarily leaves and leaf shoots, fruit, bark, flowers, buds, and insects; for this analysis I have combined the latter 4 types of food into a single class. These observations were tabulated by species to give estimates of the dietary composition of each species (Figure 3). Given the nature of the data, it is clear that the results are estimates of the time spent feeding on the 3 classes of food. Whether these proportions accurately reflect the dietary composition is open to question, and detailed study of each species might reveal slightly different proportions of food-types by weight or by

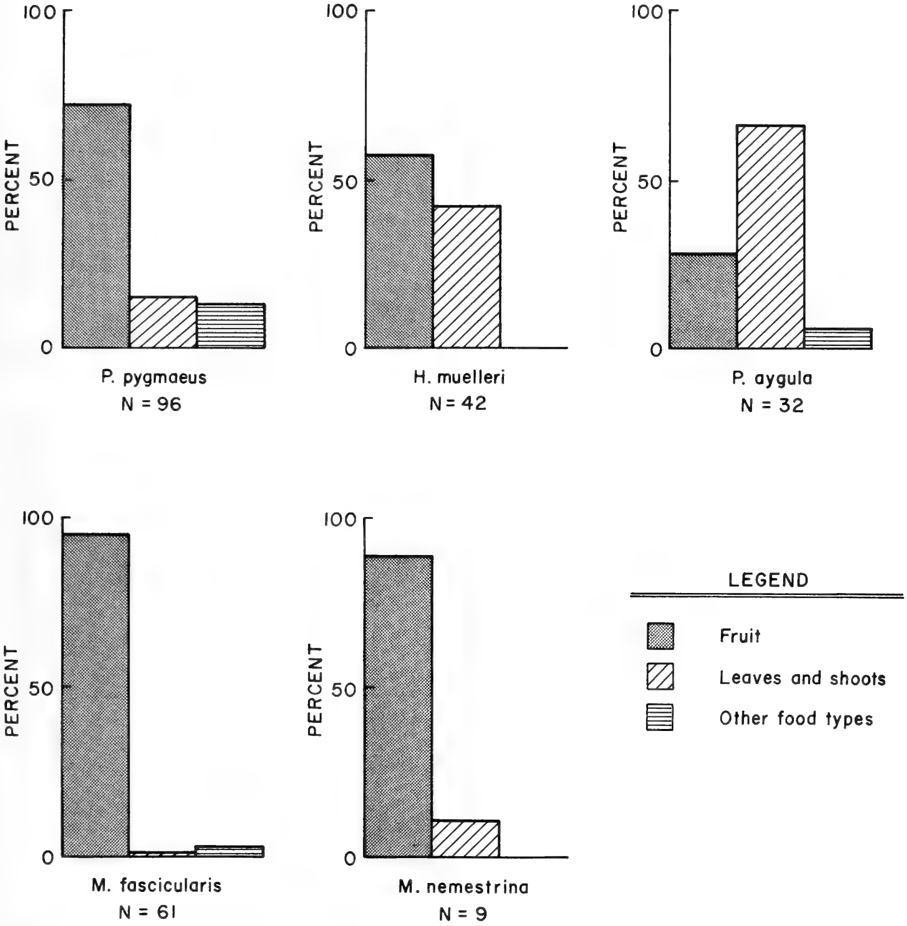


Figure 3. Proportions of food types of 5 species. These are proportions of plant parts fed upon in first contacts with feeding primates when food type was ascertained. The proportions estimate time spent feeding on each food type.

volume. But if we assume approximately equal rates of procurement, the relative time spent feeding on various foods should reflect approximately the relative amounts of those food types actually ingested.

The sample sizes presented here are small, and it may be asked whether these samples are sufficient to represent the diets of the animals accurately. Fortunately, my assistants and I collected more than 350 hours of observation of feeding by habituated orang utans (Rodman, 1978), and in these observations we recorded the numbers of minutes spent feeding on each food-type. Comparison of the 2 estimates of dietary composition of orang utans shows that the results are nearly the same for data on first contacts and for continuous observations. Observations of food-types of the other 4 species were gathered in a manner identical to those of orang utans (observed food at first contact), and this comparison of 2 calculations of dietary composition of orang utans, therefore, lends some confidence to the results for the other species.

The dietary composition of *M. nemestrina* is not demonstrated by 8 observations; the data cannot show conclusively that the diet differs from a one-to-one ratio of fruit-to-leaves ($\chi^2 = 3.13$ with 1 d.f.; $p > .05$). Several lines of evidence support the assumption that *M. nemestrina* of this study area are truly frugivorous, however. First, Fooden (1971, Table 3) reports that in 7 specimens of *nemestrina* collected in Thailand, fruit and seeds were the major component of stomach and food-pouch contents; and Davis (1962, p. 68) recorded that a specimen collected in Sabah (North Borneo) carried fruits of a palm in its cheek pouches. Second, although diets of congeners are usually reported as eclectic, most reports confirm or at least suggest that macaques are technically frugivores: *M. fascicularis* of this area are clearly frugivorous (Figure 3; also Wheatley, 1976); *M. mulatta* of the Siwaliks in India are "... on the order of 65 to 70 percent frugivorous." (Lindburg, 1977); toque macaques (*M. sinica*) of Ceylon feed on 77 percent fruit by weight (Hladik and Hladik, 1972); and Simonds (1965) reports subjectively that a large part of the diet of the bonnet macaque (*M. radiata*) of southern India consists of the fruit of banyan trees. It seems reasonable to assume that further observation of *M. nemestrina* will confirm their frugivorous diet.

In summary, among the 5 species there is 1 species, *P. aygula*, with a predominantly folivorous diet; 1 species, *H. muelleri*, with approximately equal proportions of fruit and leaves in the diet; 1 species, *P. pygameus*, that feeds on more fruit than leaves; 1 species, *M. fascicularis*, that feeds almost entirely on fruit; and 1 species, *M. nemestrina*, whose dietary composition is not established definitely, but that probably feeds predominantly on fruit. For the purpose of testing the hypothesis that species are distributed among habitats according to their mixtures of proportions of foods and the proportions of foods available in the habitats, I have calculated the ratio of leaves to fruit in the diets of each species with the following results (as percentages):

M. fascicularis	2
(*M. nemestrina*)	14
P. pygmaeus	20
H. moloch	75
P. aygula	233

If the hypothesis given by MacArthur and Levins (1964) holds, the distribution of these species in habitats that differ in proportions of fruit and leaves available as food should be directly related to the ratio of fruit to leaves in the diets.

Densities of the 5 species

Observers in this study did not identify individuals of species other than the orang utan, and as a result it is necessary to use some indirect method of estimating the densities of individuals in the area rather than a direct count. I have used the estimated number of groups of each species and the estimated mean size of groups.

Numbers of groups. All individual orang utans habitually using the study area were known (Rodman, 1973a). There were 6 population "units" (individuals or aggregations) that normally ranged independently of each other. These units had the following compositions:

2 solitary adult males;
2 adult females with single infants;
1 adult female followed by a single juvenile;
1 adult female with an infant and a juvenile.

A single group of *M. fascicularis* utilized the area, although it apparently fragmented frequently. Similarly, a single group of *M. nemestrina* ranged through the area, although it is possible that there were 2 groups. I have concluded that there was a single group because we never contacted pigtailed macaques in more than 1 location in a day. The numbers of groups of *P. aygula* and *H. muelleri* are more difficult to estimate, and my method of estimation will, therefore, be described in detail.

Observers usually made multiple contacts with groups of *P. aygula* and *H. muelleri* each day. Since these animals are quite mobile, it is often difficult to determine whether 2 contacts are with the same group or with 2 different groups. By using a systematic survey in which observers walk abreast along adjacent, parallel transects, it is possible to make decisions as to the identity of groups contacted on the basis of times of contact, locations of contact, and directions of movement or flight after contact. For example, 2 contacts with gibbons made successively by 1 observer traveling in a straight line are almost certainly contacts with different groups. Alternatively, if observer "A" contacts gibbons that flee to the southwest at 0810 hours, on transect 1, and if observer "B" then contacts gibbons at 0820 hours, on transect 2, 50 meters south of "A's" contact, it is highly likely that both observers have contacted the same group. Given many such pairs of contacts with *P. aygula* and with *H. muelleri*, it is possible to connect them or to draw lines separating them and gradually to build up a composite map showing areas that are probably occupied by different groups. Using this method, I estimate that there were 7 groups of *P. aygula* and 10 groups of *H. muelleri* whose ranges lay partially

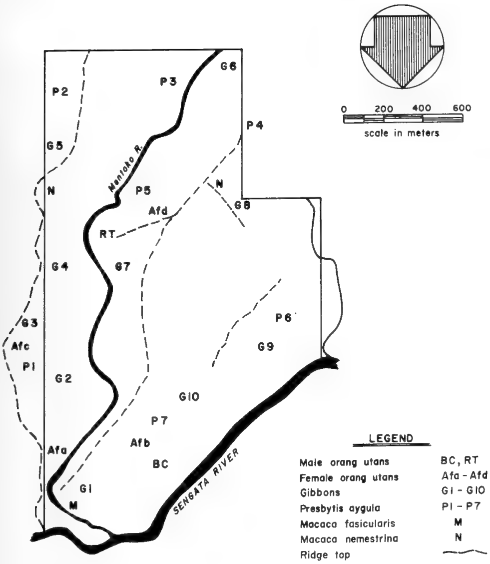


Figure 4. Estimated centers of group ranges. The centers of ranges of individual adult orang utans are given. It is likely that the 2 centers of ranges of *M. nemestrina* belong to the same group, which circled the southern end of the study area. The text describes the method of estimation of centers for gibbons and *P. aygula*.

or entirely within the study area.

The centers of ranges of all primate groups (including orang utans) are plotted in Figure 4. There were 25 groups of primates in the study area at the time of this study.

Group size. The frequencies of group counts in first contacts with each species are presented in Figure 5, but the relationship between actual group size and numbers counted at first contact is not simple. Factors such as individual size, coloration, and general activity level of a species influence "average" visibility of members of the species, and visibility must influence the relationship between numbers counted and numbers actually present. It is probably safe to say that in the forest the discrepancy between number seen and actual number present will increase with increasing group size, and that the mean number of animals counted at first contact will be lower than the actual mean size of groups observed when there are several groups of a species present. The situation is somewhat simpler if only a single group is present since, if counts are conservative and careful, the group size must be very close to the highest number of animals ever counted at 1 contact. Keeping these indefinite "criteria" in mind, it is possible to estimate the group size or mean group size of each species from data presented in Figure 5. Without explaining the details of estimation in each case, the results are as follows:

P. pygmaeus	1.83 animals per "group"
H. muelleri	4 animals per group
P. aygula	8 animals per group
M. fascicularis	16 animals in one group
M. nemestrina	15 animals in one group

Once again, observations of orang utans provide a "test" of these estimates. Orang utans are large, bright red animals who are consequently very conspicuous when they move. We would expect the mean number counted at first contacts to be close to the actual mean size of groups, and I have used the mean number counted at first contact as the estimate of group size. The mean size of the 6 population units listed previously is 1.83 also, and the correspondence of the 2 figures is partial confirmation of the criteria used for estimation.

Population densities. The estimated numbers of each species present in the study area are the simple products of the estimates of numbers of group and of sizes of groups. The area contained within the bound-

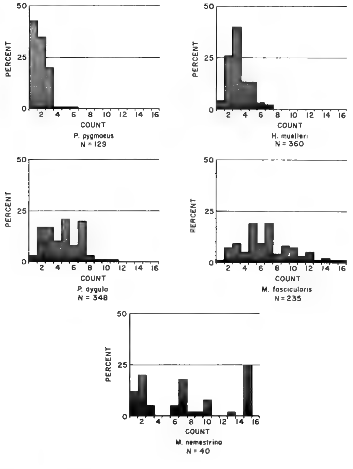


Figure 5. Frequency distributions of group counts. These are the numbers of individuals observed at each contact with a primate group. Interpretation of the figure is given in the text.

Table 2.—Population Densities of 5 Species, 1970–71*

Species	*Number of of groups*	*Groups per km²*	*Size of groups*	*Total population*	*Number per km²*
P. pygmaeus	6	2.2	1.84	11	4.0
H. muelleri	10	3.6	4	40	14.6
P. aygula	7	2.6	8	56	20.4
M. fascicularis	1	0.4	16	16	5.8
M. nemestrina	1	0.4	15	15	5.5

* Based on an area of 2.74km².

aries shown in Figure 2 is 2.74km² disregarding the additional area due to slopes. It is, therefore, possible to calculate the density of each species relative to the study area, and the results are shown in Table 2. These densities represent maximum densities achieved when all groups are present within the boundaries of the study area. The average density of a species must be lower because some groups move across the boundaries of the study area more or less frequently depending on ranging patterns.

Patterns of distribution

For the purpose of analysis of distributions, I have laid a grid of 4 hectare cells over the study area positioned so that the transects shown in Figure 3 pass through the centers of cells; the relationship between the transects and the cells of this grid is shown in Figure 6. The area sampled by the transects is larger than the area encompassed by the boundaries of the study area since observers could locate animals outside the boundaries while walking along the boundaries. Thus the area covered by the grid extends 100 meters outside the transects. In addition, contacts were made more than 100 meters outside the boundaries when observers tracked animals to the east of study area, and the cells in which such contacts were made are indicated by dotted lines in Figure 6. Finally, the arrangement of the grid of cells leaves some parts of the study area along the Sengata River that fall in cells covering primarily the river and the opposite side of the river; these cells will be excluded from subsequent analysis. I will analyze contacts made in the "principal study area" which consists of the cells lying along transects more than half of whose area lies on the south side of the Sengata River. There are 81 cells in this principal study area (Figure 6).

An initial plot of contacts within the 81 cells yielded distributional patterns that were biased by the distribution of the frequencies with which observers entered the cells. As a result, it is necessary to make some correction for bias in observation of cells. Observations have been normalized by dividing the frequency of contacts with a species in a cell by the number of walks through the cell. The range in these rates of contact has then been expanded to the range in number of original contacts. Resulting corrected values, rounded to the nearest integer, are plotted in Figure 7, and should be free of observational bias. It is the distribution of corrected contacts that is analyzed in the following discussion.

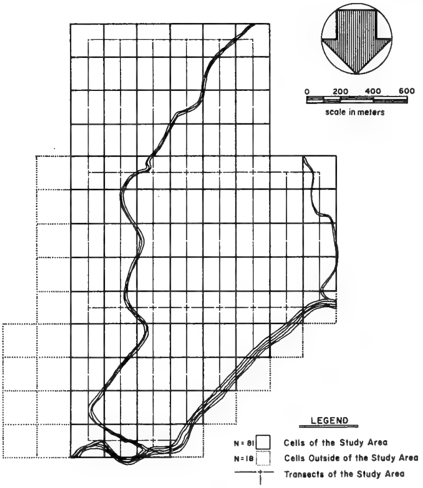
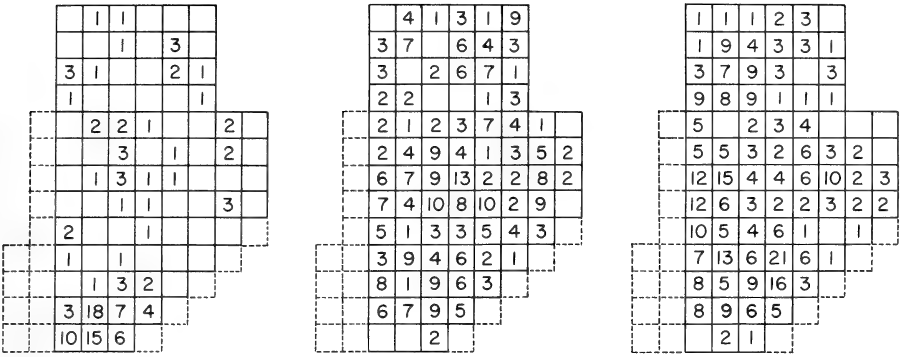


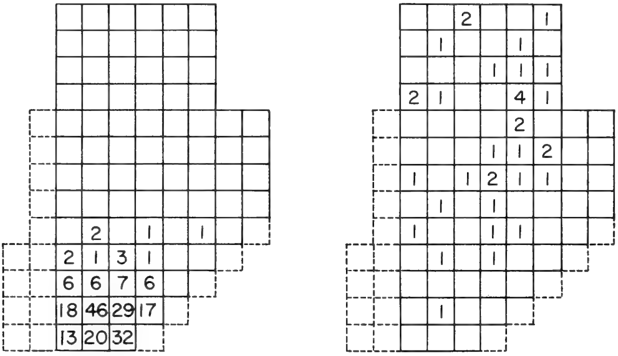
Figure 6. The Analytical Grid. A grid of .04 km² cells has been laid over the map of the area so that the transects pass through the centers of cells.



Pongo pygmaeus

Hylobates muelleri

Presbytis aygula



Macaca fascicularis

Macaca nemestrina

Figure 7. Corrected contacts with groups of primates. The numbers presented have been normalized by calculating the rate of contacts per walk into each cell, converting the rates to the range in magnitude of the raw data and rounding the results to the nearest integer.

Analysis and Discussion of Results

In the introductory paragraph I promised to test the hypothesis that a species specializing on a particular proportion of mixture of 2 or more resources will be found only where its favored proportion is found. It is possible to modify the hypothesis to fit this study more closely by stating it as follows: The density of a species feeding on a particular ratio of leaves to fruit should be positively correlated with the ratio of leaves to fruit available in cells of the principal study area. The ratio of leaves to fruit will vary directly as the quantity of leaves available and inversely as the quantity of fruit available.

Three sets of data are necessary to test the hypothesis: the relative proportions of leaves and fruit in each species' diet; the distribution of each species in cells of the principal study area; and the relative availability of leaves and fruit in cells of the study area.

Distribution of fruit in habitats

Phenological observations. Although data on plant phenology of the tropics are rare, Frankie, et al., (1974a and 1974b) have analyzed phenology of trees in Wet Forest and in Dry Forest of Costa Rica in a manner useful to the present interpretation. Comparison of fruiting activity in the 2 types of forest suggests that fruit is more constantly available, if not more abundant, in the Wet Forest than in the Dry Forest areas studied.* The 2 areas in Costa Rica were truly separated into 2 different life zones, and I am concerned in East Kalimantan with 2 habitat zones in a small section of forest. But if it is assumed that analogous differences exist between wetter and drier regions with a single forest, fruit should be more continuously available, if not more abundant, in wetter regions. Assuming rainfall to be constant over a 3km^2 section of forest, variations in moisture depend on water runoff and flooding. Zones that are relatively flat and often flooded should be the wettest sections of the forest, and, therefore, should, by analogy with observations of Wet and Dry Forests of Costa Rica, be habitat regions with more continuously available mature fruit relative to other zones.

The cells of the principal study area adjacent to the Sengata River, and particularly those that are flat, should be the cells with the most continuously available fruit. It is necessary to point out, however, that Frankie, et al. (1974b) state specifically that "Riparian species of the Dry Forest followed the same pattern as those in other communities of the Dry Forest site in respect to flowering and fruiting patterns. . ." Although this statement apparently vitiates the analogy I have attempted to draw between habitat zones of this study area and Wet and Dry Forests of Costa Rica, the authors do not provide data on monthly proportions of species bearing mature fruit in the riparian community of the Dry Forest. The analogy of interest here may, therefore, still hold, although in other respects—e.g., in seasonal patterns of fruiting—the analogy probably is not a good one.

Reproductive strategies of plants. Gaines and his co-workers have recently written the following summary statement regarding reproductive strategies of organisms:

> In an unstable environment where the usual condition is one of high density-independent mortality, selection favors those organisms (r-strategists) that allocate more energy to reproductive activities at the expense of vegetative activities. Conversely, in a stable environment where there is high density-dependent mortality, selection favors individuals (K-strategists) that allocate more energy to vegetative activities for increased competitive ability at the expense of reproductive activities. (*Gaines, et al.*, 1974, p. 889)

This summary is based on the theoretical discussions of Cody (1966), of MacArthur and Wilson (1967) and of Gadgil and Bossert (1970). The hypothesis has been tested and substantiated for various plant forms by Gadgil and Solbrig (1972; dandelions) and by Abrahamson and Gadgil (1973; goldenrod). Gaines (et al., 1974) tested and confirmed the hypothesis for sunflowers. Although the prediction of differential reproductive strategies of trees in habitats that differ in stability remains to be tested, I will assume that, given these 3 tests on other plant forms, the predictions are likely to hold for trees as well; trees in unstable environments will invest more in reproductive activities relative to vegetative activities than trees in stable environments. It is, therefore, predicted (and for the sake of this analysis, it is assumed) that trees in unstable environments will bear more fruit relative to leaves than trees in stable environments.

Tropical rain forests such as those of the study area in this research are generally perceived as stable environments, but subsections of a rain forest could be relatively unstable as a result of the normal vagaries of weather interacting with the substrate. Ridgetops subjected to intermittent windstorms may never support climax vegetation, and riverbanks subjected to intermittent flooding may support communities that are constantly in flux. The latter regions—those adjacent to rivers—may be the most unstable sections of a rain forest. The prediction is that the "riverine zone" of the study area supports trees devoting more energy to reproductive activities relative to vegetative activities than the "deep forest zone"—i.e., that the ratio of leaves to fruit available to primates in the deep forest is higher than in the riverine zone.

Habitat zones of the study area

The question now is which cells of the principal study area to assign to each zone. I have chosen to place all cells that have more than half their area below the

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* I have estimated from Figures 8, 9, and 12 of the paper by Frankie, et al. (1974b) that the average proportion of species bearing mature fruit per month was 21.2 percent in the overstory of the Wet Forest; 29.8 percent in the understory of the Wet Forest; and 16.5 percent in the Dry Forest.

40 m contour line of Figure 2 in the riverine zone; 9 cells fall into this zone. The remainder of the cells are assigned to the deep forest zone; 72 cells fall into this zone. The extent of the 2 zones is shown in Figure 8.

In 1975 I tested the prediction that fruit is more abundant in the riverine zone than in the deep forest by pacing 2350 m along paths and transects in the riverine zone and 7900 m in the deep forest, noting the presence or absence of fruit in each 50 m segment. Fecal deposits were ignored and logged areas were not included in the sample. There was at least 1 fruit on the ground in 48.9 percent of segments in the riverine zone ($N=47$) and at least 1 fruit on the ground in only 33.5 percent of segments in the deep forest ($N=158$). The 2 zones differed reliably in the predicted direction ($z = 1.74$; $p = .041$).

Diets and distributions of species in the two habitat zones

According to the principal hypothesis, it is expected that primate species will be distributed in the 2 habitat zones in relation to their dietary proportions of leaves and fruit. The figure to be used to test this hypothesis is the ratio of density per cell in the deep forest zone to density per cell in the riverine zone. It is expected that this ratio will vary directly in proportion to the ratio of leaves to fruit in the diet of species. The relevant data are presented in Table 3, and the relationship between diet and relative density in the 2 zones is plotted in Figure 9. Ignoring *Macaca nemestrina*, there is a perfect correlation between ratio of density in deep forest to density in the riverine zone and the ratio of leaves to fruit in the diet. *M. nemestrina* do not fit the prediction, and I have previously made a case for assuming the diet of *M. nemestrina* to be predominantly frugivorous.

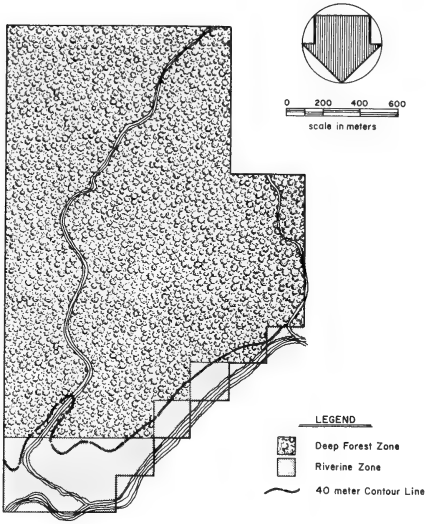

Figure 8. Habitat zones of the study area. Cells more than half of whose area falls below the 40 m contour are placed in the riverine zone; the remainder are placed in the deep forest.

The anomalous—or contradictory—relationship between diet of *M. nemestrina* and its distribution in the 2 zones is explained by its radically different utilization of vertical strata (Figure 10). Whereas the other 4 species are all quite similar and almost totally arboreal, *M. nemestrina* are predominantly found on or near the ground. This pattern can be explained simply as an efficient means of travel for an arboreal frugivore specializing on feeding in an area of low density of fruit sources. If food sources are in the forest canopy and far apart, it must be considerably more efficient to travel on the ground between them than

Table 3.—Relation of Densities in 2 Habitats to Diets of 5 Species

Species	*(A)* *Density in deep forest*	*(B)* *Density in riverine zone**	*A/B × 100*	*Diets: leaves/fruit** × 100*
1. *M. fascicularis*	0.5	19.4	2.6	2
2. *P. pygmaeus*	0.8	7.1	11.2	20
3. *H. muelleri*	4.0	3.6	111.1	75
4. *P. aygula*	4.6	3.8	121.1	233
5. *M. nemestrina*	0.4	0.2	200.0	14
6. *Macaca* (1 + 5)	0.9	19.5	4.6	3

* Density = number of corrected contacts per cell.

** Leaves/Fruit = number of times observed feeding on leaves/ number of times observed feeding on fruit at first contact.

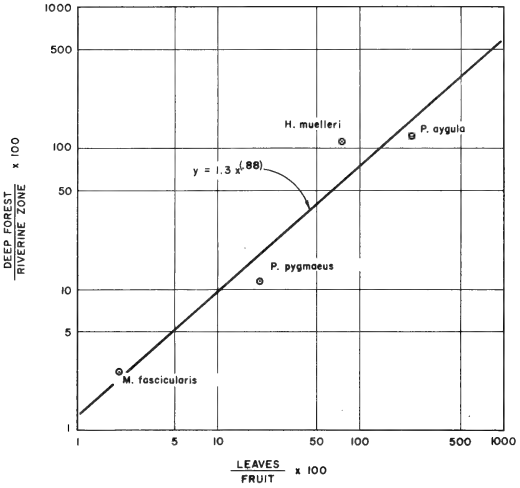

Figure 9. Dietary proportions and habitat utilization. The ratio of density per cell in the deep forest zone to density per cell in the riverine zone is plotted as a function of the ratio of leaves to fruit in the diet. The regression line is a least squares fit to the 4 points.

to follow an extended arboreal pathway with its "ups and downs." It is easy to view *M. nemestrina* and *M. fascicularis* as replacements for one another in 2 habitats that differ in density of fruit sources, each macaque with an appropriate specialization in travel patterns for the distribution of fruit in a habitat.

For the purpose of this analysis, it might be appropriate to combine observations of the diets and distributions of the 2 macaques into data on the genus *Macaca*. The results do not differ radically if this procedure is followed, but instead I will consider only the 4 species that are truly arboreal. As stated above, within this group of species the correlation between dietary proportions and distribution in the 2 habitat zones is perfect.

Alternate explanations of the result

The correlation between diet and distribution could be explained by 2 other hypotheses:

1. *The relationship occurs by chance alone.* The probability of a rank correlation coefficient of exactly +1.0 in a sample of four is only 0.04. It is highly unlikely that this result has occured by chance.

2. *The primate species are distributed in the 2 zones for some other reason that is unknown, and they feed opportunistically on the proportions of food available where they live.* This hypothesis may

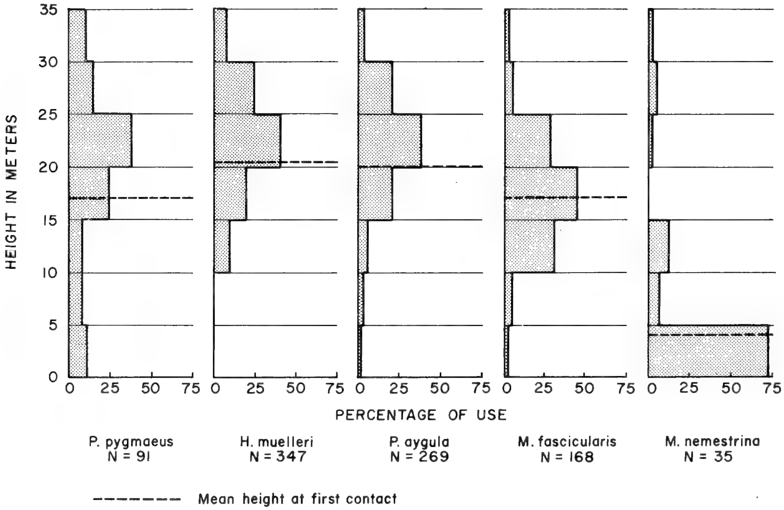

Figure 10. Utilization of vertical strata. Frequency of heights above the ground at first contact is plotted for each species. All observations are included regardless of activity of the animals when sighted.

be debated with 3 arguments:

The first argument stems from the morphology of structures related to feeding in leaf-monkeys and macaques. The alimentary tract of members of the genus *Presbytis* is long with a highly sacculated stomach characteristic of consumers of bulky, low-energy foods (Hill, 1972, p. 94). *Presbytis aygula* is, therefore, morphologically adapted to feed on a diet of leaves, and would be expected to be found in regions providing such a diet. The other primate species of this study are characterized by a "generalized" alimentary tract (Hill, 1972), and correlates of alimentary morphology are difficult to perceive. But macaques have buccal pouches for food storage typical of the Cercopithecinae, and it seems likely that such small storage facilities would be used for foods with low energy yield per unit volume such as leaves. The morphology of these structures tends to contradict the suggestion that proportions of leaves and fruit fed upon by the species are not real preferences but only the result of opportune exploitation of proportions of foods available.

A second set of data contradictory to this hypothesis comes from observation of similar species in another area of the world. As discussed previously, toque macaques of Ceylon feed predominantly on fruit (Hladik and Hladik, 1972), and bonnet macaques of southern India appear to have a predominantly frugivorous diet. These 2 close relatives of *M. fascicularis* each have diets similar to that of *M. fascicularis* although they are found in rather different regions of the world. *Presbytis senex* of Ceylon feeds on a diet of 60 percent leaves and leaf shoots by weight, 12 percent flowers and 28 percent fruits (Hladik and Hladik, 1972, p. 173), which is almost identical to the dietary proportions of *P. aygula* of this study despite a different location. Observations of macaques and leaf-monkeys elsewhere contradict the hypothesis that dietary proportions depend on the location of the animals. It should be added that *Presbytis entellus* of Ceylon have a diet consisting of approximately equal proportions of leaves and fruit (Hladik and Hladik, 1972, p. 186), and this is confusing evidence. But *P. entellus are* unusual in other respects compared with other members of the genus, and it is not surprising that their diets differ as well.

A final argument against this hypothesis results from its implication that proportions of food eaten by a species should change with different proportions of food available in the immediate habitat. Each of the 4 species observed occurs in each of the habitat zones (Figure 7). I have examined the feeding data for contacts in the 2 zones, and there is no indication that diets of the same species differ between the 2 zones in the manner implied by this hypothesis. Orang utans are predominantly frugivorous in the deep forest zone, and *P. aygula* are predominantly folivorous in the riverine zone. These observations allow rejection of the second alternative hypothesis proposed.

Summary

During a 15-month study of primate species in East Kalimantan, Indonesia, the author and several assistants made observations of the diets and distributions of 5 species in a 2.74km^2 section of forest. Observations of phenology of other tropical forests and recent theoretical work on the relationship between environmental stability and reproductive strategies of plants suggest that there are 2 habitat zones within the study area, the riverine zone and the "deep forest" zone, that differ in proportions of leaves and mature fruit available as food. Analysis of the distributions of the 5 species reveals that these species are distributed in the 2 zones according to the proportions of leaves and fruit in their diets.

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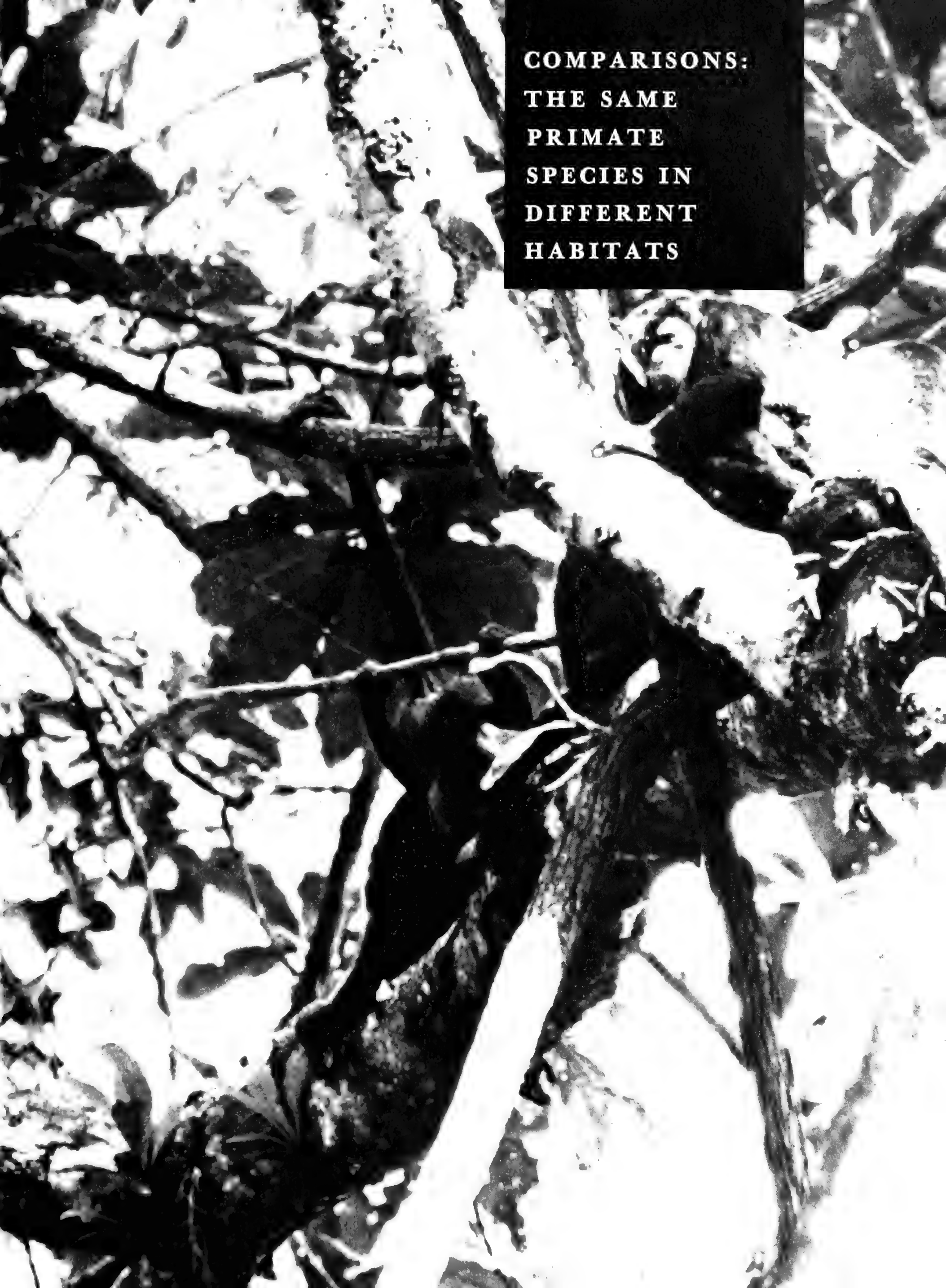
Part of a troop of ***Alouatta palliata*** *resting. (Photo by R. Thorington)*

COMPARISONS: THE SAME PRIMATE SPECIES IN DIFFERENT HABITATS



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Intergroup Dietary Comparisons and Folivorous Tendencies of Two Groups of Blue Monkeys
(Cercopithecus Mitis Stuhlmanni)

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Introduction

A field study of the ecology and behavior of blue monkeys (*Cercopithecus mitis stuhlmanni*) was conducted in the Kibale Forest (between 0° 13′ to 0° 41′ N and 30° 19′ to 30° 32′ E) western Uganda between November 1972 and October 1974 inclusive. The study area which was approximately 3.0 sq km in extent was located on undulating terrain close to the Kanyawara Forest Station at about 1450 m elevation. The forest within the study area can be described as a tropical rain forest having affinities both with montane rain forests and mixed tropical deciduous forests. Like other such plant communities, it supports a wide array of plant species and exhibits a great deal of vegetational heterogenity (Oates, 1974; Struhsaker, 1975).

Much of the time in the field was spent with 2 groups of blue monkeys, namely, Group I and Group II. The home ranges of these 2 groups were situated in different parts of the study area which partly included 2 contiguous forest compartments referred to as Compartment 30 and 14, respectively. Compartment 30 was a relatively undisturbed mature forest which included the entire home range of Group I and a small part of the home range of Group II. The major part of the home range of Group II lay within Compartment 14 which was selectively felled for commercially valuable timber in 1969. The shortest distance between the 2 home ranges was about 500 m and they were separated by the home range of another blue monkey group (Group III) which overlapped to a small extent with the home ranges of Group I and II.

Methods

Monthly feeding data were recorded during 5 consecutive days of observations of each group when group contact was maintained from dawn to dusk. Feeding-frequency scores recorded during these periods of observations (referred to as sample periods) were operationally distinguished by using a 30-minute interval between like scores. In other words, an individual monkey M_1 scored for feeding on particular food item I_1 from a particular food plant species S_1 was not scored again for the same specific food item until 30 minutes had elapsed. During this period, however, other feeding scores were obtained if:

(1) Individual M_1 utilized any other food item I_2 to I_x from the same plant species S_1, or

(2) Individual M_1 utilized any food item I_1 to I_x from food plants S_2 to S_x, or

(3) Another individual M_2 utilized food items I_1 to I_x from food plants S_1 to S_x.

A change in the plant species, specific food item, or feeding individual would lead to a score, but 30 minutes must elapse before the same combination is scored again

The frequency of exploitation of probable invertebrate food was also recorded using the same criteria. In most cases it was difficult to distinguish these food items which were small, but the type of motor patterns employed in exploitation of these food items and the substrate (such as moss-covered branches) from which they were taken did indicate that these were probably invertebrate food items. Like scores were distinguished by considering a 30-minute interval, the tree species, the substrate from which the item was taken, and the motor pattern employed in the capture and ingestion of a food item. Owing to the difficulty in distinguishing the type of invertebrate foods used, intergroup dietary comparisons which required species distinction of diet were restricted to plant foods. Invertebrate foods were included in making intergroup comparisons in the use of nonspecific food items.

Feeding data from the 2 groups were collected for different periods of time between February 1973 and September 1974. In order to show the folivorous tendencies of blue monkeys, feeding data collected from both groups through all months of study were used, but intergroup comparisons in diet were restricted to the period between February 1973 and January 1974 when monthly observations were made on both groups. In some of these months, Group I was observed for 2 successive 5-day periods (sample periods I and II) during the first 2 weeks of the month and then Group II was contacted for one 5-day period during the third or the last week of the month. Due to this sequence of observations, sometimes the time interval between a period of contact with Group II during a particular month and the first sample period of observations on Group I the following month was shorter than the time interval between sample periods on the 2 groups during the same month. Intergroup comparisons of diet were made using only those pair combinations of sample periods with the shorter time interval between them regardless of whether these periods occurred within the same month or in adjacent months. This reduced the possibility of intergroup differences in diet being affected by the time interval between sample periods. When a period of observations of a group was comparable to 2 sample periods of the other group, both pair combinations were compared.

Intergroup overlaps in diet between comparable sample periods were computed on the basis of the percentages of use of specific food items exploited by both groups. The sum of the shared percentages of mutually exploited specific food items yielded the total overlap in diet. In other words, if during a sample period the diet of Group I consisted of 40 percent of a specific food item, 30 percent of another, 20 percent of a third and 10 percent of a fourth and the extents of exploitation of the same specific food items by Group II during the most comparable sample period were 20, 20, 30 and 30 percentage points respectively, the total overlap in diet would be 70 percent. This was the same method used by Holmes and Pitelka (1968) in their study of diet overlap in sandpipers.

Results

Group I was observed during 23 5-day periods between February 1973 and May 1974 inclusive (Table 1). From March 1973 to August 1973 inclusive and in November 1973, this group was observed for 2 5-day

Table 1.—Time interval between comparable sample periods of observations on Groups I and II.

	Number of sample periods of observation		*Comparable sample periods*		
Month	*Group I*	*Group II*	*Group I*	*Group II*	*Interval (days) between sample periods*
Feb 73	1	1	Feb I 73	Feb I 73	2
Mar	2	1	Mar II	Mar I	4
Apr	2	1	Apr I	Mar I	4
May	2	1	May I	Apr I	5
Jun	2	1	Jun I	May I	3
July	2	0	July I	Jun I	4
Aug	2	1	Sept I	Aug I	2
Sept	1	1	Sept I	Sept I	10
Oct	1	1	Nov I	Oct I	3
Nov	2	1	Nov II	Nov I	7
Dec	1	1	Dec I	Dec I	7
Jan 74	1	1	Jan I 74	Jan I 74	4
Feb–May	4	3	—	—	—
Jun–Sept	—	4	—	—	—
Total	23	18		$\bar{X}$	4.58

periods and during each of the other months they were contacted during 1 5-day period. Group II was observed during 18 observation periods and contacted during all but 3 months (i.e., July 1973, May 1974, and July 1974) between February 1973 and September 1974 inclusive. In September 1974, this group was observed for 2 5-day periods whereas in other months of contact they were observed for 1 5-day period.

Eleven periods of observations of each group between February 1973 and January 1974 inclusive provided 12 pair combinations of sample periods for comparison (Table 1). The mean time interval between comparable sample periods was 4.58 days (range, 2–10 days). During these sample periods, Group I was observed for 584 hours and a total of 2329 plant and invertebrate feeding scores were collected at the rate of 4.0 feeding scores per hour of group contact; 1977 of these feeding scores were recorded from the use of 60 food plants and 102 specific food items (Table 2). Group II was observed for 558 hours and 2268 feeding scores were collected at the rate of 4.1 feeding scores per hour of contact. Feeding on plant food accounted for 1856 scores from this group and were recorded from the use of 47 plant species and 86 specific food items (Table 3). In view of the small differences in the duration of group contact and similar rates of feeding data collection, it appears that the plant diet of Group II was less diverse than the diet of Group I. The less diverse nature of the diet of Group II was also indicated by the fact that the top 13 food plants of this group were exploited to the same extent as the top 21 food plants of Group I.

Both groups exploited a total of 74 food plants, but only 33 (44.6 percent) of these were shared by them; 27 were used exclusively by Group I, and 14 were used only by Group II. In general, mutually exploited food plants were used at different frequencies, these differences being most appreciable in the use of *Ficus exasperata* and *Teclea nobilis* which were top-ranking food plants of Groups I and II. Intergroup differences in the frequency of use of *Uvariopsis congensis, Markhamia platycalyx,* and *Mimusops bagshawei* were also relatively large (Tables 2 and 3). Due to intergroup variability in the frequency of use of food plants, only 13 mutually exploited species occur among the top 20 food plants of each group. The top 20 food plants account for as much as 89.65 percent and 95.80 percent of the vegetable diet of Groups I and II respectively and, therefore, must be considered as an important component of their diet. Included among the top 20 ranks were *Pancovia turbinata* which was exclusively used by Group I and *Ficus stipulifera* which was used only by Group II. There were also several species, such as

Table 2.—Group I: Percentage use of specific plant food items during 11 observation periods most comparable t those of Group II between February 1973 and January 1974 inclusive.

Food plant species	*Leaf buds*	*Young leaves*	*Mature leaves*	*Dry leaves*	*Petioles*	*Stems*	*Flower buds*	*Blossoms*	*Fruits*	*Seeds*	*Nectar*	*Galls*	*Total frequency*	*Total % frequency*
Teclea nobilis	0.05	0.10	1.37						11.53				258	13.06
Celtis africana	0.35	0.25					0.05	0.15	10.52				225	11.39
Diospyros abyssinica		2.68						2.78	4.55				198	10.02
Uvariopsis congensis		0.15							6.83				138	6.98
Celtis durandii									6.52				129	6.52
Premna angolensis	1.27	0.05						3.80					101	5.11
Ficus exasperata									4.76				94	4.76
Mimusops bagshawei							0.20	0.56	3.85				91	4.61
Markhamia platycalyx	0.05				3.14		0.10	0.05			0.56		77	3.90
Funtumia latifolia										2.88			57	2.88
Dombeya mukole		2.07	0.40				0.10						51	2.58
Bosquiea phoberos							0.05	1.21	1.01			0.20	49	2.48
Monodora myristica	1.62	0.46	0.05					0.05				0.20	43	2.18
Parinari excelsa		0.10							2.02				42	2.13
Vangueria apiculata			1.82						0.30				42	2.13
Pancovia turbinata		0.25							1.72				39	1.97
Chaetachme aristata						0.25			1.37			0.10	34	1.72
Neoboutonia macrocalyx			1.37										27	1.37
Clausena aristata		1.27			0.05								26	1.32
Illigera pentaphylla		0.20	1.07										25	1.27
Milletia dura		0.91	0.10				0.15	0.10					25	1.27
Linociera johnsonii	0.05	0.76							0.30				22	1.11
Chrysophyllum gorungosanum								1.01	0.05				21	1.06
Olea welwitschii			0.46				0.40	0.10					19	0.96
Aningeria altissima		0.20						0.71					18	0.91
Balanites wilsoniana			0.40					0.46					17	0.86
Blighia unijugata		0.61											12	0.61
Symphonia globulifera									0.05		0.35		8	0.40
Newtonia buchanani	0.20									0.15			7	0.35
Coffea eugenoides							0.35						7	0.35
Loeseneriella apiculata								0.35					7	0.35
Trichilia splendida		0.35											7	0.35
Dichapetalum ugandense			0.05					0.25					6	0.30
Urera cameroonensis		0.15				0.10							5	0.25
Cyphomandria betaceae									0.20				4	0.20
Loxogramme lanceolata		0.20											4	0.20
Strombosia scheffleri		0.10							0.10				4	0.20
Ficus natalensis									0.20				4	0.20
Polystachya sp.			0.10					0.05					3	0.15
Ficus kisantuensis									0.15				3	0.15
Pseudospondias microcarpa									0.10				2	0.10
Fagaropsis angolensis									0.10				2	0.10
Albizia gummifera								0.10					2	0.10

Table 2.—Group I: (cont.)

Food plant species	*Leaf buds*	*Young leaves*	*Mature leaves*	*Dry leaves*	*Petioles*	*Stems*	*Flower buds*	*Blossoms*	*Fruits*	*Seeds*	*Nectar*	*Galls*	*Total frequency*	*Total % frequency*
Cardiospermum grandiflorum		0.05	0.05										2	0.10
Apodytes dimidiata								0.10					2	0.10
Belanophora glomerata									0.10				2	0.10
Erythrina sp.								0.10					2	0.10
Vangueria acutiloba									0.10				2	0.10
Spathodea campanulata		0.05											1	0.05
Ficus brachylepis		0.05											1	0.05
Randia urcelliformis			0.05										1	0.05
Diaphananthe sp.								0.05					1	0.05
Harungana madagascarensis									0.05				1	0.05
Landolphia sp.								0.05					1	0.05
Platycerium elephantotis			0.05										1	0.05
Saba florida						0.05							1	0.05
Unidentified (4 spp.)													4	0.20
Total	3.59	11.01	7.34	—	3.19	0.40	1.40	12.03	56.48	3.03	0.91	0.30	1977	

Mimusops bagshawei and *Linociera johnsonii* which occur only among the top 20 food plants of one group and occupy lower ranks in the diet of the other group.

The frequencies of use of food plants, if affected by their densities within the 2 home ranges, may not reflect any of the differences in food-plant preference between the 2 groups. In order to find out if there were any intergroup food-plant preferences, selection ratios were calculated for each of several important food plants by dividing its percentage frequency of use by a group by its density within the group's home range (Table 4). Tree density estimates from line-transect enumeration within the home ranges of Group I (by Struhsaker, 1975) and Group II (Waser, personal communication) were used for all species except *Ficus exasperata* and *Ficus brachylepis*. These 2 species did not appear in the line transect within the home range of Group I and, therefore, their true densities (obtained during a study of the phenology) within both home ranges were used. Selection ratios indicate that intergroup differences in the frequency of use of some species (*Celtis durandii, Diospyros abyssinica*) were probably due to differences in their densities within the 2 home ranges. Certain species, however, appeared to be more preferred by Group I than by Group II (e.g., *Celtis africana, Premna angolensis, Ficus exasperata, Mimusops bagshawei*), while some others were more preferred by Group II than Group I (*Ficus brachylepis, Chrysophyllum gorungosanum*). It must be pointed out that the frequency of use of food plants may also have been affected by the size of their canopy as well as the conditions of visibility within the canopy. Appropriate measures of these parameters were not available and, therefore, the selection ratios given in Table 4 do not reflect intragroup preference of food plants; however, since it is reasonable to assume that these 2 factors are more or less constant for a particular plant species, intergroup comparisons of these selection ratios must be considered valid.

Comparisons of the proportions of food items constituting the vegetable diet of the 2 groups show that Group I used 25.1 percent of foliar food (composed of leaf buds, young leaves, mature leaves, dry leaves, and petioles), while Group II used about 17.0 percent of these food items (Tables 2 and 3). This difference was largely due to appreciably higher frequencies of use of young and mature leaves by Group I. Group I also used relatively higher proportions of blossoms and lower proportions of fruits in its vegetable diet than Group II. Intergroup dietary dif-

Table 3.—Group II: Percentage use of specific plant food items during 11 observation periods between February 1973 and January 1974 inclusive

Food plant species	*Leaf buds*	*Young leaves*	*Mature leaves*	*Dry leaves*	*Petioles*	*Stems*	*Flower buds*	*Blossoms*	*Fruits*	*Seeds*	*Nectar*	*Galls*	*Total frequency*	*Total % frequency*
Ficus exasperata	3.50	0.97			0.05				15.09				364	19.61
Uvariopsis congensis									11.53				214	11.53
Celtis africana	0.65	0.32					0.65	0.70	9.16				213	11.48
Diospyros abyssinica		2.37	0.05				0.81	2.69	1.78				143	7.70
Markhamia platycalyx			0.05		2.96		0.05		0.59		3.18		139	7.49
Celtis durandii		0.05	0.05	0.05					7.00				133	7.17
Ficus brachylepis									6.63				123	6.63
Teclea nobilis			0.11						4.36				83	4.47
Funtumia latifolia										4.04			75	4.04
Monodora myristica	0.32	0.43						0.86	2.21				71	3.83
Linociera johnsonii		0.27							2.10				44	2.37
Premna angolensis	0.65		0.05					1.24					36	1.94
Chrysophyllum gorungosanum							0.05	1.40	0.32				33	1.78
Cyphomandria betaceae		0.16			0.05			0.37	0.54				21	1.13
Olea welwitschii			0.86					0.11					18	0.97
Clausena aristata		0.75					0.22						18	0.97
Illigera pentaphylla		0.22	0.54					0.05					15	0.81
Ritchia albersii		0.05							0.65				13	0.70
Ficus stipulifera									0.59				11	0.59
Bosquiea phoberos									0.59				11	0.59
Neoboutonia macrocalyx			0.54										10	0.54
Mimusops bagshawei													9	0.48
Urera cameroonensis			0.05					0.38					8	0.43
Strombosia scheffleri			0.05					0.05	0.27				7	0.38
Fagaropsis angolensis									0.32				6	0.32
Ficus kisantuensis									0.27				5	0.27
Vangueria apiculata			0.11						0.05				3	0.16
Symphonia globulifera											0.16		3	0.16
Lepisanthes senegalensis									0.16				3	0.16
Dombeya mukole		0.05	0.05										2	0.11
Angraecum distichum			0.11										2	0.11
Chlorodendrum schweinfurthii			0.11										2	0.11
Drypetes battiscombei			0.11										2	0.11
Newtonia buchanani		0.11											2	0.11
Parinari excelsa									0.11				2	0.11
Chaetachme aristata									0.05				1	0.05
Trema orientalis									0.05				1	0.05
Basella alba								0.05					1	0.05
Brachystephanus africanus			0.05										1	0.05
Diaphananthe sp.									0.05				1	0.05
Fagara angolensis		0.05											1	0.05
Ficus congensis									0.05				1	0.05
Glyphaea laterifolia		0.05											1	0.05
Tabernaemontana usamberensis									0.05				1	0.05
Unidentified (3 spp.)													3	0.16
Total	5.12	5.85	2.89	0.05	3.06	—	1.78	8.05	64.42	4.04	3.34	—	1856	

Table 4.—Selection ratios of important food plants exploited by Groups I and II

Species	*% Frequency of Use*		*Density/hectare*		*Selection ratio*	
	Group I	*Group II*	*Group I home range*	*Group II home range*	*Group I*	*Group II*
T. nobilis	13.06	4.47	21.0	12.3	0.62	0.36
C. africana	11.39	11.48	2.1	7.4	5.42	1.55
D. abyssinica	10.02	7.70	65.7	35.7	0.15	0.22
U. congensis	6.98	11.53	25.2	14.8	0.28	0.78
C. durandii	6.52	7.17	34.3	31.4	0.19	0.23
P. angolensis	5.11	1.94	1.4	1.9	3.65	1.05
F. exasperata	4.76	19.61	0.2	1.6	23.80	12.30
M. bagshawei	4.61	0.48	2.1	0.6	2.20	0.77
M. platycalyx	3.90	7.49	58.0	45.5	0.07	0.16
F. latifolia	2.88	4.04	14.7	9.9	0.20	0.41
F. brachylepis	0.05	6.63	0.1	0.4	0.40	16.60
C. gorungosanum	1.06	1.78	2.1	0.6	0.60	2.97

ferences can also be shown by considering the use of plant as well as invertebrate food items exploited by both groups during comparable sample periods (Figure 1). In the February 1973/February 1973 pair combination of sample periods from Groups I and II respectively, there were appreciable differences in the frequency of use of fruits (18.3 percent), blossoms (27.0 percent), and invertebrates (10.7 percent). Similarly in the May 1973/April 1973 pair-combination intergroup variability in diet was due to differences in the use of foliar items (13.7 percent) and blossoms (12.1 percent). In the July 1973/June 1973 pair combination, there were large differences in the use of fruits (28.5 percent) and blossoms (25.4 percent). Considerable intergroup variability in the use of food items can also be found in the September 1973/August 1973, September 1973/September 1973, December 1973/December 1973, and January 1974/January 1974 pair combinations of sample periods (Figure 1). The reader may refer to Tables 9 and 10 to assess the differences in the frequency of use of some of these food items during the above pair combinations of sample periods.

Intergroup variability in diet was also apparent in the relative importance and the frequency of use of specific food items used by the 2 groups. Among the top 20 ranks of specific food items exploited by each group, only 11 were mutually exploited, and the top-ranking specific food item of each group occupied a much lower rank in the diet of the other group (Table 5). Usually, both groups used a food plant for the same food items, but the frequency of use and relative importance of these food items were quite variable in the diet of each group. Thus, in the diet of Group I, *Monodora myristica* was included within the top 20 ranks because of the use of its leaf buds,

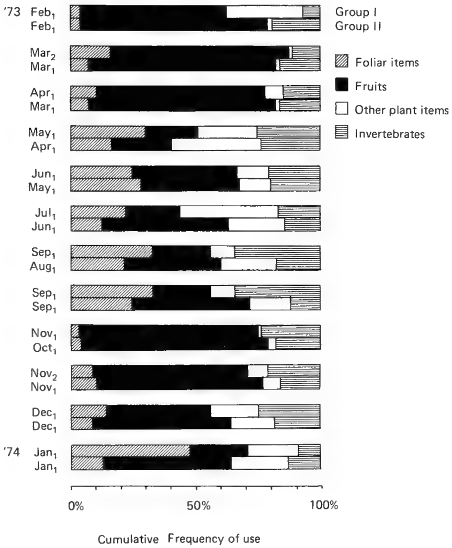

Figure 1. Cumulative percent frequency of use of different food items by Groups I and II during comparable sample periods.

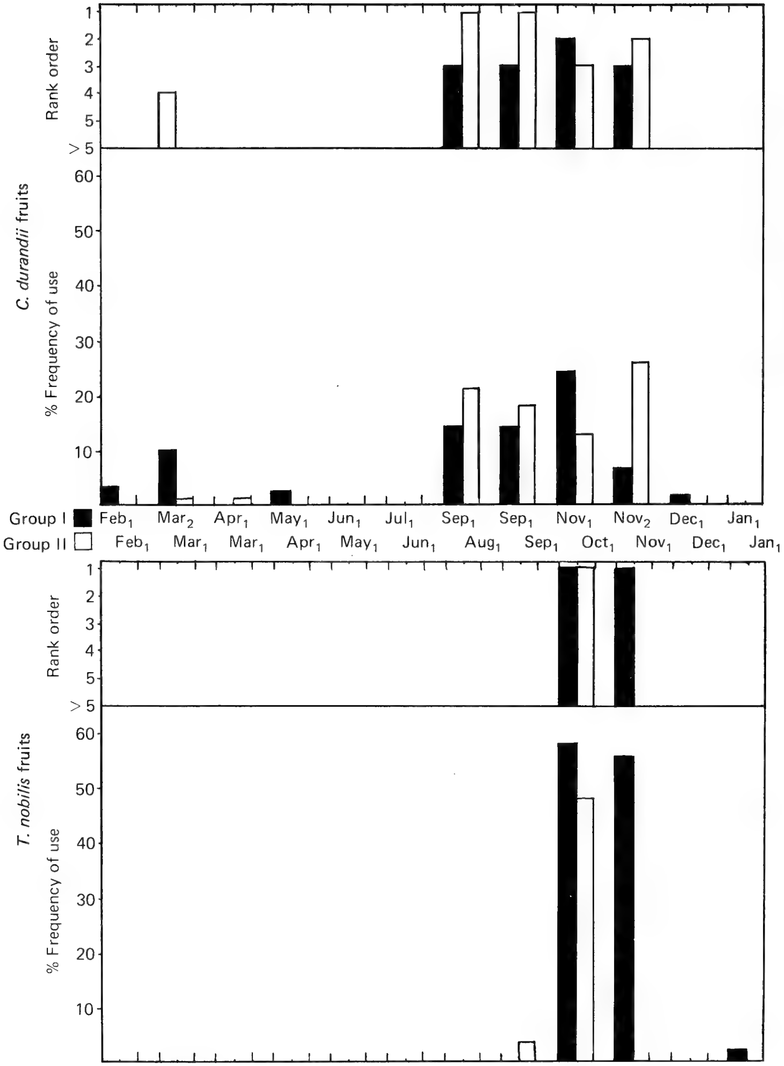

Figure 2. Rank order and frequency of use of the fruits of *Celtis durandii* and *Teclea nobilis* by Groups I and II during comparable sample periods.

and in the diet of Group II it was included among these ranks due to the use of its fruits and blossoms. Group II used the nectar of *Markhamia platycalyx* more frequently than its petioles, but Group I used the petioles more frequently than the nectar of this species. The frequencies of use and, therefore, the relative importance of food items from *Diospyros abyssinica* were also reversed in the diet of the 2 groups.

Most of the high-ranking specific food items exploited by both groups showed restricted periods of use (and importance), but their patterns of use were somewhat variable. The fruits of *Celtis durandii, Teclea nobilis,* and *Celtis africana* were used and relatively important in the diet of both groups during similar sample periods and do not show much variation in their patterns of use by the 2 groups (Figures 2 and 3). The fruits of *Diospyros abyssinica* were also used by both groups during comparable sample periods, but they were relatively important in the diet of Group I for longer periods than in the diet of Group II (Figure 3). The fruits of *Mimusops bagshawei, Uvariopsis congensis,* and *Ficus brachylepis* and the blossoms of *Premna angolensis* showed greater variability in their pattern of use and relative importance in the diet of the 2 groups (Figures 4 and 5). *Mimusops bagshawei* fruits were important in the diet of Group I during 4 sample periods, but were never important in the diet of Group II. The fruits of *Uvariopsis congensis* were important in the diet of Group II during the mid- and late-1973 sample periods, but their importance in the diet of Group I was restricted to the mid-year sample periods. The use of *Premna angolensis* blossoms showed a pattern where a specific food item was exploited during similar sample periods and assumed importance in the diet of the 2 groups during entirely different sample periods. The fruits of *Ficus brachylepis* which was the fifth ranking specific food item in the diet of Group II was important to this group in 2 sample periods, but was not at all used by Group I during comparable sample periods between February 1973 and January 1974.

Perhaps the most striking intergroup variation in the pattern of use of specific food items was found in the use of the fruits of *Ficus exasperata* (Figure 6). There were periods when Group I used little or none of these fruits, but Group II used them more or less continually from February 1973 to January 1974 and always at a higher frequency than Group I. In addition to the fruits of *Ficus exasperata,* Group II also used its leaf buds and young leaves both of which were available to but not exploited by Group I. When the use of these fruits decreased, Group II took appreciable amounts of leaf buds from *Ficus exasperata*. Therefore, this species remained important in the diet of Group II through all sample periods except June 1973, but its importance in the diet of Group I was restricted to 3 sample periods. The more or less continuous use and importance of *Ficus exasperata* in the diet of Group II was in contrast to the restricted periods of importance of other food plants and specific food items used by both groups.

The number of specific plant food items used by Group II were usually fewer than those taken by Group I and the Shannon-Weiner indices of diet diversity (Wilson and Bossert, 1971), computed on the basis of proportionate use of specific food items, showed that in 9 of the 12 pair combinations of sample periods, the diet of Group II was less diverse than the diet of Group I (Table 6). During comparable sample periods, the number of mutually exploited specific plant-food items was generally low when compared to the total number of specific plant foods used by each group. Intergroup diet overlaps due to mutual use of specific plant foods ranged from 22.6 percent to 65.2 percent (mean = 40.1 percent) which, in view of all the variables of sampling methods, vegetation, and phenology of tree species may be considered to be usually low or moderate. In 3 pair combinations of sample periods, their diets overlapped by over 50 percent. In the April 1973/March 1973 pair combination of sample periods from Groups I and II respectively, 42.7 percent of the overlap was due to the use of *Celtis africana* fruits which were top-ranking specific food items for both groups (Tables 7 and 8). In the June 1973/May 1973 pair combination, the fruits of *Uvariopsis congensis,* the young leaves of *Diospyros abyssinica,* and the fruits of *Ficus exasperata* provided for much of the overlap, and in the November 1973/October 1973 sample periods about 48 percent of the overlap was due to the fruits of *Teclea nobilis* which were top-ranking specific food items in the diet of both groups.

Both groups exploited appreciable quantities of several categories of foliar food items. Among the top 20 food plants in the diet of Group I, 9 species (*Premna angolensis, Markhamia platycalyx, Dombeya mukole, Monodora myristica, Vangueria apiculata, Neoboutonia macrocalyx, Clausena aristata, Illigera pentaphylla,* and *Milletia dura*) were either used solely for foliar food items or more frequently exploited for these than for fruits (Table 2). In the diet of Group II, 4 species among the top 20 (*Diospyros abyssinica, Markhamia platycalyx, Clausena aristata,* and *Illigera pentaphylla*) were similarly used (Table 3). The relative importance of foliar food items was also indicated by the fact that during several periods of observations on both groups foliar

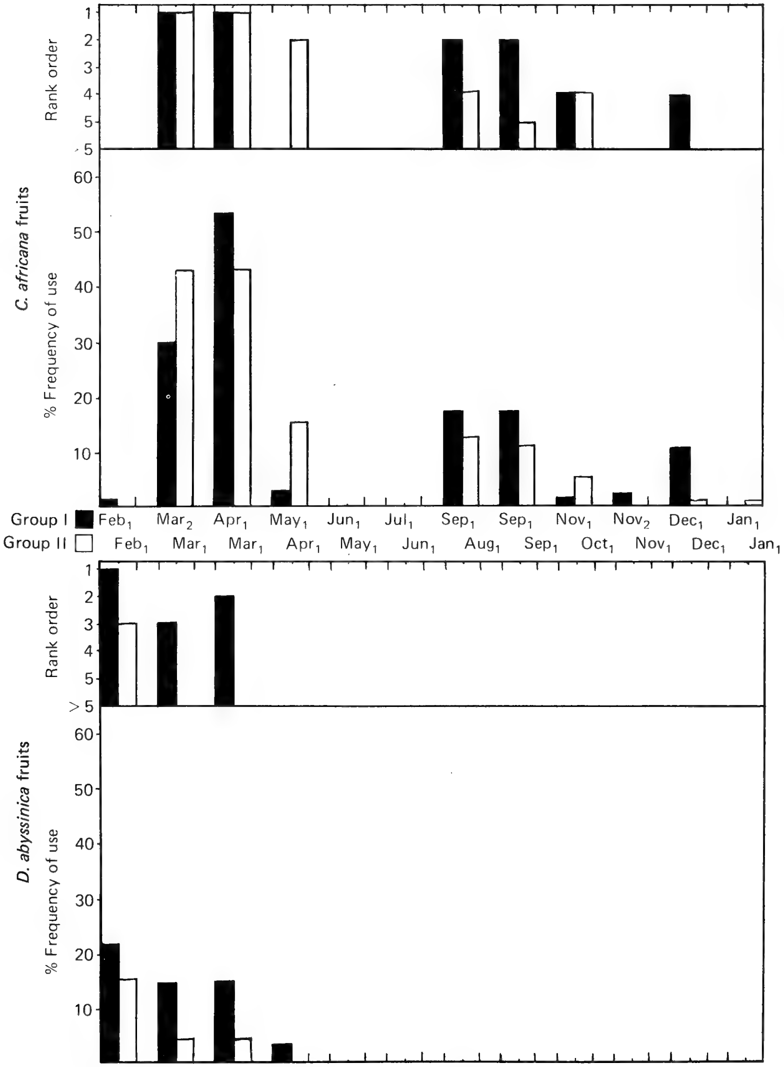

Figure 3. Rank order and frequency of use of the fruits of *Celtis africana* and *Diospyros abyssinica* by Groups I and II during comparable sample periods.

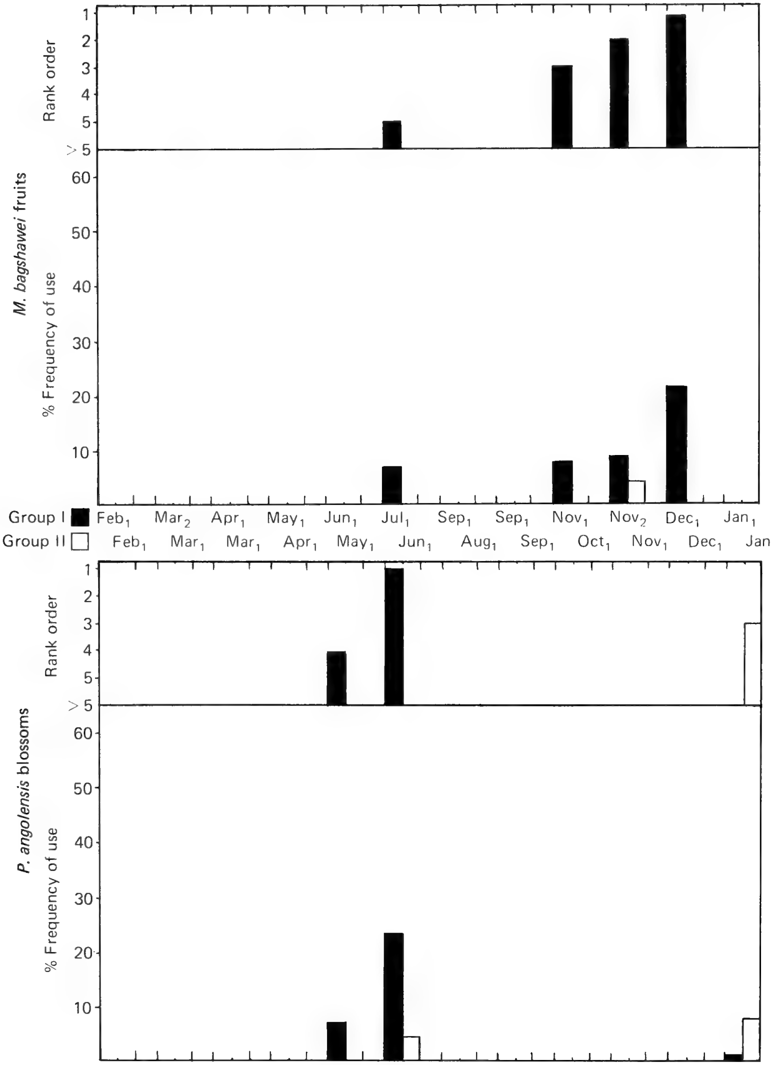

Figure 4. Rank order and frequency of use of *Mimusops bagshawei* fruits and *Premna angolensis* blossoms by Groups I and II during comparable sample periods.

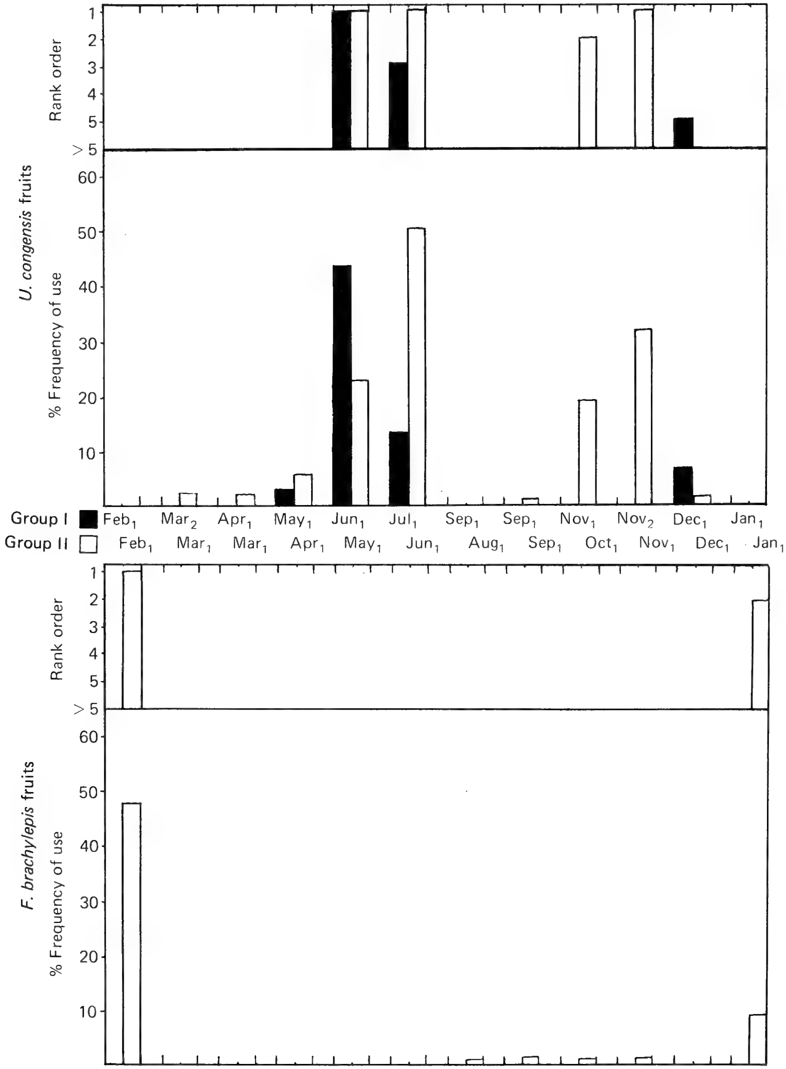

Figure 5. Rank order and frequency of use of the fruits of *Uvariopsis congensis* and *Ficus brachylepis* by Groups I and II during comparable sample periods.

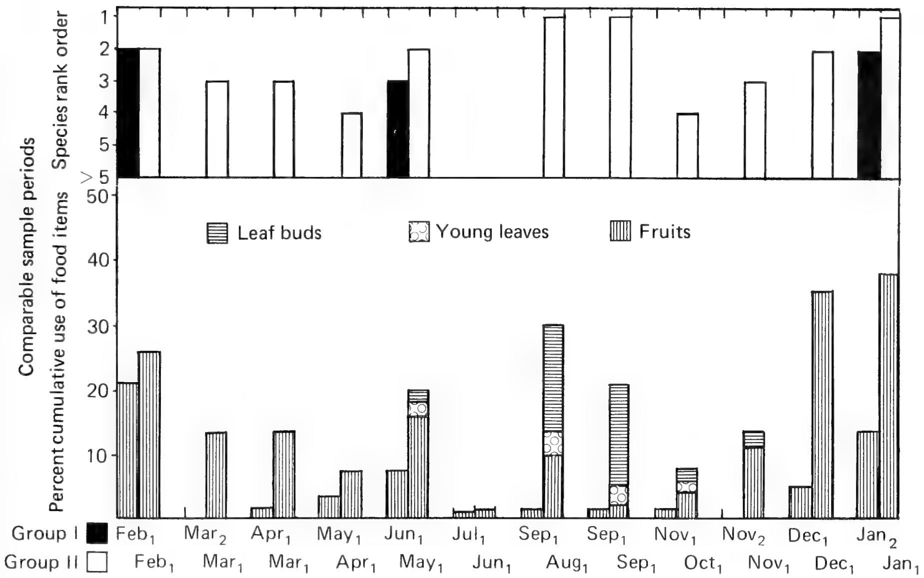

Figure 6. Frequency of use of food items from *Ficus exasperata* and rank order of its importance in the diet of Groups I and II during comparable sample periods.

food items exploited from different species were included among the top 5 ranks (Tables 7 and 8).

Of a total of 23 sample periods recorded from Group I, foliar foods were top-ranking items in 7 sample periods and their use was greater than that of fruits and invertebrates in 11 and 13 sample periods respectively (Table 9). In Group II, foliar items were top-ranking items in 3 of 18 sample periods and the frequency of use of foliar food was greater than the use of fruits and invertebrates in 3 and 8 observation periods respectively (Table 10). This suggests that foliar food items were more important in the diet of Group I than in the diet of Group II, which was also indicated in the comparison of their vegetable diet (Tables 2 and 3). Since fruits often occupied top rank and were usually taken at high frequencies, they must be considered the most important component of the diet of both groups. When fruits did not occupy this rank, foliar food occupied this rank more often than invertebrate food and their mean percentage frequency of use shows that they were taken at least as frequently as invertebrate food (Tables 9 and 10). The importance of foliar food is also shown by the fact that in both groups they were top-ranking food items during successive months from March to May 1974 when they constituted over 40 percent of the diet of Group I and 38 percent of the diet of Group II.

Both groups used foliar-food items more frequently than invertebrate food in May 1973 and around July 1973-September 1973 and February 1974-April 1974. Invertebrate food was used more frequently than foliar food by Group I from September 1973 to December 1973 and by Group II from October 1973 to January 1974 and again in June 1974 and August 1974. This suggests that foliar-food items and invertebrates show a somewhat irregular periodicity of relative importance in the diet of both groups.

Discussion

Intergroup variability in diet was expressed by the relatively low percentage of mutually exploited food plants and by differences in the total number of food plants used by each group. Since the difference between the total durations of group contact was small

Table 5.—Groups I and II - Percentage frequency of use of top 20 specific food items

Group I		*Group II*	
Rank order and specific food item	*Total % frequency of use*	*Rank order and specific food item*	*Total % frequency of use*
1 *Teclea nobilis* fruits	11.53	1. *Ficus exasperata* fruits	15.09
2 *Celtis africana* fruits	10.52	2 *Uvariopsis congensis* fruits	11.53
3 *Uvariopsis congensis* fruits	6.83	3 *Celtis africana* fruits	9.16
4 *Celtis durandii* fruits	6.52	4 *Celtis durandii* fruits	7.00
5 *Ficus exasperata* fruits	4.66	5 *Ficus brachylepis* fruits	6.63
6 *Diospyros abyssinica* fruits	4.55	6 *Teclea nobilis* fruits	4.36
7 *Mimusops bagshawei* fruits	3.85	7 *Funtumia latifolia* seeds	4.04
8 *Premna angolensis* blossoms	3.80	8 *Ficus exasperata* leaf buds	3.50
9 *Markhamia platycalyx* petioles	3.14	9 *Markhamia platycalyx* nectar	3.18
10 *Funtumia latifolia* seeds	2.88	10 *Markhamia platycalyx* petioles	2.96
11 *Diospyros abyssinica* blossoms	2.78	11 *Diospyros abyssinica* blossoms	2.69
12 *Diopsyros abyssinica* young leaves	2.68	12 *Diospyros abyssinica* young leaves	2.37
13 *Dombeya mukole* young leaves	2.07	13 *Monodora myristica* fruits	2.21
14 *Parinari excelsa* fruits	2.02	14 *Linociera johnsonii* fruits	2.10
15 *Vangueria apiculata* mature leaves	1.82	15 *Diospyros abyssinica* fruits	1.78
16 *Pancovia turbinata* fruits	1.72	16 *Chrysophyllum gorungosanum* blossoms	1.40
17 *Monodora myristica* leaf buds	1.62	17 *Premna angolensis* blossoms	1.24
(*Teclea nobilis* mature leaves 18 (*Neoboutonia macrocalyx* mature leaves (*Chaetachme aristata* fruits	1.37	18 *Ficus exasperata* young leaves	0.97
		(*Monodora myristica* blossoms 19 *Olea welwitschii* mature leaves	0.86
Total	77.10	Total	83.93

Table 6.—Indices of diet diversity and percentage overlaps in diet of Groups I and II

Comparable sample period		*Number of specific food items used*		*Indices of diet diversity*		*Number of specific items shared*	*% overlap in diet*
Group I	*Group II*	*Group I*	*Group II*	*Group I*	*Group II*		
Feb I 73	Feb I 73	20	8	2.2996	1.3455	3	38.2
Mar II	Mar I	14	12	2.0434	1.7319	4	41.8
Apr I	Mar I	22	12	1.7451	1.7319	4	56.4
May I	Apr I	38	27	3.1294	2.5340	11	34.7
Jun I	May I	22	25	2.1272	2.6369	10	53.5
July I	Jun I	25	20	2.4139	1.9214	11	39.0
Sept I	Aug I	24	15	2.5412	2.1733	7	35.4
Sept I	Sept I	24	16	2.5412	2.2159	8	38.7
Nov I	Oct I	15	15	1.3427	1.6993	6	65.2
Nov II	Nov I	20	20	1.7344	2.0934	6	22.6
Dec I	Dec I	23	19	2.4613	2.0501	9	26.4
Jan I 74	Jan I 74	30	25	2.9105	2.3894	13	29.3
						$\bar{X}$	40.1
						Range	22.6–65.2

Table 7.—Group I: Monthly percentage frequency of use of top 5 specific Plant Food Items during selected sample periods between February 1973 and January 1974

Month and sample period	*I*		*II*		*III*		*IV*		*V*	
Feb I 73	*D. abyssinica* fruits	22.15	*F. exasperata* fruits	21.48	*B. phoberos* blossoms	12.08	*P. excelsa* fruits	10.74	*A. altissima* blossoms	8.05
Mar II	*C. africana* fruits	30.00	*P. turbinata* fruits	20.67	*D. abyssinica* fruits	14.67	*C. durandii* fruits	10.00	*M. platycalyx* petioles	6.67
Apr I	*C. africana* fruits	53.33	*D. abyssinica* fruits	14.76	*P. excelsa* fruits	8.10	*M. platycalyx* petioles	7.62	*M. bagshawei* blossoms	4.29
May I	*C. gorungosanum* blossoms	16.13	*P. angolensis* leaf buds	12.90	*N. macrocalyx* mature leaves	6.45	*O. welwitschii* flower buds	4.84	*T. nobilis* mature leaves	4.03
Jun I	*U. congensis* fruits	43.06	*D. abyssinica* young leaves	13.40	*F. exasperata* fruits	7.66	*P. angolensis* blossoms	7.17	*T. nobilis* mature leaves	4.78
Jul I	*P. angolensis* blossoms	23.62	*D. abyssinica* blossoms	20.47	*U. congensis* fruits	13.38	*D. abyssinica* young leaves	8.66	*M. bagshawei* fruits	6.69
Sept I	*Clausena aristata* young leaves	20.49	*C. africana* fruits	17.21	*C. durandii* fruits	13.93	*D. mukole* young leaves	9.01	*M. platycalyx* petioles	6.55
Nov I	*T. nobilis* fruits	57.89	*C. durandii* fruits	24.34	*M. bagshawei* fruits	7.89	*F. angolensis* fruits *C. africana* fruits *I. pentaphylla* mature leaves	1.32		

(being less than 5 percent of the duration of contact with either group), this alone could not have caused the appreciable differences in the total number of food plants used by them during comparable sample periods. Differences in group size and visibility conditions within the 2 home ranges could be expected to affect the rate of collection of feeding observations and, therefore, the rate of discovery of the food plants of each group. The fact that the rate of collection of feeding observations from both groups was similar suggests that these factors were probably not important in causing intergroup food-plant diversity differences. Perhaps the effect of larger group size of Group I (Rudran, 1977) was nullified by the usually poorer visibility conditions within its home range which consisted entirely of mature undisturbed forest.

Intergroup food-plant diversity comparisons which consider all the food plants that 2 groups ever used would be independent of the above-mentioned variables. In the present study, the stage at which such comparisons could be made was closely approached when all observation periods on both groups were considered. Toward the end of the study, the rate of acquisition of new food plants by both groups had decreased greatly and during the last 200 hours of observations on each group, Group I and II acquired 9 and 3 new food plants respectively. The much slower rate of acquisition of new food plants by Group II suggests that their total food-plant list was better known than that of Group I, but at the end of observations Group II had exploited only 60 food plants while Group I had used 77 food plants (Rudran, in preparation). This would also suggest that food-plant diversity differences between the 2 groups were probably real differences rather than due to variables such as duration of group contact, group size, and conditions of visibility.

Selective felling operations for commercially valuable timber within part of the home range of Group II involved the removal of large tree species (e.g., *Parinari excelsa, Olea welwitschii, Aningeria altissima, Mimusops bagshawei,* etc.) which in the pro-

Table 8.—Group II: Monthly percentage frequency of use of top 5 specific plant food items during sample periods from February 1973 to January 1974 inclusive

Month and sample period	*I*		*II*		*III*		*IV*		*V*	
Feb I 73	*F. brachylepis* fruits	48.08	*F. exasperata* fruits	26.92	*D. abyssinica* fruits	15.38	*D. abyssinica* young leaves	5.77	*F. latifolia* seeds	2.56
Mar I	*C. africana* fruits	42.72	*F. brachylepis* fruits	19.25	*F. exasperata* fruits	13.62	*M. platycalyx* petioles	8.45	*F. stipulifera* fruits	5.16
Apr I	*D. abyssinica* blossoms	23.30	*C. africana* fruits	15.34	*C. gorungosanum* blossoms	12.50	*D. abyssinica* flower buds	8.52	*F. exasperata* fruits	7.38
May I	*U. congensis* fruits	22.15	*F. exasperata* fruits	16.11	*D. abyssinica* young leaves	8.72	*C. africana* leaf buds *F. latifolia* seeds	7.38	—	
Jun I	*U. congensis* fruits	49.43	*F. latifolia* seeds	12.07	*D. abyssinica* young leaves	8.05	*R. albersii* fruits	6.32	*D. abyssinica* blossoms	4.60
Aug I	*C. durandii* fruits	21.26	*M. platycalyx* nectar	18.11	*F. exasperata* leaf buds	16.54	*C. africana* fruits	12.60	*F. exasperata* fruits	9.45
Sept I	*C. durandii* fruits	18.14	*F. exasperata* leaf buds	17.21	*L. johnsonii* fruits	16.28	*M. platycalyx* nectar	16.74	*C. africana* fruits	11.16
Oct I	*T. nobilis* fruits	48.03	*U. congensis* fruits	18.42	*C. durandii* fruits	13.82	*C. africana* fruits	5.26	*F. exasperata* fruits	3.95
Nov I	*U. congensis* fruits	31.21	*C. durandii* fruits	26.11	*F. exasperata* fruits	10.83	*F. latifolia* seeds	7.01	*B. phoberos* fruits	3.82
Dec I	*F. exasperata* fruits	34.73	*M. myristica* fruits	24.55	*F. latifolia* seeds	10.18	*M. myristica* blossoms	7.78	*M. myristica* leaf buds and young leaves	3.59
Jan I 74	*F. exasperata* fruits	38.34	*F. brachylepis* fruits	9.33	*P. angolensis* blossoms	7.77	*M. platycalyx* fruits *C. africana* flower buds	5.70	—	
Nov II	*T. nobilis* fruits	56.04	*M. bagshawei* fruits	8.79	*C. durandii* fruits *F. latifolia* seeds	6.59			*D. mukole* young leaves	6.04
Dec I	*M. bagshawei* fruits	21.77	*F. latifolia* seeds	16.94	*M. myristica* leaf buds	13.71	*C. africana* fruits	10.48	*U. congensis* fruits	6.45
Jan 1 74	*V. apiculata* mature leaves	13.33	*F. exasperata* fruits	12.86	*F. latifolia* seeds	11.43	*Chaetachme aristata* fruits	7.62	*M. myristica* leaf buds	6.19

cess of coming down invariably destroy much of the lower story vegetation which included some of the important food plants of this group. Food items from *Aningeria altissima* and *Mimusops bagshawei* were very important food resources in the diet of Group I and therefore their removal must have seriously affected their use by Group II. The destruction of habitat provides at least a partial explanation for the less diverse nature of the diet of Group II, and the nutritional consequences of the reduction of food resources resulting from selective felling may have led to the apparent decline in group sizes in the selec-

Table 9.—*C. mitis* Group I: Percentage frequency of exploitation of plant and invertebrate food items

Month and sample period	*Foliar items*	*Fruits*	*Other plant items*	*Invertebrate food items*	*Total*
Feb I 73	5.0	57.2*	31.4	6.3	159
Mar I	5.5	75.5*	0.8	18.1	237
Mar II	17.1	70.4*	1.2	11.2	169
Apr I	10.9	66.9*	6.9	15.3	248
Apr II	21.1	58.3*	8.8	11.8	204
May I	30.6*	17.3	23.7	28.3	173
May II	30.1	33.2	1.5	35.2*	196
Jun I	25.4	41.7*	12.1	20.8	264
Jun II	5.2	73.6*	4.7	16.5	212
July I	22.6	21.3	39.3*	16.7	305
July II	37.8	11.4	41.3*	9.5	254
Aug I	35.7*	22.0	23.8	18.5	227
Aug II	42.9*	25.8	16.3	15.1	252
Sept I	33.2	22.8	10.3	33.7*	184
Oct I	18.6	50.0*	9.9	21.5	172
Nov I	3.5	71.5*	1.0	24.0	200
Nov II	8.7	63.0*	7.4	20.9	230
Dec I	13.9	42.2*	18.7	25.3	166
Jan I 74	47.6*	23.8	19.5	9.1	231
Feb I	30.6	25.7	33.6*	10.1	268
Mar I	49.6*	15.0	4.7	30.7	127
Apr I	63.9*	8.4	19.3	8.4	166
May I	40.9*	11.3	34.8	13.0	115
$\overline{X}$	26.1	39.5	16.1	18.3	

* *Indicates top ranking food item.*

tively felled areas (Rudran, 1977). The lowered frequency of use of the above species as well as some of the smaller species by Group II can be accounted for by selective felling, but it does not account for the fact that certain species (*Uvariopsis congensis, Markhamia platycalyx, Funtumia latifolia, Chrosophyllum gorungosanum*) which were found at lower densities within the home range of Group II were used more frequently by them (Table 4). Comparison of densities from the 2 home ranges also show that some important food plants (*Ficus exasperata, Ficus brachylepis, Celtis africana*) are found at higher densities within the felled area and some (*Celtis durandii, Premna angolensis*) are found at more or less equal densities in both areas. This shows that density differences between the 2 home ranges were not entirely due to selective felling and suggests that, at least in some respects, the study area was more heterogeneous prior to selective felling.

Oates (1974) and Struhsaker (1975) have documented the fact that the study area exhibited a great deal of vegetational heterogeneity. On the undulating terrain of the study area, species such as *Chaetachme aristata, Dombeya mukole,* and *Diospyros abyssinica* predominated the well-drained upper slopes while larger species like *Parinari excelsa* and *Mimusops bagshawei* were found most often on the lower slopes. In the water-logged valley bottom, trees such as *Symphonia globulifera* and *Neoboutonia macrocalyx* and semi-woody vegetation were most common. Thus, there was a conspicuous vegetational catena from ridge tops down the slopes to the bottom of valleys and different parts of the study area varied considerably in species density and composition.

These differences resulting from vegetational heterogeneity explain why both groups had exclusive access to certain species. For example, *Ficus dawei* and *Pseudospondias microcarpa* were found only

Table 10.—*C. mitis* Group II: Percentage frequency of exploitation of plant and invertebrate food items

Month and sample period	*Foliar items*	*Fruits*	*Other plant items*	*Invertebrate food items*	*Total*
Feb I 73	5.3	75.5*	2.1	17.0	188
Mar I	8.3	74.0*	1.6	16.1	254
Apr I	16.9	23.4	35.9*	23.8	231
May I	29.0	38.2*	12.9	19.9	186
Jun I	13.3	49.8*	22.7	14.3	203
Aug I	21.8	37.8*	21.8	18.6	156
Sept I	25.0	46.3*	16.8	11.9	244
Oct I	3.8	75.3*	2.7	18.3	186
Nov I	10.1	66.7*	6.4	16.9	189
Dec I	9.2	54.6*	16.9	19.3	207
Jan I 74	12.5	51.3*	22.3	13.8	224
Feb I	18.1	61.2*	5.2	15.5	116
Mar I	38.6*	15.7	28.8	17.0	153
Apr I	52.1*	24.9	3.9	19.1	257
Jun I	13.0	14.3	46.8*	26.0	77
Aug I	5.3	41.5	2.7	45.2*	188
Sept I	47.8*	32.0	5.7	13.5	334
Sept II	40.5	43.8*	2.0	13.8	153
X	20.7	45.9	14.3	18.9	

* Indicates top ranking food item.

within the home range of Group I, while *Ficus congensis* and *Drypetes battiscombei* were located only within the home range of Group II. These species were rare in the areas where they occurred and, except for *Ficus dawei,* were also infrequently used. *Ficus dawei* was the top-ranking food plant constituting nearly 35 percent of the diet of Group I during the second sample period of May 1973. Although this species does not occur in the food-plant list given in Table 2 which considers only selected sample periods most comparable to the observation periods of Group II, it exemplifies the profound intergroup differences that can be caused by the use of food plants available to only 1 group. In considering present density differences within the 2 home ranges, it is reasonable to assume that the densities of tree species that did not produce commercially valuable timber and were also large (e.g., *Ficus exasperata, Ficus brachylepis, Ficus dawei, Pseudospondias microcarpa,* etc.) would have been relatively unaffected by selective felling. Hence, any intergroup dietary variability caused by the exploitation of these species must be a reflection of density differences due to vegetational heterogeneity rather than due to selective felling. This is particularly true of large species that are presently found at higher densities within the selectively felled area (*Ficus exasperata* and *Ficus brachylepis*).

Ficus exasperata, provided for some of the greatest intergroup dietary variations through its markedly different patterns of use by both groups. A long-term phenological study of all individuals of this species found within both home ranges showed that asynchronous activity of individuals of this species provided both groups with 1 to 3 potential food items throughout all months of observations. During any particular month, however, the relative abundances of these items were much greater within the home range of Group II. Group I used only the fruits of this species, which were available only during certain periods within its home range, and therefore this species was important for restricted periods in its diet (Figure 6). Group II used all 3 food items from *Ficus exasperata* and its relative constancy of use and importance provided at least some of the intergroup dietary differences during every month. The continuous and relatively high frequency of use of this particular species was also probably responsible for the less diverse nature of the diet of Group II. *Ficus* *brachylepis* was another species that was an important food plant to Group II, but it was hardly ever used by Group I.

The diet of a group was not entirely dependent on the density of food plants found within its home range. For example, *Strombosia scheffleri* was a fairly common species within both home ranges, but it was very rarely used by the two groups, and the food plants they commonly used were exploited only for certain food items indicating that these groups were fairly selective feeders. Thus, their diet during any particular period was probably a result of this selectivity combined with the relative density of food plants and relative abundance of food items available from them.

Local variations in the phenological activity of a food plant also gave rise to dietary differences between the 2 groups. In November 1973, when *Uvariopsis congensis* became important in the diet of Group II (Figure 5) much of its feeding activity was centered around a grove of this species whose phenological activity was presumably out of phase with the majority of its individuals found within both home ranges. The variable patterns of use of *Premna angolensis* blossoms by the 2 groups were also probably due to differences in relative abundances of these blossoms caused by local variations in the activity of this species. The flowering activity of *Markhamia platycalyx* which was far more conspicuous within the home range of Group II provided an important food source (nectar) to this group during August 1973 whereas nectar was never important in the diet of Group I. This may have been due to the phenology of this species, but Struhsaker (1978) also provides evidence to suggest that these blossoms may have been less readily available to Group I owing to the more intense interspecific competition particularly with the red colobus (*Colobus badius tephrosceles*) that also used the home range of Group I. The red colobus, being best adapted to old mature forest, were found at higher densities within the home range of Group I than Group II (Struhsaker and Oates, 1975). The heavier predation of *Markhamia platycalyx* blossoms within the home range of Group I and its effect on fruit crop size (Struhsaker, 1978) was probably responsible for the fact that the fruits of this species were used only by Group II.

Comparison of the diet of blue monkeys in Kahuzi-Biega National Park, Zaire (Schlichte, 1978) and the Kibale Forest show that only 5 food plants (*Albizzia gummifera, Milletia dura, Symphonia globulifera, Basella alba, Strombosia scheffleri*) were common to both populations, and these food plants were sometimes exploited for different food items. Interpopulational differences that were found in the diet of several primate species (see Chalmers, 1968; Gartlan and Brain, 1968; Aldrich-Blake, 1970a and b; Clutton-Brock, 1972; Oates, 1974; Dunbar and Dunbar, 1974) were probably mainly due to differences in the floristic composition and phenological patterns between widely separated areas. Apparently these factors were also partly responsible in causing intergroup dietary differences in the Kibale Forest, which should perhaps be expected in view of the relatively complex and diverse nature of the habitat.

Cercopithecines have been variously classified as opportunistic omnivores (Struhsaker, 1967, 1969), arboreal frugivores, frugivore-omnivores (Eisenberg, Muckenhirn, and Rudran, 1972) and frugivore-insectivores (Dittus, 1974). The broad ecological categories used to describe their diet sometimes obscures the varying degrees of importance of different dietary components which in the case of sympatric cercopithecines could cause substantial differences between their feeding niches. In the Kibale Forest *Cercopithecus mitis* is sympatric with 3 other species of cercopithecines, namely *C. ascanius, C. lhoesti,* and *Cercocebus albigena*. Although *C. mitis* and *C. ascanius* and *C. albigena* are mainly frugivorous and supplement their diet with invertebrate food, the folivorous tendency of *C. mitis* strongly contrasts its diet with that of *C. albigena* which uses only 5.4 percent of foliar food (Waser, in press). The diet of *C. mitis* and *C. ascanius* differ in that the latter species uses a higher proportion and also a wider spectrum of invertebrate food (Struhsaker and Rudran, in preparation). Very little is known of the diet of *C. lhoesti,* but the dental structure of this species (see Kay and Hylander, 1978) indicates that it may be the most folivorous of the 4 cercopithecines found in the Kibale Forest. Similar differences were found between the diets of *Cercopithecus pogonias, C. cephus,* and *C. nictitans* which are sympatric in Gabon, West Africa (Gautier-Hion and Gautier, 1974). Although they were mainly frugivorous, *C. pogonias* was the most insectivorous, while *C. nictitans,* which belongs to the same superspecies as *C. mitis* was the most folivorous in food habits.

In view of the possible interspecific competition between *Colobus badius* and *C. mitis,* examination of their diets provides some useful comparisons. Dietary differences between the 2 species are shown by the variable proportions of food items, especially fruits and petioles used by them (compare Table 2 here and Struhsaker's Table 1, 1978). Also, many important food plants of *C. mitis* were either not used by *C. badius* or used infrequently and sometimes for different food items. Similarities are found in the many mutually exploited food items from *Celtis africana* and *Markhamia platycalyx*, both of which were relatively important in the diet of the 2 species and the fact that 32 food plants (over 50 percent) of *C. mitis* were also used by *C. badius*. Direct interspecific dietary comparisons cannot be made from their food lists given in this volume since the periods of observations were different, but in general their diets seem to bear greater similarity than the diets of *C. mitis* and *Colobus guereza* living in the same area. The diet of *C. guereza* consists of nearly 35 percent of *Celtis durandii* young leaves (Oates, 1974) which was not used as a food item by *C. mitis*.

The relatively small cecum of the blue monkey suggests that this species may be quite inefficient in digesting and probably derives little nutritional benefit from the use of foliar material. Therefore, periods when foliar material were frequently used food items probably reflect times when more nutritious food items such as fruits and invertebrates were in short supply. Several studies have stressed the fruit and insect components of the diet of cercopithecines (Gartlan and Brain, 1968; Jones and Sabater Pi, 1968; Bourliere et al., 1970), but Ellefson (1968) has pointed out that the seeming abundance of plant food in a tropical rain forest is partly illusory and this is especially so in the case of fruits which tend to be produced more or less seasonally. There is also some evidence that insect populations of the tree canopy undergo seasonal fluctuations in tropical forests (Smythe, personal communication; Leigh and Smythe, 1978). Therefore, when these items are scarce, species that largely depend on them either have to rely on more readily available supplementary foods such as leaves or range over extensive areas at relatively high-energy cost. In the Kibale Forest the large-bodied and mainly frugivorous species, such as the mangabey (*C. albigena*), have large home ranges and cover extensive areas in search of fruits and invertebrates while the smaller species such as the blue monkey, being limited to relatively small home ranges, rely heavily on leaves when more nutritious items are in short supply. Freeland and Janzen's hypothesis (1974) suggests that by incorporating foliar food into the normal diet, the blue monkeys may maintain certain enzymatic pathways which are periodically very important in degrading noxious compounds taken along with foliar food.

Summary

A field study of the ecology and behavior of blue monkeys was conducted in the Kibale Forest, Uganda, between November 1972 and October 1974 inclusive. Much of the time in the field was spent with 2 groups of blue monkeys (Group I and II) whose home ranges were situated about 500 m apart. Dietary differences between these 2 groups were expressed as differences in the total number of food plants used and the pattern and frequency of use of important food plants and food items. The number of food plants common to the diet of both groups amounted to only 45 percent of the total used by both groups. The monthly diet of Group I was usually more diverse than that of Group II and overlaps in their diets were either low or moderate ($\bar{X} = 40.1$ percent, range 22.6 —65.2 percent). Dietary differences between the 2 groups can be explained by tree species density differences between the home ranges (caused by vegetational heterogeneity and selective felling within the home range of Group II) and by local variations in the phenological activity of food plants. Different degrees of interspecific competition within the 2 home ranges may also have given rise to some dietary variability between the 2 groups.

Although blue monkeys are generally regarded as frugivores or frugivore-insectivores, it was found that leaves and parts of leaves form an appreciable proportion of their diet. The monthly frequency of use of foliar food was often greater than the use of invertebrate food and sometimes greater than the use of fruits. The folivorous tendencies of blue monkeys were probably important in causing a substantial separation of their feeding niches from those of other cercopithecines found in the Kibale Forest.

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The Ecology of Two Groups of Blue Monkeys, *Cercopithecus mitis stuhlmanni*, in an Isolated Habitat of Poor Vegetation

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Introduction

The distribution of the blue monkey extends from west Africa through central Africa to the coast of east and southeast Africa (Gartlan and Brain, 1968). Their habitats include a variety of vegetation forms: swamps, mountains, coastal forests, gallery forests, and cultivated forests, such as the exotic soft-wood forest of Mount Kenya (Omar and deVos, 1970). This presents an excellent opportunity for the study of arboreal primates under a variety of ecological conditions.

The study area is located in the western mountain range of the African rift valley in the Kahuzi-Biega National Park on the shores of Lake Kivu (1460 m) (Figure 1), near the Institute pour la Recherche Scientifique en Afrique Central (IRSAC), situated 40 km north of Bukavu. A strip of vegetation approximately 100 m wide ran along the small Lwiro River at a height of about 2000 m, at one point forming a deep valley which at the end joined the extensive mountain forest of the park (Figure 2). The area was bordered on one side by a cultivated meadow, on the other, by cleared and burned slopes from which I was easily able to locate and observe the monkeys. In spite

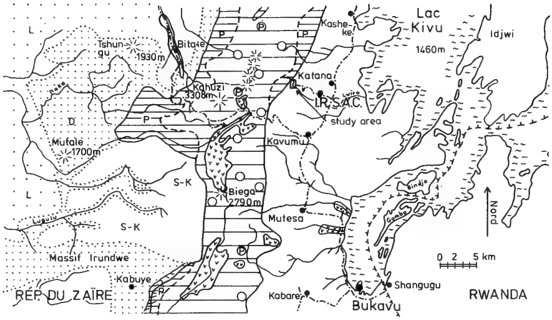


Figure 1. Vegetation of the Kahuzi-Biega National Park (according to a map (1:50,000) of A. Leonard, 1957-58), and the location of the study area. Thin lines = rivers; dashed-stippled lines = streets and roads; thick and dashed lines = boundaries of vegetation; large black dots = towns and villages. Vegetation: wide hatched area = mountain forest of high altitude with *Arundinaria alpina;* narrow hatched area (P) = mountain forest of high altitude with *Podocarpus* division; narrow stippled (D) = mountain forest of middle altitude with *Drypotes* division; wide stippled = mountain forest of low altitude with *Lebrunia bushaie*, etc.; areas with small hooks = swamps with *Cyperus latifolius*; empty areas (S-K) = savannah with *Setaria sphacelata* and *Kotschya africana*.

of its exceptional vegetation composition and isolation, the study area can be considered a natural habitat of the blue monkeys to which they have successfully adapted. Description of the vegetation and climate conditions have appeared elsewhere (Schlichte, 1975).

Methods

I started intensive systematic observation in June 1972, but was forced to break off in November of the same year, due to transfer of the program in which the study took place.

For quantitative data collection, the monkeys were observed continuously in weekly intervals over a period of 12 hours (from 12 noon to 6 P.M. and on the following day from 6 A.M. to midday), at a distance of 30 to 50 m (maximum 200 m) by means of binoculars (10 × 40). In addition, protocols of the activities, neighbors, food, and other relevant information were recorded for each visible individual on a cassette recorder every 5 minutes, resulting in 5-minute units for each animal. These units were summarized as needed. For feeding habits, the data for the whole day (12 hours) were added.

The fundamental difficulties in collecting data on arboreal primates have been discussed by Aldrich-Blake (1970b) and Schlichte (1975). The main problem is that not all animals in the group are visible at the same time. The quantitative data then could be influenced by certain activities during which the monkeys are more likely to be seen or by certain group members which are more active than others. The effects of some factors were analyzed, based on my knowledge of the individual monkeys.

Five minutes was the shortest period of time in which I could record the activities of all group members, keeping the group constantly in view. In addition, I was able to locate the group each day at midday and evening, between the 12-hour observation periods. In this way an additional 1- to 2-hours of observation daily supplemented the weekly systematic observations (Table 1).

Results

SPATIAL UTILIZATION. In locating the group twice daily and during the 12-hour observation periods every half hour, I obtained the information which allows a determination of the areas inhabited by the groups. Group A occupied Zones I to XII; Group B, Zones V to VII and XII to XVII, each about 25 ha (Figure 2). The two living areas were found to overlap about 11 ha. Group C was also seen in parts of the areas of both A and B, in Zones VII to XII.

GROUP COMPOSITION. Group A was composed of 1 large male, 2 smaller males, 2 big females (1 of which could be identified by a missing right lower leg), 2 smaller females, 2 juveniles and 1 infant. Group B consisted of 11 animals, with 1 big male and 1 infant. Group C had 16 animals, with 1 big male and 2 infants.

SLEEPING PLACES. The group members slept alone or in groups of twos and threes scattered throughout the trees and bushes at distances of up to 30 m apart. A preference for certain trees was not determined. Figure 2, however, indicates a concentration of sleeping places in certain regions.

VERTICAL STRATIFICATION. The blue monkeys observed occupied mainly the middle layer of the canopy. Of 7945 5-minute observation periods of Groups A and B, 51 percent were in the canopy, 48 percent at shrub level, and 1 percent on the ground (Table 2a). The groups moved along the ground and crossed open areas with no vegetation quickly and in closed formation. Group B was seen for days at a time feeding in the 1- to 2-meter shrubs outside of their home range (see below). A specific pattern of

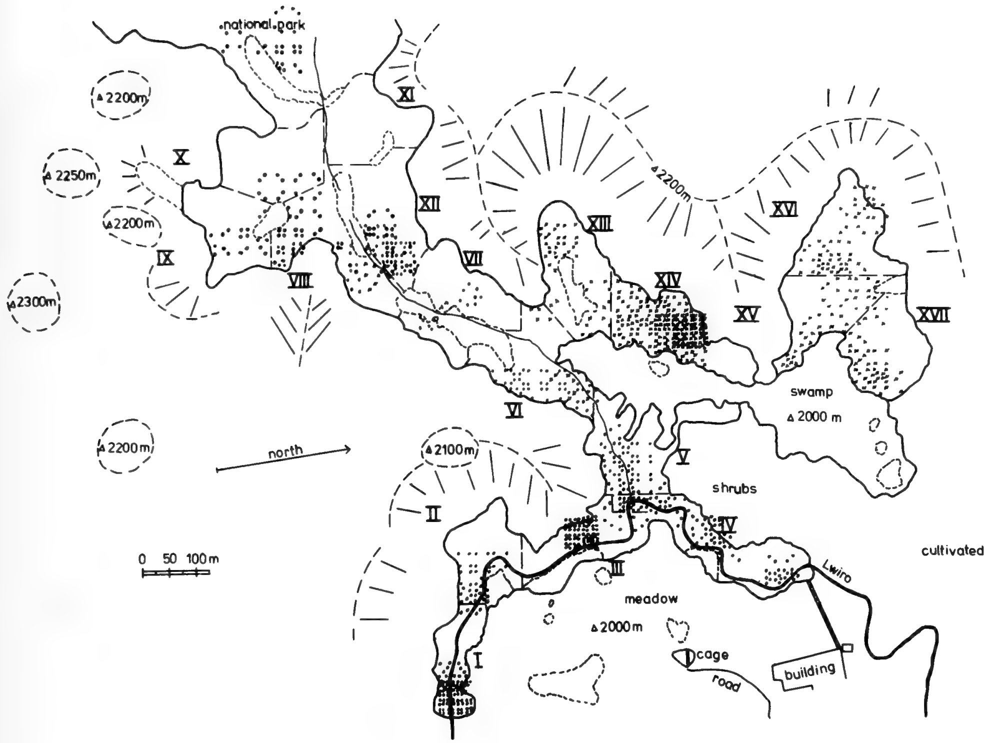


Figure 2. Study area and distribution of sleeping places of Group A (●), Group B (x) and Group C (○). Two of the symbols mark the place in which the group or at least 1 member has been observed. The boundaries of the Zones – –XVII = long broken lines. The empty areas enclosed by short broken lines are swamps, clearings, or secondary vegetation; mountain ridges = middle broken lines; slopes = long lines; river or creek = thick or thin lines.

preference for a certain height for various activities (for example, resting) may exist, but there were no statistically significant differences. From Table 2a, it appears that during the rainy season Groups A and B prefer the shrubs while during the dry season they like to stay in the canopy. Only for the rainy season are data available to analyze the preference of Group A for certain heights during various activities (Table 2b). It seems that Group A prefers the shrubs for resting, moving and social behavior, but at the same time looks for food mainly in the canopy. For statistical treatment, additional data are necessary.

RELATIONSHIP TO NEIGHBORING GROUPS. The groups tolerated the presence of neighboring groups at relatively close distance. On 3 days (16.10, 3.11, 12.11), for example, it was observed that Groups A, B, and C retired to sleeping places in the overlapping areas, each at a distance of about 50 m. On these encounters and on the ones during 3 other occasions (17.8, 27.9, 22.10), no interactions or vocalizations that could be related to threatening, or other aggressive behavior occurred. One excited encounter of Groups A and B was recorded on January 9. This relatively peaceful reaction against strange blue monkeys in the home range stands in contrast to the results of an experiment carried out in the area of Group A. Upon encountering 3 young male captive animals, which had been set out the previous evening in the center of the home area, the large male of Group A pursued the strangers until these monkeys, frightened and

Table 1.—Total observation Time during each of the Months of the Study.

Group	*Mar.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Total*
				Observation Time (5-minute protocols)					
A	—	1020	1800	1440	1080	1560	2520	300	9720 min
B	—	540	1380	1440	720	—	—	—	4080 min
C	—	—	—	—	—	—	120	—	120 min
Sum	—	1560	3180	2880	1800	1560	2640	300	13920 min

Group	*Mar.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Total*
				Observation Time (written protocols of general terms)					
A	—	1140	1140	1560	1200	840	1890	840	8610 min
B	480	510	960	1500	720	540	1380	450	6540 min
C	—	270	—	—	60	30	270	270	900 min
Sum	480	1920	2100	3060	1980	1410	3540	1560	16050 min

Table 2a.—Vertical Stratification: Number of 5-minute Periods during the Study in which Blue Monkeys were observed at certain Heights above the Ground. Ground = 1 m, Shrubs = 1–10 m, Canopy = 10 m.

			Ground		*Shrubs*		*Canopy*		*Sum*	
Group	*Period*	*Date*	*5-min*	*%*	*5-min*	*%*	*5-min*	*%*	*5-min*	*%*
A	Summer n = 4	7/7–1/9	9	—	1014	43	1318	56	2341	100
B	Summer n = 4	14/6–24/8	42	2	813	36	1418	62	2273	100
A	Winter	13/9–25/10	30	1	1998	60	1303	39	3331	100
Total			81	1	3825	48	4039	51	7945	100

Table 2b.—Vertical Stratification for Group A during the Winter Period.

Group A Winter 13/9–25/10 n = 5	*Ground 5 min*	*%*	*Shrubs 5 min*	*%*	*Canopy 5 min*	*%*	*Sum 5 min*	*%*
Resting	7	1	767	66	393	33	1167	100
Moving	16	2	620	79	145	19	781	100
Social behavior	—	—	237	77	70	23	307	100
Feeding	7	1	374	35	695	64	1076	100
Total	30	1	1998	60	1303	39	3331	100

badly bitten, were able to hide themselves. The other group members did not participate in the chase.

BEHAVIOR TOWARD OTHER *CERCOPITHECUS* SPECIES. For a short period of time, Group B formed a mixed group (polyspecific association) with a group of *Cercopithecus l'hoesti* which was passing through. All but 1 female and the large male joined the *C. l'hoesti* group and moved with them, usually near the ground. The remaining *C. mitis* remained in the canopy and middle layer. Juveniles of both species played together.

Blue monkey groups did not show any visible reaction toward groups of baboons (*Papio anubis*).

MOVEMENTS. The distance covered by the group was recorded every half hour for each observation day. The distance was measured in so-called distance units (ca. 33m = one unit). The subsequent locations of the groups were marked on an aerial photograph and the distance then expressed in units by means of a grid pattern placed over the photograph. Group A moved an average of 18 ± 6 units (n = 9) daily. The animals tended to avoid regions which they had visited on the previous day, moving regularly back and forth within their beltlike home range. Omar and DeVos (1971) described the same behavior by *C. mitis kolbi,* Sykes monkey, in Kenya. The average distance for each half hour of the day is given in Figure 3. An impressive maximum of moving activity is to be seen at about 4 P.M. Other smaller peaks are between 6 and 7 A.M., 9 and 10 A.M., and at about noon. A resting period is between 1 P.M. and 3 P.M.

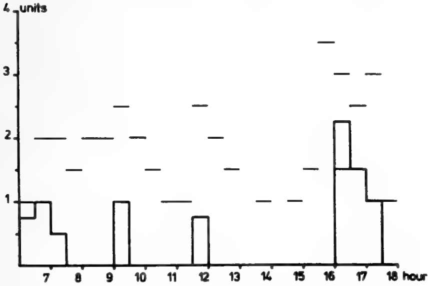


Figure 3. Median of traveled distance per half hour of Group A for 12 observation days. The distance in units: one unit = about 33 m. The thin lines are 95 percent confidence intervals.

FEEDING BEHAVIOR. The distribution of trees and shrubs within the zones of the study area are included in Table 3a. A list of the more important plant species is included in Table 3b. Table 4 lists plants and plant parts which were eaten during the observation period from May to November 1972.

FLOWERS, LEAVES, AND FRUITS. The blue monkeys selected certain parts of the fruits, leaves, and blossoms on which they fed. For example, from 1 leaf they ate only the stem or vein of the leaf; from others, they chose only the immature leaves or buds. From blossoms, they chose the bases. In certain plants, more than 1 part served as food: from *Albizzia gummifera,* the fruits and buds; from *Milletia dura,* the fruits, buds, and flowers. A detailed description of feeding behavior on various edible plants has been published elsewhere (Schlichte, 1975). A short description of the feeding behavior on the 3 most important plants follows.

- ALBIZZIA GUMMIFERA: Blue monkeys ate the fruits of *A. gummifera,* a 15 to 25 m tree with pinnate leaves, yellow-white flowers, and fruit pods 10 cm long. The monkeys, sitting on a branch, opened the pods at the tops and ate the fruits directly with their mouths. Usually, only a part of the fruit was eaten. The pod was then dropped and fell to the ground, similar to a parachute, turning propeller-like on its own axis. The pods, when opened artificially, possess an advantage in flight ability compared to the pods which normally remain closed. Without doubt, the blue monkeys contribute in this way to the distribution of *A. gummifera.* In addition to the fruits, the buds as well as the flowers were eaten.
- MILLETIA DURA: *Milletia dura* (Papilionaceae) is a tree, 10 to 15 m tall, with pinnate leaves, fruit pods of 10 cm, and blue-to-red flowers 2 cm long. The pods were eaten in the same manner as with *Albizzia.* The buds were also eaten. Flowers were eaten more often and in greater amounts than those of *Albizzia gummifera.* The monkeys picked the blossoms and stuck the base into their mouths first, as though to suck on them. The petals were spat out.
- BRIDELIA BRIDELIIFOLIA: This bush-like tree (about 5 m tall) with strong elliptical leaves provided fruit to the monkeys. The fruits consist of green, fleshy elliptical berries, 1 cm in length, which contain numerous seeds 2 mm in diameter. The berries sit spike-like on the ends of small twigs. The monkeys pulled these twigs toward them and picked off the berries with their mouths. When overripe, the berries are brown and rotten and were no longer eaten by blue monkeys. The shoots and buds were also eaten frequently.
- BAMBOO (*Arundinaria alpina*): Outside the area of study, in regions where bamboo commonly grows, blue monkeys were known to eat its seeds, young leaves, and shoots. It is not known up to what age of the shoots feeding is done. A reconstruction, by means of the plant remnants, indicates that the tips

Table 3a.—Frequency of Occurrence of the most important Tree and Shrub Species in Zones I to XVII. Scientific Names of the Plants are abbreviated; full Names are given in Table 3b. SE = secondary, SK = sclerophyl, M = mesophil Vegetation.

	Alb	*Sap*	*Mac*	*Mil*	*Syz*	*Bri*	*Mae*	*Con*	*Neo*	*New*	*Nau*	*Dich*	*Sym*	*Pol*	*Myr*	*Par*	*Dom*	*Hag*	*Chr*	*Size of each Zone (ha)*	
Occurrence	*SK*	*?*	*SE*	*?*	*?*	*?*	*SE*	*M*	*SE*	*M*	*?*	*M*	*M*	*SE*	*M*	*M*	*SE*	*SE*	*M*		
mean height in m	*10–12*	*5–6*	*5–6*	*5–6*	*3–4*	*3–4*	*3–4*	*3–4*	*5–6*	*10–12*	*3–4*	*3–4*	*10–12*	*5–6*	*10–12*	*10–12*	*5–6*	*5–6*	*10–12*		
Zone I	15	8	15	10	15	7	6	—	3	6	—	—	11	—	4	—	—	—	—	100	1.3
II	14	9	9	7	7	7	8	—	1	—	—	4	—	—	1	—	—	—	—	67	1.7
III	15	23	15	18	24	5	—	1	3	3	—	7	—	—	2	—	—	—	—	116	1.6
IV	13	37	5	33	10	19	—	—	6	—	4	—	—	—	2	1	7	—	—	137	2.3
V	10	18	9	3	24	4	—	1	—	3	13	10	2	—	—	1	1	—	—	99	2.4
VI	20	11	6	2	8	5	—	7	5	5	9	3	1	1	2	2	—	2	—	89	2.3
VII	11	11	15	16	—	7	9	5	4	—	1	2	—	1	—	—	—	2	—	84	1.9
VIII	25	21	13	11	—	3	7	5	6	—	—	—	—	2	—	—	—	—	—	93	2.1
IX	15	5	7	4	—	—	6	3	3	5	1	—	2	8	1	1	—	1	—	62	2.0
X	15	3	7	2	—	—	4	5	—	10	—	—	3	3	—	1	—	—	—	53	2.4
XI	10	4	5	—	—	—	—	12	—	5	—	—	8	3	1	5	—	—	2	55	2.0
XII	16	11	20	1	—	—	3	9	—	6	—	—	1	2	1	2	—	—	—	72	2.4
XIII	12	8	12	9	1	10	4	—	3	—	—	—	—	1	—	—	1	1	—	62	2.1
XIV	20	25	33	2	22	12	—	3	—	—	10	12	3	—	2	4	—	—	—	148	2.4
XV	23	20	13	—	6	3	5	3	3	—	4	4	2	1	1	2	—	—	—	90	2.0
XVI	23	16	13	11	—	6	7	1	13	—	1	—	—	—	2	—	4	—	—	97	2.2
XVII	16	25	7	35	—	15	6	2	5	—	—	—	—	—	—	—	2	—	—	113	2.1
Sum	273	255	204	164	117	103	65	57	55	43	43	42	33	22	19	19	15	6	2	1537	35.2

of the young plants were split open and the contents eaten.

BARK. Many authors (Omar et al., 1970) have indicated that guenons feed upon bark, thus under certain circumstances damaging cultivated forests. This behavior was not seen among the blue monkeys, who occasionally chewed, but did not eat a piece of the bark of *Albizzia gummifera*. *Urera* was also chewed and spat out; however, this behavior cannot be clearly distinguished from the behavior when feeding on arthropods, as was described by Bourliére et al. (1970) for *Cercopithecus campbelli lowei*.

ARTHROPODS. Small animals and all species of arthropods, especially insects, were eaten. I was able to record the typical behavior in catching arthropods by observing 3 male blue monkeys which were kept in cages on the institute grounds. The monkeys investigated every crack and removed the arthropods with their fingers. The arthropods found in old leaves and under tree bark which had been removed from the trunk were eaten directly with the mouth. The monkeys caught flies in the air with their hands. Spiders were preferred, but grasshoppers and the praying mantid were also eaten. In one instance, these monkeys consumed a young bird which they had stolen from a house cat. In the field, I observed members of Groups A and B as they searched for arthropods by investigating old leaves, bark, and tree trunks. I was able to record in 5 instances that the arthropods were actually eaten. The search for arthropods was easy to distinguish from foraging.

DRINKING. Blue monkeys were never seen drinking at open water holes on the ground. The monkeys probably lick water from the leaves or tree holes (Bourliere et al., 1970). When the monkeys seemed to lick water running down the trunks of the trees after a rainstorm, I scored this as drinking behavior.

GROUP SPECIFIC FOOD PREFERENCE:

Kotschya africanum—Only Group B was observed to feed on the yellow flowers of this shrub-like, man-sized plant, which grew on the cleared slope bordering the study area, in competition with *Pteridium africanum* (a fern). Group B advanced far into this region, moving partly on the ground, partly springing from bush to bush. Here, they remained for a week during the day, returning to the forest area at night. Group A was never observed eating the *Kotschya* flowers, although these plants on the cleared slopes could easily be reached from their position. We have

Table 3b.—Scientific Names of Plants occurring in the Study Area.

Genus	*Species*	*Family*
Trees		
1. Albizzia	gummifera	Mimosaceae
2. Sapium	ellipticum	Euphorbiaceae
3. Macaranga	kilimandcharica	Euphorbiaceae
4. Milletia	dura	Papilionaceae
5. Neoboutonia	macrocalyx	Euphorbiaceae
6. Newtonia	buchanii	Mimosaceae
7. Symphonia	globulifera	Guttiferaceae
8. Polyscias	fulva	Araliaceae
9. Myrianthus	holstii	Moraceae
10. Parinari	holstii	Rosaceae
11. Dombea	goetzenii	Sterculiaceae
12. Hagenia	abyssinica	Rosaceae
13. Chrysophyllum	sp.	Sapotaceae
14. Albizzia	grandibracteata	Mimosaceae
15. Lebrunia	bushai	Guttiferaceae
16. Myrica	salicifolia	Myricaceae
17. Bersama	ugandensis	Melianthaceae
Shrubs		
18. Chasalia	subochreata	Rubiaceae
19. Syzygium	guineense	Myrtaceae
20. Bridelia	brideliifolia	Euphorbiaceae
21. Bridelia	micrantha	Euphorbiaceae
22. Maesa	lanceolata	Myrsinaceae
23. Conopharyngia	durissima	Apocynaceae
24. Nauclea	sp.	Rubiaceae
25. Dichaethanthera	corymba	Melastomaceae
26. Canthium	hispidum	Rubiaceae
27. Galiniera	coffeoides	Rubiaceae
28. Mitragyne	rubrostipulata	Rubiaceae
29. Allophyllus	griseotomentosa	Rubiaceae
30. Alchornea	hirtella	Euphorbiaceae
31. Kotschya	africana	Papilionaceae
32. Xymalos	monospora	Monimiaceae
33. Cyathea	manniana	Cyatheaceae

here an instance of a group specific food preference.

Pennisetum purpureum—It is also of interest to note that only Group B ate the *Pennisetum purpureum,* in the same manner that was observed with captive monkeys. This plant, growing on damp ground and abandoned garden plots, was regularly fed to the primates (guenons, chimpanzees, and gorillas) kept in cages on the institute grounds. The blue monkeys sat on the poles and with both hands broke the shaft two-thirds of the way up and pulled it apart, thus obtaining the young leaf inside. The monkeys in Group B employed the same method in feeding on *P. purpureum* found on the border of their area.

Quantitative Analysis

Description of food preference

The results of the quantitative analysis for 12 observation days are presented as corrected raw data in Table 5. An adjustment of the data was necessitated by the fact that the visibility of the monkeys varied according to the type of vegetation (shrubs versus trees). A visibility of 50 percent was assumed for the majority of the plant species which were being eaten. This value has been obtained by rounding off the estimation of the total activity observed (sum of column vis., Table 5c). A visibility of 90 percent was assumed only for those plants in which the monkeys were easy to locate: *Albizzia gummifera, Milletia dura* and *Symphonia globulifera.* The corrected values used for interpretation of the results were calculated from these data. Because differences in vegetation composition and feeding behavior between the groups could not be found, the data of the 2 groups, A and B, were pooled.

Group feeding behavior is concentrated on a few plants (Figure 4). A large part, 35 percent, of the total feeding activity is limited to *Albizzia gummifera,* followed by *Bridelia brideliifolia* with 13 percent, *Milletia dura* with 12 percent and *Symphonia globulifera* with 6 percent. The feeding on arthropods received a relatively high value of 11 percent. All remaining food sources represent only 23 percent of the total feeding activity. Figures 5a-5e show that the monkeys preferred different food items according to season. Only a few other plants have proved to be of importance on individual observation days. On June 12, *Sapium ellipticum* with 13 percent; on September 13, *Urera hypselodendon* with 11 percent and on September 30 with 10 percent; on October 19, *Conopharyngia durissima* with 15 percent. Feeding on arthropods is not subject to as great a seasonal variation as is feeding on plant life (Figure 5).

On certain days, the group fed upon extremely few plant species. Evidently the preferred plant provided sufficient nourishment. Corresponding to this plant preference is the fact that sometimes considerably more fruit is eaten; other times, more flowers are eaten. It should be mentioned that the number of flowers eaten is generally great. Possibly the flowers provide the vitamin requirements. Leaves are seldom eaten. Insects and other arthropods, in forming a large share of the total food source, provide the

Table 4.—Plant Parts used as Food by blue Monkeys during the Study.

Species	*Eaten part*
Trees	
1. Albizzia gummifera	fruit: beans of the pod flower: observed only rarely, part not identified leaf: unfolded tips of the new leaf
2. Sapium ellipticum	fruit
3. Milletia dura	fruit: beans of the pod flower: base of the flower leaf: young leaf
4. Symphonia globulifera	flower: base of the flower
5. Myrianthus holstii	fruit: from information of others, outside of the study area
6. Parinari holstii	flower: part not identified
7. Hagenia abyssinica	leaf: stem of the leaf
Shrubs	
8. Syzygium guineense	fruit
9. Bridelia brideliifolia	fruit
10. Maesa lanceolata	flower: part not identified
11. Conopharyngia durissima	flower: base of the flower
12. Nauclea sp.	leaf: base and stem of the leaf
13. Dichaethanthera corymba	flower: base
14. Mitragyne rubrostipulata	leaf: stem
15. Canthium hispidum	fruit
16. Alchornea hirtella	flower: part not identified leaf: young leaf
17. Chasalia subochreata	flower: total leaf: total
18. Kotschya african	flower: part not identified
19. Xymalos monospora	leaf: total
20. Cyathea sp.	leaf: unfolded, young leaf
Lianas	
21. Ficus sp.	fruit
22. Acacia monticola	fruit: beans of the pod leaf: young leaf
23. Cissus sp.	fruit
24. Basella alba	leaf: stalk of the leaf
25. Mikaniopsis sp.	leaf: stalk
26. Embelia pellweida	flower: total leaf: total
27. Urera hypselodendon	flower: total fruit
28. Sarcostachys scandens	leaf: young leaf
29. Mikania caudata	leaf: total
30. Begonia meyeri-johannis	flower: part not identified
31. Leptoderis congolensis	flower: total leaf: young leaf
32. Loranthus woodfordioides	flower: base
Herbs	
32. Pteridium africanum	leaf: total except the stalk
34. Pennisetum purpureum	leaf: young leaf
Outside of the study area	
35. Strombosia schefferi	fruit
36. Arundinaria alpina	fruit flower shoots: identified through reconstruction, by means of the plant remnants

monkeys with an important source of protein.

Of interest, but difficult to interpret, is the fact that the amount of arthropods eaten varies according to sex. During the entire observation period, the males of Group A were observed to eat arthropods twice as often as the females (Table 6). No such difference, however, is shown in the total feeding behavior. The difference in the feeding on arthropods according to sex is statistically significant on the 0.05 level (Mann-Whitney U test; $p = 0.04$ arthropods; $p = 0.22$ total food).

Discussion

The vegetation of the study area in which the blue monkeys were living was described as one with a low diversity of plant species, insofar as it was a poor vegetation when compared with the primary forest. Indeed, 80 percent of the tree and shrub vegetation is made up of 6 plant species only. To this was added the disadvantage of a small belt of vegetation along a river enclosed by cleared slopes and cultivated areas, conditions which limited the extension of the home range. Certainly some observations on the blue monkey's habitat utilization and feeding behavior may be interpreted as adjustments to these poor conditions.

With 25 ha the group utilized a larger area as a home range than that observed by Aldrich-Blake (1970a) for blue monkeys with 8 ha. Omar and DeVos (1970) calculated a home range of 13 ha for Sykes monkeys. The relatively large overlap in home range, which was not observed on Sykes monkeys (Omar and DeVos, 1971), correlated with the rela-

Table 5a.—Total Time spent feeding on the major Food Plants within the Study Area for 2 groups of Blue Monkeys.

Date	*Group*	*Alb.*	*Mill.*	*Sym.*	*Bri.*	*Others*	*Arthr.*
12.7.	B	39	69	3	54	78	16
21.7.	A	58	20	—	72	86	16
26.7.	B	105	72	1	120	24	52
11.8.	A	288	9	—	24	92	78
23.8.	B	293	17	—	66	14	66
1.9.	A	281	7	—	22	12	24
13.9.	A	44	55	9	18	76	16
30.9.	A	41	87	47	—	76	42
11.10.	A	22	39	1	124	88	16
19.10.	A	78	20	—	6	184	62
25.10.	A	60	15	168	10	82	24
14.11.	A	69	48	2	4	138	24
Sum		1378	458	231	520	950	436
%		35	12	6	13	23	11

Table 5b.—Preferred Plant Parts for the major Food Plants utilized by Blue Monkeys.

Plant Part	*Alb.*	*Mill.*	*Sym.*	*Bri.*	*Others*
leaf	12	—	—	—	216
fruit	939	100	—	322	128
flower	11	259	206	130	190
leaf shoot	214	34	7	14	34
searching	202	65	18	54	282

Table 5c.—Total Time Spent Feeding on Various Plant Parts and Arthropods for 2 Groups of Blue Monkeys.

TOTAL Date	*Group*	*Leaf*	*Fruit*	*Flower*	*Shoot*	*Search*	*Arthr.*	*Sum*	*Vis.*	*Poss.*
12.7.	B	6	123	11		100	16	256	477	1440
21.7.	A	27	83	21		108	16	255	517	1584
26.7.	B	6	221	12		82	52	373	625	1440
11.8.	A	41	292	35		46	78	492	883	1584
23.8.	B	4	356	4		28	66	456	724	1440
1.9.	A	—	307	7		8	24	346	530	1584
13.9.	A	6	42	72	48	34	16	218	584	1584
30.9.	A	18	18	139	31	45	42	293	638	1584
11.10.	A	24	26	136	41	47	16	290	571	1584
19.10.	A	16	9	81	73	109	62	350	767	1584
25.10.	A	44	4	199	63	25	24	359	763	1584
14.11.	A	36	8	82	47	88	24	359	414	770
Sum		228	1489	797	303	720	436	3973	7542	17762
%		6	37	20	8	18	11	100		

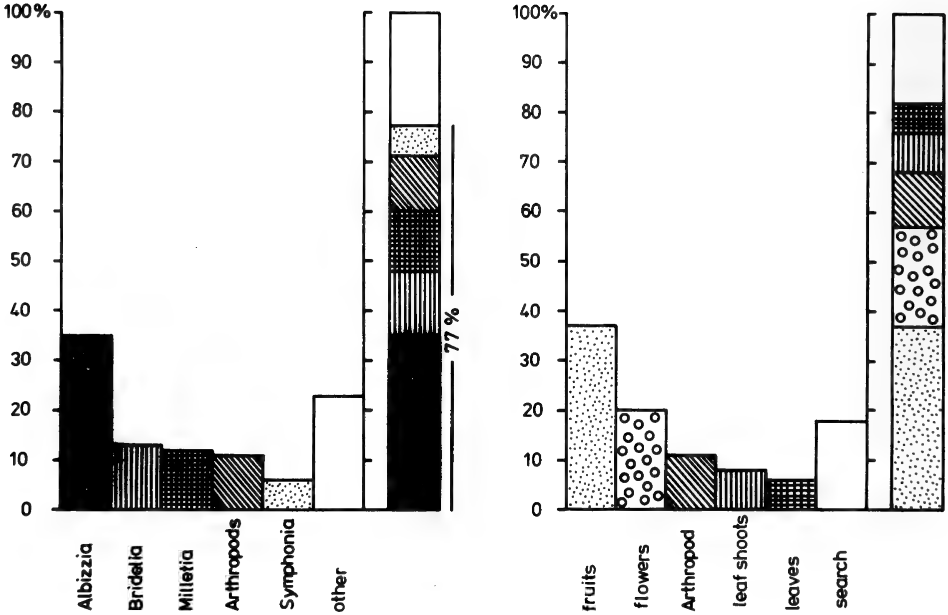
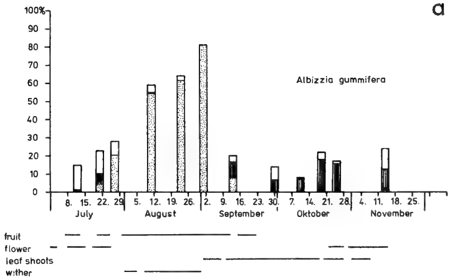
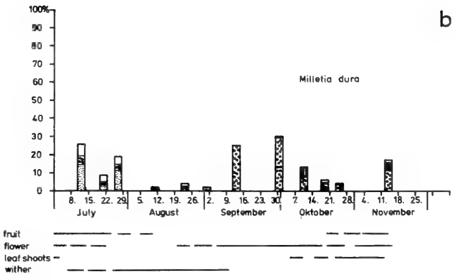
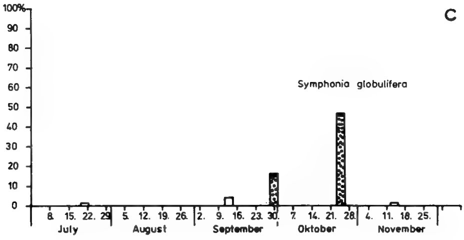


Figure 4. Proportion of feeding activity on various food sources calculated from 12 observation days from July to November.



Figures 5a–5e. Proportion of feeding activities at different observation days for the respective sources. Symbols as in Figure 4, right diagram.


b
Milletia dura
100%
90
80
70
60
50
40
30
20
10
0
8. 15. 22. 29. 5. 12. 19. 26. 2. 9. 16. 23. 30. 7. 14. 21. 28. 4. 11. 18. 25.
July
August
September
Oktober
November
fruit
flower
leaf shoots
wither


c
Symphonia globulifera
100%
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80
70
60
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8. 15. 22. 29. 5. 12. 19. 26. 2. 9. 16. 23. 30. 7. 14. 21. 28. 4. 11. 18. 25.
July
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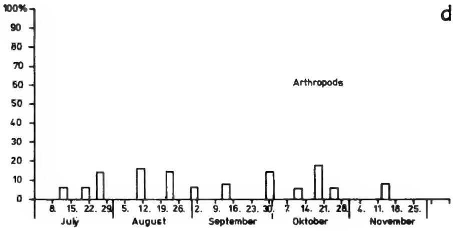
November


d
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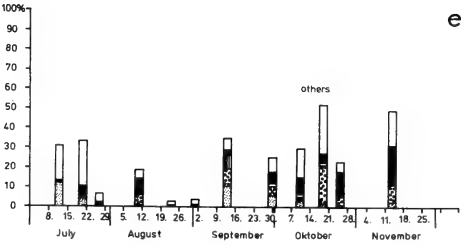
July
August
September
Oktober
November


e
others
100%
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80
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40
30
20
10
0
8. 15. 22. 29. 5. 12. 19. 26. 2. 9. 16. 23. 30. 7. 14. 21. 28. 4. 11. 18. 25.
July
August
September
Oktober
November

Table 6.—Food derived from arthropods and other plant substrates expressed as number of 5-minute intervals spent feeding differentiated for the 2 sex classes.

Food derived from Arthropods

Date:	*21. 7.*	*11. 8*	*1. 9.*	*13.9.*	*30. 9.*	*11.10.*	*19.10.*	*25.10.*	*sum*
per ♂	1.33	7.33	1.00	1.67	3.67	1.33	4.00	1.67	22.00 5-min
per ♀	0.25	2.25	0.50	0.75	1.75	0.25	2.25	0.75	8.75 5-min

Mann-Whitney-U-test: U = 15; one-tailed p = 0.041

Total Food

Date:	*21. 7.*	*11. 8.*	*1. 9.*	*13. 9.*	*30. 9.*	*11.10.*	*19.10.*	*25.10.*	*sum*
per ♂	11.33	36.67	12.67	14.33	22.00	17.00	15.67	30.00	159.67 5-min
per ♀	8.50	37.75	42.50	15.25	20.00	19.75	21.00	22.25	187.00 5-min

Mann-Whitney-U-test: U = 24; one-tailed p = 0.221

tively greater tolerance for neighboring groups. This overlap may be due to the pressure of poor feeding conditions on the blue monkey population. Through home-range overlap, it is guaranteed that every scarce feeding place is found by 1 group which otherwise would not be utilized by the home group because of lack of time and mobility. The regular pattern of moving back and forth in their belt-like home ranges should be considered in view of the poor feeding conditions, since this allowed a group at any time to inspect the area for every potential food resource.

By altering the feeding behavior, a species may respond to different feeding conditions. Rudran (1978) in his investigation on the feeding behavior of 2 groups of blue monkeys in the primary forest of Kibale, Uganda, gives an example of how "the pattern of use of *Ficus exasperata* was due to differences in its density within the two home ranges and in the relative abundance of food available from it." One group used only fruits of *F. exasperata,* while the other used leaf buds as well. In Kibale, *Albizzia gummifera* and *Milletia dura* were also food plants used by the blue monkeys, but unimportant ones, while the groups in my study area ate extensively on these plants. They not only fed on the flowers of *Milletia dura* but, unlike the blue monkeys in Kibale, fed on the fruits and leaf buds as well.

Not only the density of the plant species but also the composition of the vegetation as a whole influence the feeding behavior. The reasons for the differences in feeding behavior may be complex. An animal feeds on a certain food item with an indigestible or harmful secondary compound as an accessory which can only be neutralized by eating another food plant which by absence of the first would be of no use.

While the feeding conditions influence the feeding behavior, it may be also true that the diet is an indicator of the feeding conditions. One may speculate that Group B was forced to look for additional food items because of poor feeding conditions based on the low diversity of the vegetation and the small dimension of the living area, compared to the conditions met by Group A. Thus, Group B explored the adjacent slopes to feed on *Kotschya africanum,* while Group A had no need to do so.

In this way, the blue monkeys showed an astonishing flexibility in feeding behavior, also illustrated by the observation that in other parts of the Kahuzi-Biega Park they seemed to be adapted for living over a long period in the extremely limited vegetation of the bamboo forest. Flexibility in feeding behavior correlates with the large geographic range of this species. It must adapt to a range of living conditions, and this study helps to clarify the total niche which the blue monkey occupies in the tropical forest.

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Variability in the Feeding Behavior of a Malagasy Prosimian, *Propithecus verreauxi*: Lemuriformes

Acknowledgments

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Introduction

The lemurs, variously classified as the Infraorder Lemuriformes in the Suborder Prosimii (Simpson, 1945), or the Suborder Lemuroidea in the Grade Strepsirhini (Hill, 1953), are found uniquely on the island of Madagascar and are probably the best known among members of the 6 mammalian orders represented there. Between April 1970 and September 1971, a study was carried out on 4 groups of one of the largest and most widely distributed of the lemurs: *Propithecus verreauxi.* Two groups of the sub-species *P. v. coquereli* were observed living in rich, mixed deciduous and evergreen forest in the northwest of the island. The habitat of the other 2 groups (sub-species *P. v. verreauxi*) was semi-arid Didiereacae forest in the extreme south. Data were collected on various aspects of the ecology and social organization of these groups, but this paper reports only findings concerning their feeding behavior (full results are in Richard, 1978).

The study had 2 primary focuses which are reflected in the presentation of results here. First was the investigation of flexibility through time and space in the social organization and ecology of a prosimian species by comparing over an extended period groups from populations living in widely contrasting habitats. Second, data were gathered on a prosimian species a high percentage of whose diet consisted of leaves and shoots (Jolly, 1966), in order to provide comparative material for a broad assessment of the behavioral and ecological characteristics of primate folivores: such information was already available for Old and New World anthropoid species (e.g. Chivers, 1969; Clutton-Brock, 1972; Struhsaker, 1978), but until this study there was little on any Malagasy folivore. A number of classification systems have been proposed for primate social organizations which assume a close and simple relationship between ecology and social organization (Crook and Gartlan, 1966; Crook, 1970; Eisenberg, et al., 1972). Further information on another "leaf-eater" would, it was felt, aid in assessing the validity of this assumption.

The two study areas (Figure 1) are described in detail elsewhere (Richard, 1978), but a brief account is given here to provide some background for the data on feeding behavior presented subsequently. The northern study area (16°35″ South and 46°82″ East) was situated in the forestry reserve at Ampijoroa, in a region known as the Ankarafantsika. The southern study area (24°85″ South and 46°50″ East) was situated in semi-arid forest 1 km from Hazafotsy, around 1500 kms south of Ampijoroa. Hazafotsy lies on the northwest boundary of Reserve Nationale No. 11, and the study area was inside the reserve.

The vegetation of both habitats was sampled systematically and aspects of its structure, density, diversity, and phenology recorded. In the north, most trees were between 3 and 13 m in height, with emergents occasionally exceeding 21 m. The small stature of trees was probably a function of the poverty of the sandy, hilltop soil as well as of the age of the forest. Except for the forest's low profile, the usual characteristics of a very young secondary succession (Richards, 1966) were absent. In the south, most trees were between 3 and 7 m high, and none exceeded 21 m. There appeared to be a critical size beyond which 2 of the most abundant *Alluaudia* species present, *A. procera* and *A. ascendens,* became top-heavy, with the entire branching superstructure ultimately being torn off the trunk by its own weight. In addition to being generally lower, trees in the southern study area provided less cover than in the north. Summing the maximum spread of all trees sampled, the mean summed spread of trees per sample (a circle with a radius of 5 m) was 214 m. In the north it was 493 m. The estimated density of trees was similar in both areas: 13,878 per ha in the north and 13,370 per ha in the south.

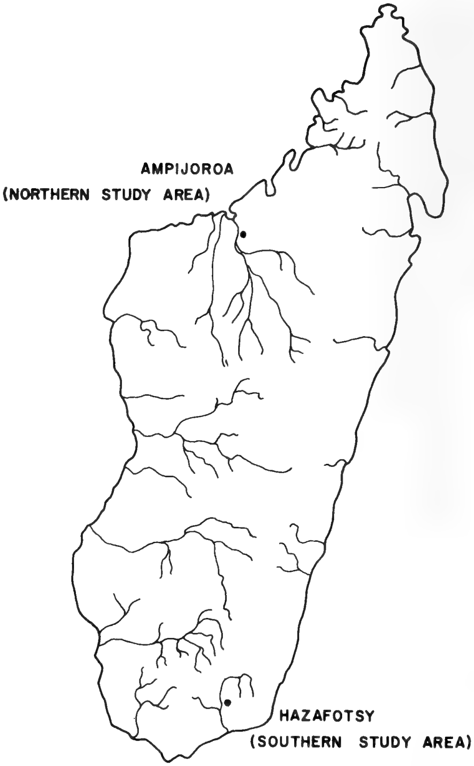

Figure 1. Location of the two study areas.

A greater diversity of tree species was found in the north than in the south; 194 species, belonging to a minimum of 35 families, were identified in the north compared with only 99 species, belonging to a minimum of 23 families, in the south. In both forests, most tree species occurred rarely and only a few were abundant and widely, though not necessarily uniformly, distributed.

Seasonal changes in climate were clear in the north, and even more marked in the south. Between mid-October and December in the north, 385.4 mm of the annual total of 1619 mm of rain fell and maximum and minimum temperatures of 29.5°C and 18°C were recorded. These months are referred to as the "wet season." Between July and September, only 1.8 mm of rain fell, and temperatures ranged between 31.5°C and 14°C. These months are referred to as the "dry season." In the south, 613.8 mm of the annual total of 629.8 mm of rain fell during January,

Table 1.—Composition of the four groups studied at the outset of observations

Group	*Adult male*	*Adult female*	*Subadult*	*Juvenile*	*Infant*	*Total*
I	2	5	—	—	—	7
II	1	1	1	1	1	5
III	2	2	1	1	2	8
IV	1	2	1	—	2	6
	6	10	3	2	5	26

February, and March (the wet season), and temperatures ranged between 39°C and 16°C. During the rest of the year (the dry season), practically no rain fell and temperatures ranged between 36°C and 8°C. (Rainfall data were supplied by Météorologie Nationale de Madagascar).

In both the north and the south, some trees shed their leaves at the beginning of the dry season, while leaf production continued throughout the year in others. Unlike the north, the southern forest was dominated by xerophytic vegetation, and many species exhibited water-conserving adaptations such as extreme reduction of leaf-size, huge-girthed bottle trunks, or water-retaining tubers.

Sampling Methods

The northern study groups, I and II, were observed during 3 dry season months and 3 wet season months. Observations of the southern groups, III and IV, were similarly distributed between seasons. The composition of these groups is given in Table 1. All 4 groups were habituated to my presence before the start of quantitative data collection. A group was regarded as habituated when all its members would approach and feed within 2 m of me.

An animal was recorded as feeding if it was chewing or ingesting. The animals' remarkable tolerance of and apparent indifference to my presence, the low stature of the forest in both study areas and, in the south, the low density of foliage, all facilitated accurate observation of both the food species and the part being eaten. Animals could almost always be seen, and were rarely more than 10 m-15 m away from me.

One animal was followed for 12 hours each day, from 6 a.m. until 6 p.m. Each day, the age and sex class of the subject was changed so that observations were equally distributed between the different categories as well as between different times of day. Data on feeding behavior were recorded at timed minute intervals. Seventy-two hours of data collected in this way were recorded for each group in each of the observation months. Data included total time spent feeding and its distribution through the day, time spent feeding on different food species and food parts, animals' posture and height above ground when feeding, and their ranging behavior. The animals' location was recorded relative to 50 m-sided quadrats marked by trails at ground level. If a member of a given group was seen in a quadrat more than once, that whole quadrat was included within the range of the group; this probably resulted in an over-estimate of the real area used by the group, for there were certain portions of most quadrats where the group was never seen and which individuals probably never entered.

Results[1]

General characteristics of feeding behavior

FEEDING TECHNIQUES. Animals detached food parts with their teeth, using their hands only to pull food-carrying branches toward their mouths. Food carrying was rare, and generally occurred only when there was a large, rare, and greatly relished fruit in question: its finder would sometimes carry it away from the rest of the group if and when another animal tried to seize it. Usually, however, food was consumed where it was found. Bark and dead wood were gouged out with the tooth-comb and then torn off, gripped between the upper and lower molars and premolars.

FEEDING HEIGHTS, SITES, AND POSTURE. Eight height categories were established in each forest: ground, off-ground to 1.5 m, 1.5 m-3 m, 3 m-5 m, 5 m-7 m, 7 m-10 m, 10 m-13 m, and over 13 m. Both seasonal and regional differences were found in the heights at which animals most commonly fed (Figure 2). In the north during the dry season, animals spent significant amounts of time feeding high in the forest, often on the buds and leaves of emergent trees. During the wet season, they tended to concentrate their feeding ac-

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[1] Discrepancies between some of the results presented here and those in Richard (1977 and 1978) are due to a more detailed reanalysis of the data and to recent access to a fuller identification list of samples collected from tree species in the course of the study. These identifications were generously made by the Royal Botanical Gardens, Kew.

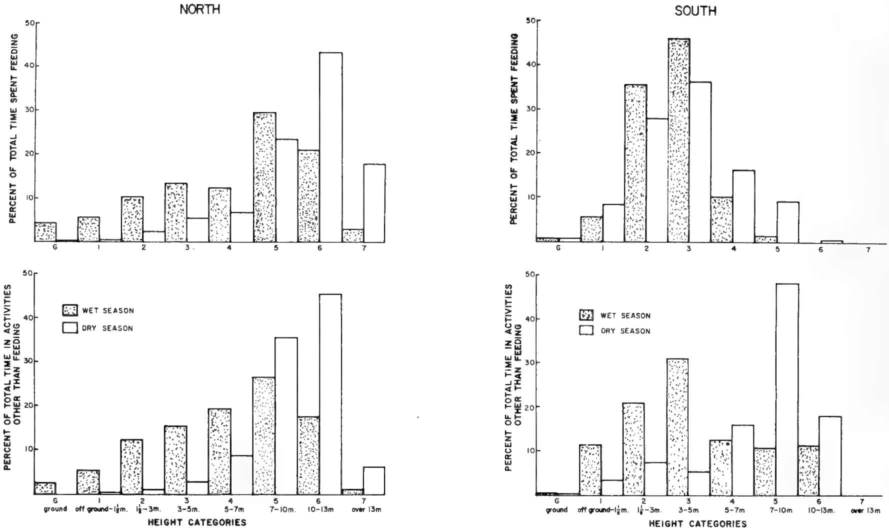

Figure 2. Distribution of time between different height categories by the 4 groups when feeding, in wet and dry seasons.

tivity in the dense and more or less continuous vegetation between 3 m and 10 m. In the south, unlike the north, there was little difference in feeding heights between the wet and dry seasons. Although animals in both study areas used all the height categories available to them to some extent in the course of observations, there was no significant correlation between the 2 study areas in the time spent feeding in each. This difference was probably associated with differences in the height and structure of the 2 forests.

Five main substrate types were defined for this study: Ground, Main Vertical, Main Horizontal, Smaller Branches (less than 6 cm in diameter) and Twigs (less than 1.5 cm in diameter). Although animals in both areas spent little time on the ground, all other substrate categories were used extensively. When feeding, however, animals tended to take up stations on smaller branches and twigs rather than on main trunks and branches (Figure 3).

P. verreauxi has been allocated to the locomotor category "Vertical Clinging and Leaping" (Napier and Walker, 1967). This label well describes the bounding progress of animals through the forest between vertical trunks, when moving from one food source to another or when fleeing. It does not do justice, however, to the wide range of postures adopted by animals, particularly when feeding: 75 percent of feeding was done in a sitting or vertically clinging posture, but for the remaining 25 percent animals hung by assorted limbs or spread-eagled over a network of fine twigs. This great postural versatility enabled them to reach food located in all parts of the tree including peripheral twigs.

The similarity of results concerning posture and substrate for animals in both study areas is the more striking in view of the considerable differences apparent between the physical structure of the 2 forests.

TIME SPENT FEEDING. In both study areas there were seasonal differences in the mean amount of time animals spent feeding each day. During the wet season in the south, animals fed for about 4 hours (32.8 percent of total time) each day while in the dry season this dropped to under 3 hours (24.2 percent of total time). This difference was highly significant (Mann-Whitney U Test, p. < .004). A similar, although statistically insignificant, trend was found in the north where animals fed for 4 1/2 hours (37 percent) each day in the wet season and only 4 hours (30 percent) in the dry.

Comparing results from the north and south for each season, there was no significant difference dur-

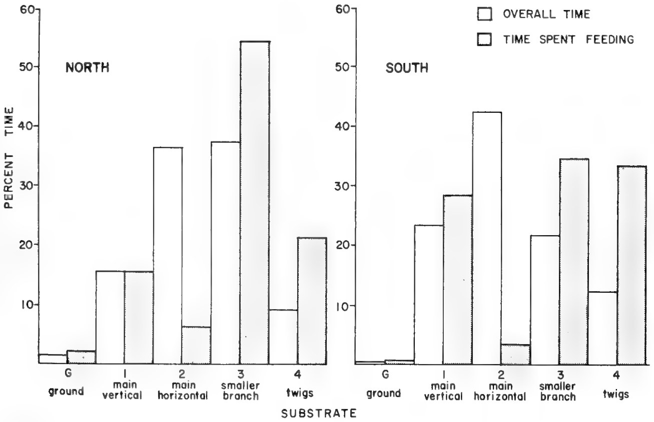

Figure 3. Distribution of time between different substrate categories by the 4 groups overall and when feeding.

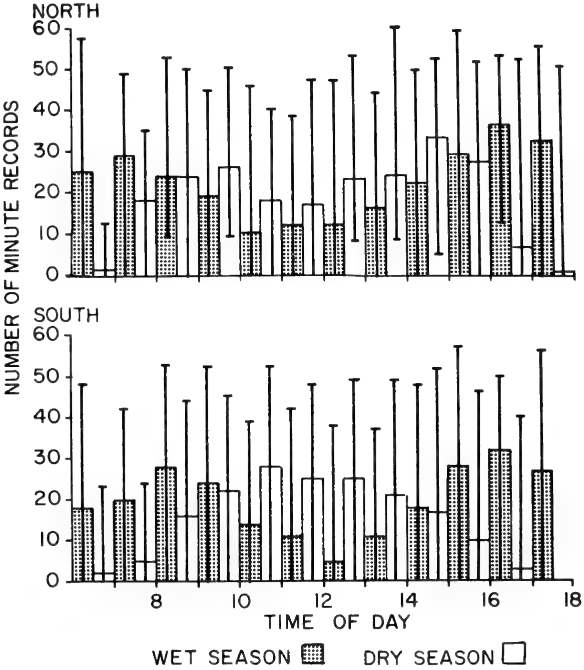

Figure 4. Mean number of minute records per hour on which subjects were recorded feeding throughout the day, in each season and study area.

ing the wet season. In the dry season, however, the southern groups fed less than those in the north (Mann-Whitney U test, $p < .001$).

These results were calculated combining data from all animals except 1 juvenile who was found to feed longer each day in the wet season than other animals. Time spent feeding by adult males or by lactating or gestating females did not differ from other animals.

DAILY PATTERN OF FEEDING. In both areas, the pattern of feeding in each season and the nature of the change between seasons were clear and similar (Figure 4): during the wet season, feeding began early, reaching a peak between 7 a.m. and 9 a.m. This was followed by a gradual decrease until midday, by which time very little feeding was taking place. Between 1 p.m. and 2 p.m. the amount of time animals spent feeding began to increase once more, reaching a peak in the late afternoon. During the dry season, intensive feeding began later and ended earlier in both study areas. In the south, feeding rates slowly built up throughout the morning to reach a peak between 10 a.m. and 11 a.m. and then decreased in the afternoon at almost the same speed. In the north, a similar pattern was present although a slight midday depression in feeding still occurred.

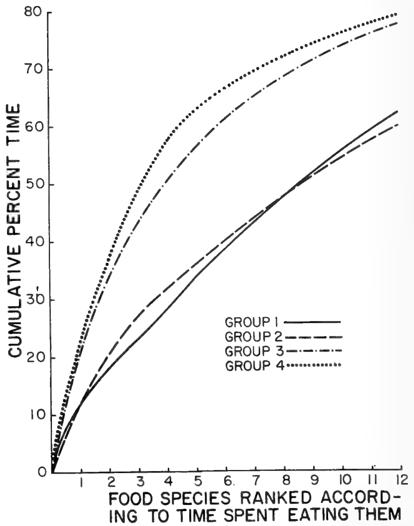

Figure 5. Overall amount of time each group spent feeding on the 12 food species eaten more commonly by each group than any other food species.

Variability in feeding behavior

In this section, regional, seasonal, and local variation in the breadth and composition by species and food part of the animals' diet are considered. "Local" variation refers to that observed between groups living in the same forest. Throughout the discussion, data from adult and sub-adult animals of both sexes are combined. No animal aged 5 months or more was seen eating a food part or food species which was not also eaten by another animal at some point during observations and, although it is not known whether individuals had different food preferences, if such variation existed it was not noticeable to the observer. Only infants are excluded from the analysis: between the ages of 3 weeks and 1 1/2 months infants did attempt to eat food parts not eaten by other members of the group (Richard, 1977).

BREADTH OF DIET. The northern groups' diet contained more species than that of the southern groups. In 6 months of observation, Group I was seen feeding on 85 different food species (including 18 liana species), and Group II on 98 (including 18 lianas). In the south, Group III was seen to eat 77 different food species (including 14 lianas) and Group IV 65 (including 13 lianas). These represent 34.5 percent (Group I), 41 percent (Group II), 64 percent (Group III) and 52.5 percent (Group IV) of all *tree* species identified in each forest.

In both areas, groups fed primarily on a few species despite the broad overall diversity of diet. Indeed, all four groups spent more than 65 percent of total feeding time eating only 12 food species (Figure 5). Figure 5 also shows that this tendency to concentrate on a few foods was more pronounced in the south than in the north.

A similar pattern of a trend common to both areas, but more pronounced in the south, is apparent in results concerning seasonal variation. In both areas, the number of food species eaten by each group declined in the wet season. This difference is statistically significant for all groups when only foods eaten for more than 1 percent of total feeding time are compared (Table 2, Mann-Whitney U test, $p < .01$). When all food species were included in the analysis, this trend was masked in the north by the long "tail" of rarely eaten foods.

SPECIES COMPOSITION OF DIET. Table 3 shows the 12 species which each group spent most time eating throughout the study, and indicates a total regional difference. This difference was largely, but not entirely, due to differences in the composition of the 2 forests. Only 4 species were identified which were common to both forests. Of these, ***Baudouinia flug-***

Table 2.—Number of food species on which each group spent more than 1 percent of its total time spent feeding in each season.

	Number of species			*Number of species*	
Month	*Group I*	*Group II*	*Month*	*Group III*	*Group IV*
July and August	18	22	May and June	18	19
Nov. and Dec.	13	17	Jan. and Feb.	8	6

Table 3.—Twelve species on which each group spent most time feeding throughout the study, and percentage of total feeding time spent eating each.

Group I		*Group II*	
Food species	*Time spent*	*Food species*	*Time spent*
Drypetes sp. no. 1*	12.4	*Drypetes* sp. no. 1	11.7
Cedrelopsis sp. no. 1	5.4	*Cedrelopsis* sp. no. 1	8.9
Combretum sp. no. 1	5.3	*Bussea perrieri* R. Vig.	4.5
Dead Wood	5.3	*Commiphora pervilleana* Perr	4.4
Capurodendron microlobum (Baker) Aubreville	5.1	*Bathiorhamnus louveli* Perr	3.9
Rheedia arenicola Jerm and Perr	4.5	Dead Wood	3.9
Commiphora pervilleana Perr	4.2	*Rhopalocarpus similis* Hemsley	3.7
Apaloxylon madagascariense Drake	4.0	*Combretum* sp. no. 1	3.6
Liana sp. no. 1	3.7	Liana sp. no. 1	3.1
Protorhus deflexa Perr	3.4	*Boscia* sp.	3.3
Hippocratea sp.	3.3	*Protorhus deflexa* Perr	2.4
Mundulea sp.	2.9	*Capurodendron microlobum* (Baker) Aubreville	2.3

Group III		*Group IV*	
Terminalia sp. no. 1	21.5	*Terminalia* sp. no. 1	21.0
Mimosa sp. no. 1	16.8	Liana sp. no. 2	15.4
Liana sp. no. 2	12.3	*Mimosa* sp. no. 2	11.2
Grewia sp. no. 2	7.7	*Grewia* sp. no. 1	9.9
Terminalia sp. no. 2	5.0	*Hagunta modesta* (Bak.) M. Pichon	4.8
Diospyros humbertiana Perr	4.1	*Terminalia* sp. no. 2	4.3
Grewia sp. no. 1	5.2	*Grewia* sp. no. 2	2.6
Euphorbia plagiantha Drak.	2.3	Liana sp. no. 3	2.5
Liana sp. no. 4	2.1	*Diospyros humbertiana* Perr	1.9
Liana sp. no. 3	1.9	*Rothmannia decaryi*	1.6
Hagunta modesta (Bak.) M. Pichon	1.8	*Commiphora* sp. no. 1	1.6
Liana sp. no. 5	1.7	*Grewia* sp. no. 3	1.5

* Where species identification could not be made, samples were numbered serially.

geiformis (found in 92 percent of vegetation samples in the north and 23 percent in the south) was an important dietary component in the north but untouched in the south. *Cedrelopsis grevei* (17 percent in the north, and 77 percent in the south) was eaten commonly in the south, but never in the north. *Commiphora pervilleana* (66 percent in the north, and 77 percent in the south) was eaten commonly in the north but rarely in the south. Finally, ***Rothmannia*** *decaryi* (79 percent in the north and 3 percent in the south) was eaten in quantity in the south where animals fed exclusively on its green ripe fruit; in the north it was eaten rarely, and the only part eaten was its large white flowers.

These regional differences were clearly the most sweeping, but some variation was also seen between the diets of the two neighboring groups studied in each area. Groups I and II each ate one species which the other was never seen to eat, for example. In the south, although no single food species was eaten exclusively by one group, there was some variation in the way animals distributed their time between different food species. Of the food species eaten for more than 1 percent each of total time spent feeding by Group III, 41 percent were eaten for less than 1 percent of total feeding time by Group IV, and 33 percent of Group IV's more commonly eaten foods were eaten rarely by Group III. Equivalent values for Groups I and II were 23 percent and 33 percent.

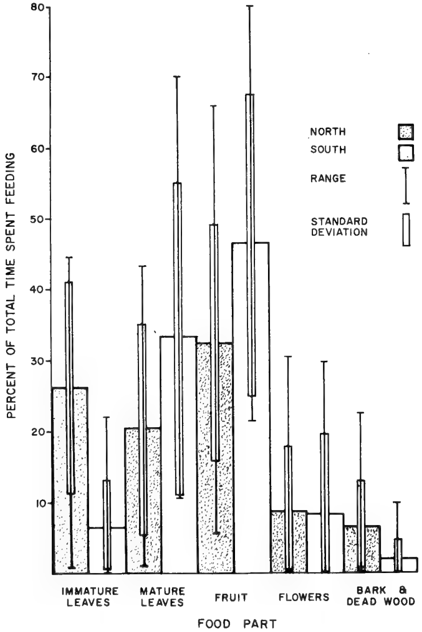

Figure 6. Amount of time spent eating different food parts, irrespective of season, by the groups in each study areas.

Within each study area, the composition of the animals' diet changed almost completely between seasons. Only 5 food species out of a total of 77 eaten in the course of observations were utilized by the southern groups for more than 1 percent of total feeding time in both seasons. The northern groups ate 9 out of a total of 99. Species eaten throughout the year tended to be those which produced leaves throughout the year, and animals fed regularly on these leaves at an immature and/or mature stage. Species that dominated the animals' diet for a short period and then disappeared from it were commonly those that produced flowers and fruit with close synchrony between individuals and that shed their leaves during the dry season.

FOOD PARTS EATEN. There were marked differences in the overall quantity of various food parts eaten by the groups in each study area. In the north, immature leaves were a primary dietary item whereas in the south animals tended to spend more time eating fruit and mature leaves (Figure 6).

Comparing data from the 2 study areas by season, further regional distinctions emerge. Although in both seasons the southern groups ate more mature leaves and fewer immature leaves than the northern groups (Mann-Whitney U Test, $p < .01$), in only the wet season did they eat more fruit than the northern groups (Mann-Whitney U Test, $p < .008$). In neither season was there any regional difference in the time spent eating flowers.

For each group, the preponderant food part in their diet changed seasonally, and the nature of this change was similar for all 4 groups. In both forests, these dietary changes mirrored quite closely phenological changes and, hence, the relative abundance of different food parts in the forests. Figure 7 shows the percentage of total feeding time which each group spent eating fruit, flowers, and flower buds each month together with counts of the presence of these items on the 100 trees sampled for phenology each month. Similar data for leaflets, shoots, flush and buds, immature, and mature leaves are shown in Figure 8.

In the north, a general peak in immature leaf consumption occurred at the same time as a decrease in mature leaf consumption at the beginning of the wet season. This was followed by an increase in the consumption of flowers in November and fruit in December. In the dry season, there was a general

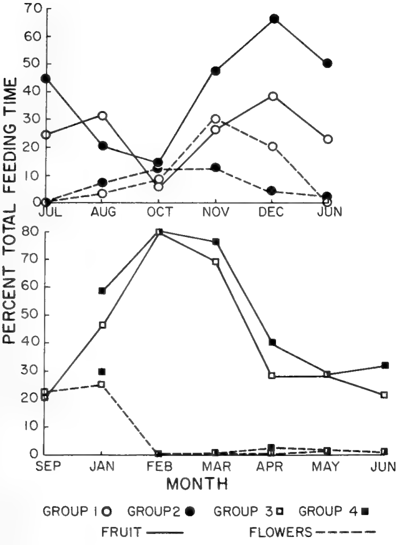

Figure 7. Percentage of total feeding time each month which each group spent eating fruit, flowers, and flower buds.

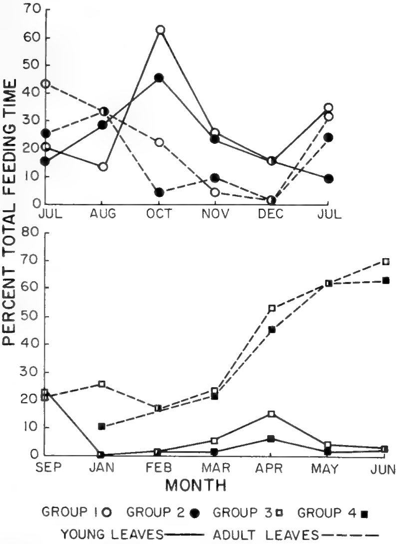

Figure 8. Percentage of total feeding time each month which each group spent eating immature and mature leaves.

reduction in time spent eating fruit and flowers and an increase in time spent eating mature leaves. Immature leaves also figured less in the animals' diet during the dry season, with 1 exception: Group I spent a large part of the dry season month of July (1971) eating immature leaves and leaf shoots on a single tree of *Capurodendron microlobum*. Phenological data indicate that at that time budding occurred uniquely in this 1 tree.

In the south, flowers and then fruit were primary food parts in the wet season as in the north. The dry season saw a big increase in time spent eating mature leaves. Only toward the end of the dry season did flowers become important; these came uniquely from *Alluaudia ascendens* and *A. procera*, both of which were abundant in the forest and, alone of all the tree species present, flowered toward the end of the dry season each year. September, usually one of the driest months of the year preceded as it is by several months of almost total drought, was the only observation month in which immature leaves constituted an appreciable proportion of the diet. This apparent anomaly—an abundance of new leaves in an arid month—was caused by light rain falling atypically at the beginning of the month which was sufficient to stimulate leaf production in many species. It is perhaps some measure of the successful adaptation of this xerophytic vegetation that so little rain could prompt such a rapid and full response.

Groups fed for long periods on bark and/or dead wood at certain times of year. Although dead wood was never eaten in the south, bark was eaten in quantity during the dry season: in September 1970 Group III spent 15.5 percent of total feeding time eating the bark and cambium of *Operculicarya decaryi*. This wood contains 81 percent water by weight. Animals gouged out the thin-barked, soft moist wood with their "tooth-combs," leaving scars on the trunk up to 1 cm deep and 4 cm long. At the onset of the following dry season, animals again began to feed on this wood. In the north, animals also ate bark, but in small quantities, during the dry season; further, they did not gouge out the underlying cambium and the bark itself appeared to contain little moisture. Most bark was eaten from thin branches of *Commiphora pervilleana*. In the wet season, however, animals in the north spent long periods gnawing at stumps of dead wood. On most days, each group would cluster around 1 of 2 stumps in their range (although there were other sources of dead wood in both ranges which did not differ noticeably from those eaten) and spend half an hour to an hour tearing off splinters of wood with their tooth-combs and premolars. This wood was very dry,

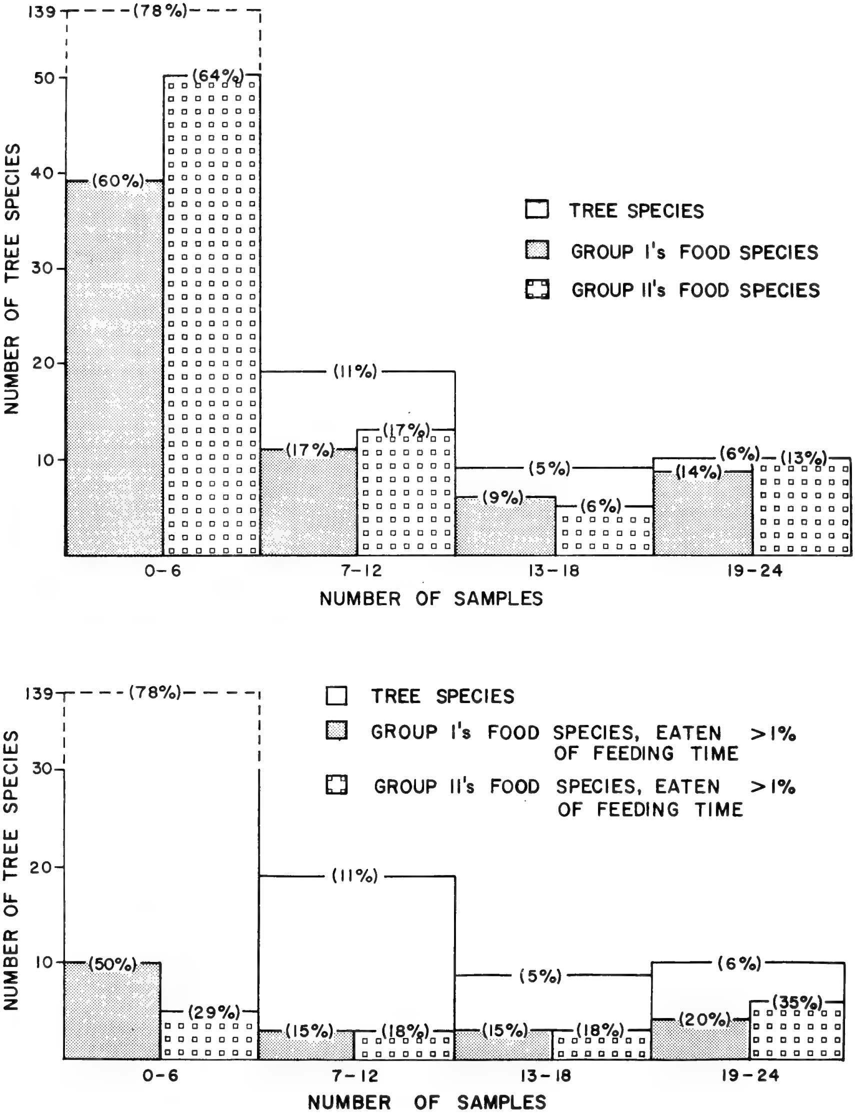

Figure 9. Tree species in the northern study area grouped according to the frequency with which they occurred in vegetation samples, showing the number of rarely eaten and preferred foods in each grouping.

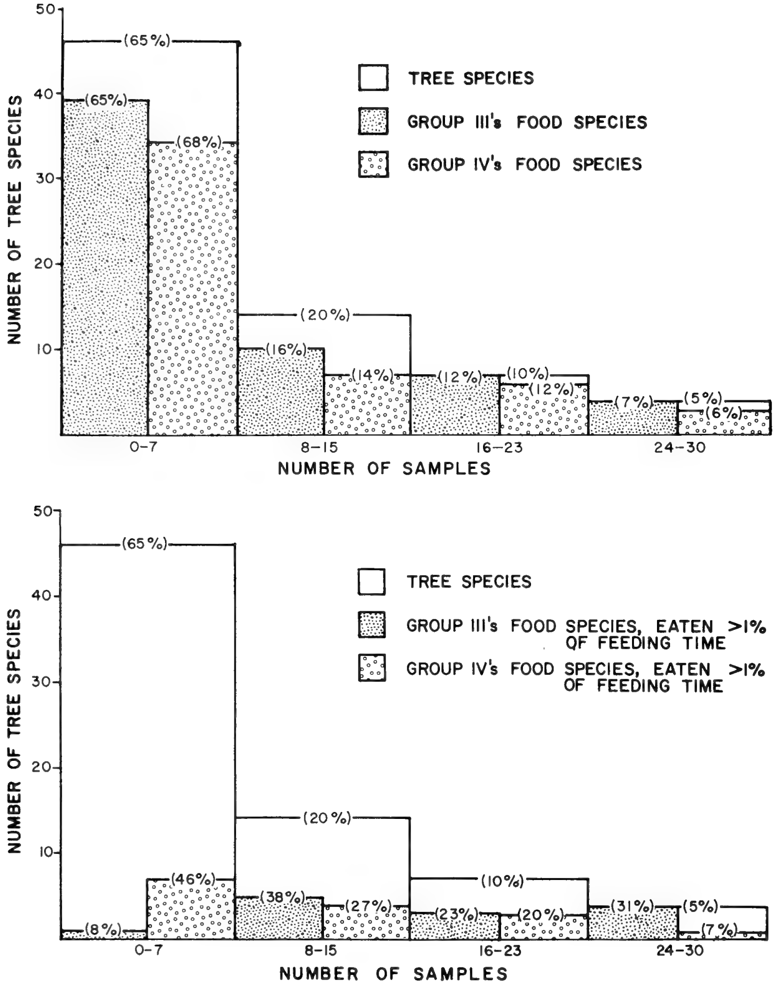

Figure 10. Tree species in the southern study area grouped according to the frequency with which they occurred in vegetation samples, showing the number of rarely eaten and preferred foods in each grouping.

very hard and dense, and did not appear to contain any kind of insect life.

Diet and the abundance of food

In both study areas, animals ate rarely and commonly occurring foods. In Figure 9 (top), tree species identified in the vegetation analysis in the northern study area are grouped according to the frequency with which they were present in vegetation samples (this was found to be a good measure of relative abundance). Four categories are shown: rare species (present in 1-6 samples, or identified only because animals ate them), moderately rare species (present in 7-12 samples), moderately abundant species (present in 13-18 samples) and abundant species (present in 19-24 samples—the latter being the total number of samples made in the north). In Figure 9 (top), the total number of food species eaten by Groups I and II in each of these categories is shown.

In Figure 9 (bottom), only preferred food species—i.e., foods eaten by groups for more than 1 percent of total feeding time—are included. While rare species formed a major component numerically (60 percent for Group I and 64 percent for Group II) of the animals' diet, over half the total number of rare species present in the forest were untouched by either group. In contrast, although abundant species constituted a small proportion numerically (14 percent for Group I and 13 percent for Group II) of the animals' total diet almost all abundant species present in the forest were eaten. When only preferred foods are considered, the numerical proportion of abundant species is higher (20 percent and 30 percent). In other words, these few abundant species were almost all eaten in considerable amounts.

Figure 10 shows comparable results for the southern study area where a total of 36 vegetation samples were made. Parallels with results for the north are obvious: animals fed on almost all of the few species which were abundant in the forest, although these constituted a small proportion numerically (7 percent for Group III and 6 percent for Group IV) of their total diet. As in the north, over half the total number of species eaten by each group were rare; in contrast to the north, animals ate a much higher proportion of the total number of rare species present in the forest. It should again be noted, however, that the diversity of the southern forest was much lower: only 46 rarely occurring species were identified in the vegetation analysis compared with 139 in the north. When only preferred foods are considered, an unexplained difference between Groups III and IV arises. The distribution of Group III's foods between categories is similar to that of the northern groups: almost all the abundant species in the forest were included among their preferred foods and indeed constituted close to one-third of them. In contrast, only one of Group IV's preferred foods was abundant in the forest, and about half of them were rare.

In summary, 3 of the 4 groups studied ate each of almost all the most abundant tree species in the forest for significant amounts of time. Their diet was supplemented by a wide variety of rarer species, only some of which were eaten commonly. In the north, many rare species were untouched by either group whereas in the south (where overall species diversity was lower) animals fed on most of these rare species too.

Ranging patterns

HOME-RANGE USE. Each group occupied an area of between 6.75 ha and 8.50 ha, but all of them used small pockets intensively and large areas quite rarely within this total range: all spent at least 60 percent of observation time in only 10 quadrats (i.e., 2.5 ha).

The term "core area" was used to describe quadrats that, in 4 or more months, were among those in which a group spent 75 percent of its time when quadrats were ranked according to time spent in them. Group I had 6 such quadrats, Group II seven, Group III 10 and Group IV 5. Although this differentiation of the home range could be made according to time spent in different parts of it, no comparable differentiation could be made according to activity: core areas were not necessarily areas in which animals preferred to feed or to rest, but rather localities in which animals spent extended periods and engaged in a whole spectrum of activities.

The 4 groups each had quadrats within their home ranges where no other groups were seen, which were called "areas of exclusive use." In the north, Groups I and II had exclusive use of 46 percent and 43 percent of their total home ranges. Intergroup interactions occurred throughout the extensive areas of overlap with neighboring groups, and there was no evidence that these encounters defined or defended the boundaries of that part of the home range used exclusively by the resident group. Exclusivity of use was not related to amount of use: core areas were not necessarily areas of exclusive use and, conversely, little-used quadrats were not necessarily areas of overlap.

In the south, Group III and IV had exclusive use of 87 percent and 91 percent of their total home ranges. Intergroup encounters occurred along the periphery of this area of exclusive use and apparently served to define and/or defend its borders. In contrast with the north, core areas almost all lay within the area of exclusive use within each group's range.

RANGING BEHAVIOR. All 4 groups visited most parts of their home range within 10 to 20 days. Characteristically, each group followed the same general patterns and direction of movement for 2 or 3 days, usually feeding in many of the same trees each day, and then suddenly both the sleeping tree and the ranging pattern would change.

DAILY DISTANCE MOVED. The northern groups moved farther each day than the southern groups (Mann-Whitney U Test, $p < .025$). All 4 groups moved farther each day during the wet season than during the dry season (Mann-Whitney U Test, $p < .001$-south; U-3, $p < .008$-north). There was no significant difference in the distance moved by the different age and sex classes within each group, nor between the groups in each area. The data from each area were, therefore, combined.

In the north, mean distance moved each day in the wet season was 1100 m; in the dry season it was 750 m. In the south, the mean distance moved each day in the wet season was 1000 m; in the dry season it was 550 m.

Discussion and Conclusions

P. verreauxi is a vegetarian and, overall, a high proportion of its diet consists of mature and immature leaves. It can, thus, be called a "folivore" within the broad conceptual framework proposed by Eisenberg (1978). The exigencies of a generally folivorous diet are such (Kay and Hylander, 1978; Janzen, 1978; Parra, 1978) that *P. verreauxi*, in common with many folivorous species, has a number of physiological and morphological characteristics which facilitate exploitation of the leafy component of the forest. These include relatively large bulk, molar tooth pattern and digestive tract formation (Richard, 1978).

Behaviorally, *P. verreauxi* shows the depressed activity level and low frequency of interaction characteristic of many folivores relative to frugivores, but there is no evidence that this species has a "folivorous type" social structure or, indeed, that such a "type" social system exists. Comparison of the data from this study with those from other studies of folivorous primates suggests that, while there may be a preponderance of 1-male groups among these species, no single social system is so prevalent as to support any proposed correlation between specific social systems and broad niche categories, such as "folivory."

Within the limits of folivory discussed by Eisenberg, *P. verreauxi* provides no exception to the dietary "opportunism" of many so-called specialized species (e.g., *Cercopithecus mitis,* Rudran, 1978). For example, overall figures giving the proportion of leaves in the diet of the southern groups mask the preponderance of fruit eaten, almost to the exclusion of leaves, toward the middle of the wet season. In this study, a systematic investigation was made of variation through space (locally and regionally) and time (seasonally) in aspects of the ecology and social organization of 4 groups. Their diet showed marked variation in both these respects. Considering first the variation through space, local differences were mainly restricted to the species composition of the diet of the 2 neighboring groups under study in each area. In both, only 8 of the 12 species most commonly eaten by each group in that area were the same. This may have been due to "cultural" differences or differing traditions between groups, or to local differences in the availability and distribution of the various food species.

Regional differences were more impressive. In comparison with the southern groups, animals in the north fed longer each day during the dry season, had a more varied and almost totally different diet, ate fewer fruit in the wet season and more immature and fewer mature leaves in both seasons. Much of this variation may have been due to regional differences in the distribution and availability of foods, but the data nonetheless contain enigmas: 4 tree species were common to both forests, yet the frequency with which animals fed on them and the parts of the tree eaten varied between study areas. Frequency differences could not be explained as a function of differing abundances of the tree species in each forest. There are a number of possible reasons for this: "traditional" food preferences may have been different in the 2 study areas. When a species was eaten little or not at all in one area, another species may have been a preferred alternative, providing equal or greater nutritional value, or possibly a lower detoxification cost (Janzen, 1978).

Considering variation through time, seasonal changes in feeding behavior were clear in both study areas, and the direction of these changes was similar in both although more pronounced in the south. This was probably because of the greater climatic extremes in this area. In comparison with the dry season, animals in the wet season fed for longer periods each day on a narrower and almost completely different range of food species. They ate more flowers, fruit, and immature leaves and fewer mature leaves. These seasonal changes were associated with, and reflected closely, seasonal changes in the vegetation.

Home-range use and ranging patterns also varied regionally and seasonally. The southern groups could be described as "territorial" in Burt's (1943) sense of an area defended against conspecifices. Overlap between the ranges of neighboring groups was minimal and it is probable that encounters in the narrow overlap area served to re-define and defend geographically fixed areas of forest. In the north, in contrast, intergroup encounters took place throughout extensive overlap areas, and there was no evidence that these encounters defined geographical boundaries. Certainly, the animals' "interpretation" of encounters in the north differed from the south; for in the former, animals might continue on their initial route after an encounter, even if that route was taking them away from the center of their range and toward the exclusive area within the encountered group's range. In the south, however, animals always moved away from the edge of their range toward its center after an encounter.

These basically different patterns of dispersion did not change seasonally; however, the movement of animals around their range did show seasonal as well as regional variation. In both study areas, animals moved further in the wet season than in the dry, thereby covering their range faster rather than expanding it. All four groups tended to concentrate their time in core areas, particularly during the dry season.

Altmann and Altmann (1970), working with baboons, emphasized the importance of the distribution of vital resources such as water on home-range size and utilization, and began to formulate testable hypotheses concerning the relationship between baboon strategies and their environment. This trend within primate studies away from "simple correlation combined with *post hoc* explanation" (Altmann, 1974:222) has been further stimulated by ecological models predicting optimal feeding strategies for animals (though rarely primates) living in diverse habitats (e.g., Emlen, 1968; Levins and MacArthur, 1969; MacArthur and Pianka, 1966; Schoener, 1971). More recently, attention has also focused on the importance of potentially toxic plant secondary compounds in determining the dietary choices made by herbivores (Freeland and Janzen, 1974; Janzen, 1978; McKey, 1978).

My general approach at the time of this study was one of "simple correlation . . . ." However, some of the predictions arising from the research referred to above provide a valuable basis for preliminary interpretation of the significance of the variation found in feeding behavior in this study. These inferences are discussed extensively in Richard (1978) and are presented here in summary form.

Using the data on feeding and ranging behavior presented in the results section of this paper, and the data on the distribution of tree species in each forest presented in the introduction, hypotheses can be constructed concerning the feeding strategy of *P. verreauxi* in each study area. In the north, the widely scattered distribution of the many rare species included in the animals' diet determined the minimum area over which the group must range in the course of a year. Animals monitored all these foods throughout the year and ate them as they became available. A consequence of this strategy was that at any one time the *total* food available to animals within the range was in excess of the group's immediate needs and overlap between groups could therefore be extensive. Intergroup encounters functioned to preserve group integrity and, on occasion, to dispute access to a favored food source.

In contrast, the dispersion of the southern groups was determined by *total* food availability at certain times of year rather than by the distribution of critical but scattered food sources. The whole range was required to support the group toward the end of the dry season, when total food availability was low. Round-the-year maintenance of a largely exclusive range was a more efficient means of assuring this seasonally crucial resource area than seasonal conflicts to establish exclusivity at just that time when resources were scarce.

Despite these differences, it is still true that in both areas animals fed on a wide range of plant species, some of which were abundant but many of which were widely and unevenly scattered through the forest. Seasonal and regional variations in this basic strategy accord well with the predictions of the foraging strategy models. In both areas, animals fed on a wider range of foods in the dry season when the abundance of food was lower. In the south, which appeared to have lower overall productivity and more patchy, less predictable resources than the north, animals ate a wider range of food species relative to the total number present. Although the size of each group's home range was no greater than in the north, overlap between the ranges was less and the ratio of biomass to area was thus lowered. The presence of territorial behavior in the south but not in the north fulfills another of the feeding strategy models' predictions: a lowering of food density will favor switching from lack of defense to defense, if the area in question is not too large (Schoener, 1971).

These hypotheses still fail to account for some aspects of *P. verreauxi's* feeding behavior. For example, animals often fed briefly on what appeared to be extensive food resources and sometimes traveled several hundred meters to do so. It is possible that such foods contained critical nutrients only required in trace quantities. Recent research, however, has indicated that various secondary compounds synthesized by plant species may have toxic effects on herbivores ingesting them (Freeland and Janzen, 1974; Janzen, 1978). In many potential toxins, a dosage effect is found, and much further research will be needed to investigate the possibility that the diversity of this species' diet and the failure of animals to eat apparent food present in large quantities are due to the species' inability to detoxify many secondary compounds.

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Behavioral Adaptations to Leaf-eating by the Mantled Howler Monkey (*Alouatta palliata*)

Introduction

The foraging behavior of neotropical primates has as yet been little investigated, but thus far the howler monkey, *Alouatta,* is the only New World genus whose diet is known to include a substantial proportion of leaves (Carpenter, 1934; Altmann, 1959; Hill, 1962; Fooden, 1974; Hladik and Hladik, 1969; Eisenberg and Thorington, 1973; Mittermeier, 1973; Smith, 1977; Glander, 1978). The howler is described as having specialized features in the digestive tract that may be associated with leaf-eating and is viewed as occupying a dietary niche in the neotropical forest similar in many respects to that of Old World folivorous primates, the Colobinae and Indriidae (Hill, 1962; Hladik and Hladik, 1969; Richard, 1970; Jolly, 1972; Eisenberg et al., 1972; Eisenberg and Thorington, 1973; S. A. Altmann, 1974; C. M. Hladik, 1978). The howler is said to depend on abundant and readily available foods (Carpenter, 1934; Altmann, 1959; Hladik and Hladik, 1969; Smith, 1977; C. M. Hladik, 1978), which it takes from a limited number of common plant species (Hladik and Hladik, 1969; C. M. Hladik, 1978).

The data presented here suggest that the above view of the howler monkey is an oversimplification. I believe that much of the complexity of the howler's foraging behavior has been overlooked because researchers have tended to see the howler as a New World analogue to highly specialized Old World folivores. These folivores—the colobines, with sacculated stomachs analogous to those of ruminants (Bauchop and Martucci, 1968; Bauchop, 1971, 1978); the indriids, with enormous intestinal tracts, including ceca 2 to 3 times total body length (Hill,

Table 1.—A comparison of 4 sections of the digestive tract of *Alouatta* with those of 20 primates not generally regarded as specialized folivores and three highly specialized folivores. Relative surface area = actual surface area in cm²/ (length of body + head)² × 1000. N = number of individuals in sample. All data except means and ranges are from C. M. Hladik (1967).

		Relative Surface Area			
	N	*Stomach*	*Small intestine*	*Cecum*	*Colon*
Arctocebus calabarensis	1	30	300	20	60
Perodicticus potto	1	30	200	15	140
Galago demidovii	4	44	275	35	85
Galago elegantulus	1	65	160	45	140
Galago alleni	3	58	317	27	135
Microcebus murinus	1	45	300	15	55
Cheirogaleus major	4	56	290	14	66
Leontocebus midas	1	20	195	10	40
Cebus griseus	2	35	308	3	25
Ateles paniscus	1	60	280	35	80
Papio leucophaeus	2	15	145	15	155
Papio papio	1	25	200	5	80
Cercocebus albigena	3	32	190	22	217
Cercopithecus nictitans	4	40	224	24	189
Cercopithecus neglectus	1	70	260	35	340
Cercopithecus vervet	1	25	120	10	100
Cercopithecus pygerythrus	1	10	150	20	65
Cercopithecus talapoin	4	55	225	25	165
Gorilla gorilla	1	40	220	15	190
Pan troglodytes	1	70	250	25	260
Mean		41	230	21	129
Range		10–70	120–317	3–45	25–340
Alouatta seniculus	1	50	300	40	160
Colobus polykomos	1	320	180	10	180
Avahi laniger	3	92	547	253	280
Lepilemur mustelinus	1	70	105	270	250

1953; Hladik, 1967); and *Lepilemur* with a greatly elongated cecum and colon (Hladik, 1967; Charles-Dominique and Hladik, 1971)—have specialized features in the digestive system of a magnitude that clearly sets them apart from other primates (Table 1).

The large, complex stomachs of the colobines contain vast quantities of bacterial flora which aid in the breakdown of food substances high in structural cellulose (Bauchop and Martucci, 1968; Bauchop, 1971, 1978) and appear to play an important role in the detoxification of secondary compounds (Scheline, 1968; Williams, 1971). The greatly enlarged caecum and colon of the indriids presumably also contain extensive bacterial flora that perform similar functions. Wherever studied, species from these groups have been shown to have diets that at times are heavily dependent on tough, bulky food items, particularly mature leaves (Ripley, 1970; Hladik and Hladik, 1972; Richard, 1973; Clutton-Brock, 1974, 1975). The extensive gut flora of these animals must help them to exploit such foods efficiently.

From the literature, it might appear that howler monkeys have similar digestive specializations. Depending on the source consulted, howlers are described as having specialized stomachs (Böker, 1932; S. A. Altmann, 1974) or specialized ceca and colons (Hladik and Hladik, 1969; Richard, 1970; Eisenberg et al., 1972; Jolly, 1972). A comparison of 4 sections of the digestive tract of howler monkeys with those of 20 primate species not generally regarded as specialized folivores shows that howlers have unremarkable digestive tracts both in actual size and in surface area relative to body size (Table 1). The stomach of the howler monkey is a simple, nonsacculated primate stomach (Hill, 1962; Cramer, 1968) that is only slightly above the mean in relative surface area (Hladik, 1967). The small intestine and cecum of the howler are in the upper range for this group, but they are similar to those of *Galago* and *Ateles*, neither of which is described as a leaf-eating primate.

When howlers are compared with 3 members of the highly specialized groups, one can clearly see the magnitude of the difference between the stomach of the howler monkey and that of the *Colobus* monkey, and between the cecum and colon of the howler and those of *Avahi* or *Lepilemur*. The howler may indeed have some specializations in the digestive tract associated with leaf-eating (e.g., Hladik and Hladik [1969] have pointed out the unusual villi in the small intestine), but thus far there is little morphological evidence to support the view that it can be considered a folivore in the same sense as colobines and indriids.

Behaviorally, however, the howler monkey may be considered a relatively folivorous primate as all of the studies done so far, except that by Schlichte (1978), show that its diet includes a substantial proportion of leaves (Carpenter, 1934; Altmann, 1959; Fooden, 1974; Hladik and Hladik, 1969; Mittermeier, 1973; Smith, 1977; Glander, 1978). Many other primate species also have diets that include considerable amounts of foliage (see C. M. Hladik, 1978) and yet do not appear to have digestive specializations of a magnitude comparable to those of colobines and indriids. This list includes mountain gorillas (Schaller, 1965), lowland gorillas (Sabater Pi, 1974), orangutans (MacKinnon, 1974), siamangs (Chivers, 1974), various cercopithecine monkeys (Haddow, 1952; Gautier-Hion, 1973) and some lemurs (Petter and Peyrieras, 1970; Sussman, 1972). Since so many primates eat substantial proportions of foliage, I would suggest that a distinction be made between those primates that have highly specialized gastro-intestinal features associated with leaf-eating, which I would call *anatomical folivores*, and those primates that lack such specializations, which I would call *behavioral folivores*. Though digestive processes involving some extent of microbial fermentation presumably occur in all leaf-eating primates, the magnitude of differences between the digestive tracts of the 2 groups indicates that there is considerably less scope for such processes in the less specialized animals.

Behavioral and anatomical folivores may have evolved 2 different basic approaches to the opportunities and problems of leaf-eating. While folivory might appear to be an attractive way of life, offering arboreal animals an omnipresent and abundant food source, the high ratio of plant to animal biomass in the tropical forest supports the view that much of this leafy material cannot be used by primary consumers (Bourliere, 1973). Much of it contains high proportions of structural materials, which most animals are unable to digest (Moir, 1965). Further, all plant parts contain secondary compounds, which may present problems for herbivores. Many such compounds are distasteful and/or harmful; some may act as proteinase inhibitors; and the cost of detoxifying them may be energetically expensive (Fraenkel, 1959; Ehrlich and Raven, 1965; Feeny, 1970; Williams, 1971; Ryan and Green, 1974; Freeland and Janzen, 1974). In addition, in a tropical forest the leaves that are generally abundant throughout the year are *mature* leaves. Feeny (1970) found that mature oak leaves had much higher concentrations of tannins than immature oak leaves, and McKey (1974) has suggested that the mature leaves of trees in general may have higher concentrations of certain secondary compounds. Feeny (1970) also found that mature oak leaves were over 7 times as tough as immature oak leaves and had lower protein contents. C. M. Hladik (1978) states that the protein content of mature leaves he has analyzed is generally 10 to 20 percent compared with 25 to 35 percent in immature leaves. Mature leaves might be less desirable as a food source since they probably contain less soluble carbohydrates and more structural materials than immature leaves (H. Rice, personal communication; Milton, in preparation).

To some extent, an arboreal herbivore might overcome the problems of eating mature leaves through specialized adaptations in the digestive system and thus benefit from the great advantage of mature leaves as a food source in a tropical forest—their general and perennial availability. An animal might circumvent these problems to some extent by feeding on immature leaves; however, even immature leaves contain secondary compounds and in some cases are known to have high concentrations of toxins such as alkaloids (McKey, 1974). And immature leaves are considerably less abundant and less continuously available both in space and time than mature leaves, so the problem of food procurement is greater. Thus, to be a successful folivore, an animal must have anatomical and/or behavioral adaptations to enable it to benefit from the advantages and overcome the disadvantages of leaves as a food source.

In the following sections of this paper, I shall present data on the foraging behavior of the howler monkey, *Alouatta palliata*, in a heterogeneous moist forest habitat. I shall discuss the patterns suggested by the data as possible behavioral adaptations to leaf-eating by a primate that does not appear to have gastrointestinal specializations of a type and/or magnitude comparable to those of colobines and indriids and is therefore, according to my definition, a behavioral folivore. It should be noted that the results are preliminary in that they are part of a long-term study that has not yet been completed.

Research Site

The study was carried out on Barro Colorado Island, a 15 m² nature preserve located in Lake Gatun, Panama Canal Zone. Detailed accounts of the history, topography, climate, flora and fauna of Barro Colorado can be found in the literature (Allee, 1926; Kenoyer, 1929; Enders, 1935; Woodring, 1958; Bennett, 1963; Chivers, 1969; Foster, 1973; Croat, in press; Knight, 1975; Leigh and Smythe, 1978; and others).

I studied the behavior of two troops of howler monkeys that lived in different areas of the island (see Figure 1) because I was interested in comparative data. Both study troops were approximately the same size: 3–4 adult males, 6–7 adult females, and 4–6 immature animals. One of the study sites, the Lutz Ravine, an area adjacent to the laboratory clearing on the eastern side of the island, was selected because it had been the site of *all* previous detailed investigations of howler behavior on Barro Colorado Island (Carpenter, 1934; Collias and Southwick, 1952; Altmann, 1959; Bernstein, 1964; Chivers, 1969; Hladik and Hladik, 1969; Richard, 1970; Mittermeier, 1973; Smith, 1977). I felt that a long-term study in this area would help to confirm and tie together many of the scattered pieces of information on howlers in the Lutz Ravine. The second study site, which I call the Old Forest, was located some 45 minutes by foot from the laboratory clearing in an area which is roughly bordered by the junctions of the Wheeler-Drayton and Zetek-Armour trails.

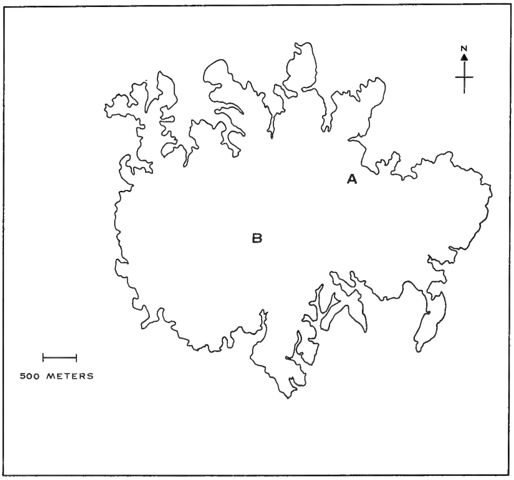

Figure 1. . Approximate locations of 2 study areas on Barro Colorado Island. Area A is Lutz Ravine near laboratory clearing. Area B is Old Forest.

The forest in Lutz Ravine is largely composed of trees less than 100 years old (Bennett, 1963; Foster, personal communication). Much of this area is known to have been cleared some 60 to 80 years ago before Barro Colorado was established as a nature preserve. This apparently allowed the growth of a large number of nonstrangler (Pharmacosycea) fig (*Ficus*) trees which typically begin growth only in relatively open areas. There are approximately 127 large nonstrangler fig trees of this type in the 25 ha making up the Lutz Ravine. Quantitative data show that this is about 9 times as many fig trees per hectare as are generally found on the island (Knight, 1975).

The second study site, the Old Forest, has in large part been undisturbed for at least the past 130 to 150 years and is believed to be structurally mature (Foster, personal communication). There are patches of younger secondary forest in this area which the troop regularly included as part of its home range. Most nonstrangler fig trees in this area are clustered in this younger growth. I found a comparatively high number of nonstrangler fig trees in one sample hectare in this younger section (6) and none in two other sample quadrats in the older area. Only 22 nonstrangler fig trees have been located in the entire home-range area of this troop. This is an important difference between the 2 areas since many fig species are asynchronous with respect to intraspecific fruiting cycles and individual trees may produce two huge fruit crops in an annual cycle (Morrison, 1975; Milton, in preparation). Because of the high number of fig trees in the Lutz Ravine, howlers here are living in a habitat where fruit appears to be always available.

Sample quadrats in the Lutz Ravine (Thorington, 1975) and in the Old Forest (Milton and Tarak, in preparation) provided data on the structure and composition of the forest in each of the study areas (Table 2). Three ha were sampled in each area and all trees 60 cm in circumference (breast height) and over were identified and their locations mapped. The

Table 2.—Tree data from sample quadrats. Numbers in parentheses are numbers of individuals of respective species in sample quadrats. Old Forest data are from Milton and Tarak (in preparation) and Lutz Ravine data from Thorington et al. (in preparation).

	Old Forest			*Lutz Ravine*		
	Quadrat			*Quadrat*		
	1	*2*	*3*	*1*	*2*	*3*
Number of trees:	214	168	173	208	200	201
Number of species:	58	52	57	60	63	58

Most common species:

Quadrat I	*Quadrat I*
Jacaranda copaia (18)	*Macrocnemum glabrescens* (22)
Gustavia superba (16)	*Hyeronima laxiflora* (19)
Alseis blackiana (12)	*Alseis blackiana* (17)
Alchornea costaric	*Anacardium excelsum* (11)
Hura crepitans (9)	*Luhea seemannii* (10)
Cordia alliodora (8)	*Poulsenia armata* (9)
Pterocarpus rohrii (8)	*Ficus yoponensis* (8)
Pseudobombax septenatum (6)	*Gustavia superba* (7)
Hasseltia floribunda (5)	*Pterocarpus rohrii* (6)
Zanthoxylem panamense (5)	*Virola sebifera* (6)
Luhea seemannii (5)	
Quadrat 2	*Quadrat 2*
Trichilia cipo (24)	*Alseis blackiana* (23)
Virola sebifera (9)	*Pterocarpus rohrii* (12)
Alseis blackiana (9)	*Spondias radlkoferi* (11)
Quararibea asterolepis (8)	*Trophis racemosa* (8)
Tetragastris panamensis (6)	*Luhea seemannii* (7)
Heisteria concinna (6)	Gustavia superba (7)
Hura crepitans (5)	*Macrocnemum glabrescens* (6)
Beilschmiedia pendula (5)	*Swartzia simplex* (6)
Hirtella triandra (4)	*Hasseltia floribunda* (5)
Quadrat 3	*Spondias mombin* (5)
Quararibea asterolepis (16)	*Hyeronima laxiflora* (5)
Poulsenia armata (13)	*Quadrat 3*
Virola nobilis (12)	*Virola nobilis* (17)
Guatteria dumetorum (8)	*Macrocnemum glabrescens* (13)
Trichilia cipo (7)	*Anacardium excelsum* (12)
Gustavia superba (6)	*Luhea seemannii* (11)
Alseis blackiana (5)	*Virola sebifera* (9)
Cecropia eximia (4)	*Swartzia simplex* (6)
Virola sebifera (4)	*Spondias radlkofera* (7)
	Gustavia superba (6)
	Spondias mombin (5)
	Alseis blackiana (5)

data showed that there was a great diversity of tree species, with most species having very low densities and/or clumped distributions. Phenological data showed that there were pronounced peaks and valleys in the overall production of new leaves, fruits, and flowers, and that individuals of most species were to some degree synchronous in their phenologies (Foster, 1973; ESP Report, in progress). Thus, such products from particular species were shown to be very patchy in both space and time.

Methodology

The behavior of each howler troop was sampled for 5 consecutive days each month. Both troops were always sampled within the same 15-day period. Since it was not practical to use the focal-animal method in the Barro Colorado forest, I used a scan sampling method described by J. Altmann (1974). This method works well for howlers as they tend to perform most activities as a unit. From dawn until dusk on each sample day, I observed the study troop at 5-minute intervals and recorded the activity of each animal that was visible. Each of these animal-activity states was counted as an activity record for the relevant 5-minute interval. Percentages for each type of activity—such as feeding, travel, resting—were then calculated in relation to the total activity records for each 5-minute interval. These percentages were added and divided by the total number of 5-minute intervals in the sample day to arrive at the percent of time spent at each activity. Only full sample days (observation from dawn to dusk) were used for this purpose.

Feeding activity included the inspection of food, bringing it to the mouth, chewing, and swallowing. Whenever an animal was feeding, the particular food item was recorded (e.g., young leaf, fruit, etc.) and a sample was collected or the tree was marked for later identification. To calculate the percent of feeding time spent on different food categories and species, I related the feeding activity records for each food category and species to the relevant activity records for the 5-minute intervals and proceeded as above; the resulting percentages were divided by the percent of time spent feeding in the sample day.

The data thus compiled for sample days were used for analyzing and comparing the results for the 2 study areas. The daily data for the two areas were also combined for the purpose of determining overall patterns; unless otherwise specified, the results described in the following sections of this paper are based on such combined data. Differences between two samples (e.g., between the 2 study areas, between seasons) were tested for significance by using the Mann-Whitney test. The Spearman rank correlation coefficient was used to measure correlation between 2 data sets.

As the animals traveled through the trees, the travel routes were marked at intervals with plastic surveyor's tape. These routes were later surveyed and mapped.

The 5-day samples were taken during 1974–75 in 5 months of the wet season (which lasts about 7 months) and in 3 months of the dry season (which lasts about 4 months). In the Lutz Ravine area, all 8 monthly samples were taken on the same howler troop. In the Old Forest, because of initial problems with troop identification, 2 monthly samples were taken on 1 troop and 6 on another. All 8 samples in the Old Forest should be equally representative of howler foraging behavior in this area and thus are included in these analyses.

Results

FOOD CATEGORIES. In the Lutz Ravine and in the Old Forest, the two troops showed a similar overall dietary pattern (Table 3). They ate foods from 3 categories: (1) leaves, 43.5 percent of feeding time, (2) fruit, 46.5 percent, and (3) flower buds and flowers, 10 percent. Insects, particularly beetle larvae (Curculionidae), were inadvertently eaten with some foods (e.g., *Ficus* fruit, fruit of *Quararibea asterolepis*).

Leaves were a substantial part of the howler diet in all 8 sample months and were eaten on every sample day. Leaves were eaten significantly less in the dry season than in the wet (Mann-Whitney (M-W), $p < 0.01$), but even then 35 percent of the feeding time was spent on leaves. Of all leaves eaten, very young leaves (flush) were the preferred items, with less than 5 percent of the overall feeding time spent on leaves that might be considered mature. Many leaves eaten by howlers that appeared mature from a distance were found on examination to be soft and tender in comparison with other leaves that were rejected. Leigh and Smythe (1978) report that the number of trees with new leaves was at a maximum during the last month of the dry season and the first 2 months of the wet season.

Fruit was also eaten throughout the study. It was eaten on every sample day in the Lutz Ravine (total 40 days) and on every sample day but 5 in the Old Forest (total 35 days). There was no significant difference between fruit consumption in the wet and dry seasons, even though the canopy tree species on Barro Colorado show a peak in fruit production during the latter part of the dry season (Smythe, 1970; Foster, 1973; Leigh and Smythe, 1978). Flower buds and flowers were much more seasonal items and were eaten significantly more in the dry season (M-W, $p < 0.001$).

Thus, in both areas there was a common overall dietary pattern in the proportions of the 3 food categories. As shown by Table 3, howlers in the Lutz Ravine spent more time eating fruit and less time eating leaves than those in the Old Forest, but neither of these differences is statistically significant.

When analyzed on a daily or monthly basis, however, the proportions of each food category show a far more dramatic fluctuation in the Old Forest than in the Lutz Ravine, even though the overall results are very similar. The very even pattern shown by the Lutz Ravine troop appears to be largely due to the continuous availability and greater use of fig products, both fruits and young leaves, in this area.

FOOD SPECIES. The data show that during the 8-month sample period, howlers ate foods from a minimum of 105 plant species including canopy trees, subcanopy trees, lianas, epiphytes and hemi-epiphytes (Table 4). Combined data from my other work on the island and that of earlier researchers (i.e., Carpenter, 1934; Hladik and Hladik, 1969; Mittermeier, 1973) bring the total number of food species used by Barro Colorado howlers to at least 145. This dietary diversity is due mainly to the great number of plant species that howlers use as flush leaf sources; considerably fewer species are used as fruit sources. Further, a large number of different species were used as food

Table 3.—Food categories. Data are means of percentages of feeding time spent on respective food categories during sample days.

Food	*Study area*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Wet season*	*Feb.*	*Mar.*	*Apr.*	*Dry season*	*Eight months*
Leaves	Old Forest	29	19	83	66	65	49	43	51	41	45	47
	Lutz Ravine	37	54	63	51	36	48	36	27	12	25	40
Fruit	Old Forest	71	81	1	33	14	43	41	27	53	40	42
	Lutz Ravine	61	42	37	50	55	49	51	62	47	53	51
Flowers	Old Forest	1	0	14	0	20	7	15	22	6	14	10
	Lutz Ravine	2	5	0	0	8	3	12	11	41	21	10

Table 4.—Overall diversity of food sources. Data are totals from 8 sample months.

	Old Forest	*Lutz Ravine*	*Combined*
Total number of different species used	70	70	105
Number of different species used as:			
Leaf sources	55	54	80
Fruit sources	20	20	32
Flower sources	14	17	28

sources in all sample months (Table 5).

During the sample period, howlers in both the Old Forest and in the Lutz Ravine ate foods from 70 different species. Only 35 of these species were shared in common, which may reflect the different composition of the forest in each area or the need for different supplementary items in the Lutz Ravine where the overall diet was based substantially on fig products, both fruits and young leaves. Though the same number of different species were eaten in each area, there was a much greater concentration on some species in the Lutz Ravine. This appears to be due mainly to the presence of so many fig trees in the Lutz Ravine area. Forty-eight percent of the feeding time in the Lutz Ravine was spent eating fig products as compared to 25 percent in the Old Forest. Fig products were used on 38 of 40 sample days in the Lutz Ravine and on only 20 of 35 sample days in the Old Forest. Fig leaves were the most important leaf source in the Lutz Ravine, accounting for 25 percent of feeding time spent on leaves, and the fig was by far the most frequently used primary food source in this area. (For the purpose of this analysis a "primary" food source is a species that accounted for 20 percent or more of feeding time in a sample day and a "secondary" source, less than 20 percent.)

As Table 5 shows, most food species eaten by howlers changed from one sample month to the next. There was also considerable turnover in food species from day to day. With few exceptions, there was continuous turnover in leaf sources and many species were eaten on only one sample day. The turnover of fruit sources was much less than that of leaves; fruit species were often eaten for several consecutive days. Most species used as primary food sources also changed from month to month.

The howlers showed strong preferences in the species they used as food sources; the ones they used most were not necessarily the most common species in their home ranges (Table 6). In the Old Forest, for example, *Ficus yoponensis* makes up 0.4 percent of the total trees in the combined data from the 3 sample quadrats in this area. Yet 17.5 percent of feeding time during

Table 5.—Monthly diversity and turnover of food sources. Only identified species were included. Identified species accounted for 92 percent of total feeding time for 8 sample months in Old Forest and 94 percent in Lutz Ravine.

Old Forest	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Feb.*	*Mar.*	*Apr.*
Number of species used during sample:								
All sources	8	7	4	21	31	17	26	17
Leaf sources	7	5	3	17	30	11	14	9
Number of species not used during previous sample:								
All sources	—	6	3	19	23	9	15	10
Leaf sources	—	4	2	15	22	6	6	6
Lutz Ravine								
Number of species used during sample:								
All sources	11	17	13	22	22	18	17	19
Leaf sources	9	11	12	20	15	12	11	13
Number of species not used during previous sample:								
All sources	—	9	7	19	16	16	10	13
Leaf sources	—	5	7	16	10	10	6	8

Table 6.—Thirty species most used as food sources. F = fruit, L = leaves, Fl = flowers or flower buds. Feeding time is total from 8 sample months. Tree data are from combined 3 sample quadrats in each study area.

Species	*Categories eaten*	*% of feeding time*	*% of trees in sample*
Old Forest			
Ficus yoponensis	F,L	17.50	0.40
Brosimum bernadettae	F,L	12.86	0.60
Poulsenia armata	L	6.90	3.13
Ficus insipida	F,L	6.25	0.80
Platypodium elegans	L	4.19	1.41
Hyeronima laxiflora	F,L,Fl	3.69	1.00
Cercropia eximia	F,L,Fl	3.05	1.00
Pseudobombax septenatum	Fl	2.52	1.20
Ficus costaricana	F	2.33	0.20
Quararibea asterolepis	F,L	2.13	5.28
Anacardium excelsum	F,L,Fl	2.05	0.40
Tabernamontana arborea	L	1.87	0.40
Trichelia cipo	F,L	1.71	6.83
Eugenia oerstediana	F,L	1.67	0.80
Inga fagifolia	L	1.41	0.40
Arrabidea patallalerum	L	1.30	—
Bignoniaceae, sp.	L	1.29	—
Crysophyllum panamense	F	1.10	0.40
Dipteryx panamensis	F	1.04	1.00
Clusia odorata	L,Fl	1.00	—
Ormosia sp.	L	0.83	1.57
Topobaca praecox	L,Fl	0.78	—
Abuta racemosa	L	0.77	—
Maripa panamensis	L,Fl	0.73	—
Acacia hayesii	L	0.73	—
Cordia alliodora	L	0.63	2.01
Tetragastris panamensis	F,L	0.57	1.81
Protium panamense	L	0.55	0.80
Hiraea sp.	Fl	0.51	—
Paragonia pyramidata	Fl	0.48	—
Lutz Ravine			
Ficus yoponensis	F,L	27.15	2.18
Ficus insipida	F,L	21.27	1.17
Platypodium elegans	L,Fl	7.81	1.17
Spondias mombin	F,L	5.58	1.68
Lacmellea panamensis	F	3.56	0.17
Pterocarpus rohrii	F,L,Fl	2.79	3.02
Inga fagifolia	L	2.30	0.17
Maguira costaricana	F,L	1.79	1.17
Brosimum bernadettae	F,L	1.67	—
Poulsenia armata	L	1.64	2.18
Ficus trigonata	F,L	1.59	—
Luhea seemannii	L	1.24	4.70
Inga sp.	L	1.20	—
Cercropia eximia	F,L,Fl	1.08	0.17
Inga goldmanii	L	1.02	0.17
Inga punctata	L	0.98	—
Zanthoxylum panamense	L,Fl	0.92	0.84
Eugenia coloradensis	F,L	0.83	—
Anacardium excelsum	F,L	0.72	3.86
Dioclea sp.	Fl	0.62	—
Socratea durissima	F	0.55	—
Protium panamense	L	0.54	1.01
Entata gigas	L	0.49	—
Hasseltia floribunda	F,Fl	0.48	0.84
Trophis racemosa	F,L,Fl	0.48	2.01
Gnetum leyboldii	Fl	0.41	—
Cordia alliodora	L	0.40	0.67
Ficus tonduzii	F,L	0.36	0.17
Tetragastris panamensis	F,L	0.31	—
Prioria copaifera	L	0.30	—

the 8-month sample was spent eating foods from this species. In contrast, *Alseis blackiana* makes up 7.8 percent of the total trees in the Lutz Ravine sample and only 0.1 percent of feeding time was spent eating it. Certain families seem highly preferred as well. Eight of the 10 most used leaf sources in the Lutz Ravine, accounting for 68 percent of the feeding time spent on leaves, were from 2 families, Moraceae and Leguminoseae, and species of the Moraceae were the most used fruit sources. Howlers are also selective with respect to which individual trees of a species they use for food. Sample quadrat 2 in the Old Forest, for example, has a total of 24 trees of *Trichilia cipo* and yet only a few of these were used as food sources during the 8-month sample.

Howlers did not eat from certain tree species common in the sample quadrats. *Macrocnemum glabrescens* makes up 7 percent of the total tree species in the 3 quadrats in the Lutz Ravine and was never noted as a food source. Likewise, in the Old Forest, *Jacaranda* *copaia* and *Hura crepitans* make up, respectively, 4.2 percent and 3.4 percent of the total trees in the sample and neither was used as a food source. On the other hand, howlers eat a great many food items, particularly young leaves, that appear to be undesirable. In their pursuit of young leaves, howlers seemed little deterred by flush densely coated with hairs (*Inga goldmanii*), by extremely sharp thorns (*Poulsenia armata*), by soft thorns on the leaves and sharp thorns on the branches (*Zanthoxylem* sp.), by biting ants (*Cecropia eximia*), by presumably caustic saps (*Omphalia diandra*), or by sticky exhudations (*Ficus* sp.; *Tabernamontana arborea*).

DAILY FOOD PATTERNS. In both areas, howlers showed a common daily pattern of food selection. On the average, each day howlers ate foods from 6 different plant species—4 leaf sources and 2 fruit sources, supplemented at times by flower buds and/or flowers. This number varied from day to day and from month to month. There were also seasonal differences in the number of food species eaten daily. In both areas, howlers used more species in the dry season than in the wet season (M-W, $p < .005$). This reflects the greater number of species used for fruit, flower buds, and flowers during the dry season, while the number of leaf species was about the same in both seasons. Howlers also traveled significantly more during the dry season (M-W, $p < .001$), and there was a strong positive correlation between the number of food species used each day and the distance traveled (Spearman Rank, $R_s = 0.59$, $p < .001$).

In both areas there was a persistent pattern of 1 to 2 primary resources and 4 to 5 secondary resources used each day. Fruit species were more likely to be primary resources than leaves. Both primary and secondary resources were constantly changing. The 2 study areas were basically similar with respect to this pattern of primary and secondary food sources except for the fact that in the Lutz Ravine howlers more often used fruit species as primary sources than in the Old Forest. Also, there was less turnover of primary sources in the Lutz Ravine.

RANGING PATTERNS. Howler monkeys have been described as having a ranging pattern in which they remain in one particular locale for several days and then travel some 1000 m to a new area of their home range (Carpenter, 1934; Richard, 1970). Though there were times when this pattern was noted, my data show that howlers usually travel a certain regular amount each day and within a 5-day period generally manage to cover about a quarter of their home range by moving some 450 m a day (Table 7).

Table 7.—Daily travel distance. Data are means of distances in meters traveled during sample days.

	Old Forest	*Lutz Ravine*
July	322	304
August	351	594
September	307	561
October	405	498
November	393	361
Wet Season	355	463
February	396	495
March	604	590
April	441	564
Dry Season	480	550
Eight Months	399 (± 124)	486 (± 164)

Because howlers eat an average number of six species a day and because of the way their food is distributed in the Barro Colorado forest, howlers presumably have to move a certain amount each day to meet their dietary requirements. Typically they move out in a given direction from a set point and forage from tree to tree, moving forward and doubling back. Often, over a period of several days they make a wide loop and come back to their original starting point.

The Lutz Ravine howlers travelled significantly farther each day than the Old Forest howlers (M-W, $p < .01$). Having a great many fig trees in the home range seems to ensure an even balance of fruits and young leaves in the diet, but apparently howlers must travel farther either to find the fig products, particularly fruit, which appear to be always available in this area but which are spread out over the home range, or to obtain the supplementary foods needed to balance a diet highly dependent on fig fruits and leaves in an area of secondary forest demonstrated to be somewhat more clumped in species distribution than the Old Forest.

TIME BUDGETS. The time budgets for daily activities of howler monkeys are remarkably consistent throughout the year (Table 8). Also, as Table 8 shows, the time budgets of Lutz Ravine and Old Forest howlers are virtually identical. The percentage of time alloted to the 4 primary activities of a howler day—resting, moving (changing location within a tree), traveling (changing location from tree to tree), and feeding (defined above)—is very regular and there are no significant differences between the wet and dry seasons in either area.

Discussion

The data presented above show that the diet of the howler monkey on Barro Colorado regularly includes

Table 8.—Howler time budget. Data are means of percentages of time spent at 4 primary activities during sample days.

Activity	*Study area*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Wet season*	*Feb.*	*Mar.*	*Apr.*	*Dry season*	*Eight months*
Feeding	Old Forest	15.2	14.1	14.8	14.3	15.1	15.0	14.0	20.9	14.9	16.8	15.7
	Lutz Ravine	17.4	14.5	14.8	14.3	18.1	15.8	12.9	19.8	12.5	15.1	15.5
Traveling	Old Forest	9.9	8.8	6.4	10.8	10.6	9.3	8.5	14.9	10.8	11.6	10.2
	Lutz Ravine	8.6	12.8	10.4	11.2	8.1	10.2	11.7	9.7	8.6	10.0	10.1
Moving	Old Forest	2.0	6.0	4.4	3.2	3.0	3.7	2.3	3.2	1.2	2.2	3.1
	Lutz Ravine	3.9	7.0	2.5	1.2	4.8	3.9	4.0	1.8	1.7	2.5	3.4
Resting	Old Forest	67.8	61.9	71.8	68.0	66.5	66.9	68.8	55.7	70.3	64.7	66.0
	Lutz Ravine	64.4	58.9	68.8	68.8	66.0	65.4	64.9	64.5	74.0	67.7	66.3

a substantial proportion of foliage. The leaves eaten, however, are almost entirely *young* leaves. Smith (1977), in his study of the Barro Colorado howler, also noted that with 1 exception (some *Cecropia* leaves), all leaves eaten by howler monkeys were either still growing or the youngest leaves on the branch. As noted above, some young leaves have been shown to have higher contents of protein and soluble carbohydrates and lower contents of structural materials and toxic compounds than mature leaves. Thus, howlers may prefer young leaves because they provide a higher return of energy and nutrients per unit weight.

Howlers almost always ate *both* leaves and fruit each day. On certain days when a study troop was feeding in a particular tree, there seemed to be enough flush or fruit available (as evidenced by the fact that occasionally another howler troop would enter the tree on the same day and feed heavily from it) so that the monkeys could have spent the entire day feeding only on leaves or fruit. The fact that they generally did not indicates that howlers prefer to feed each day on both food categories, and that leaves and fruit together provide them with the best balance of energy and nutrients. Eventually, chemical analyses extending the work of Hladik et al. (1971) should give a clearer picture of the energetic and nutritional components of the howler diet.

The diet of the Barro Colorado howler is quite diverse. Howlers eat large numbers of plant species and most of these species are constantly changing over time. Freeland and Janzen (1974) have pointed out that herbivores may be forced to eat small amounts of several kinds of food both because they need a range of nutrients and because they can safely ingest and degrade only a limited amount of any given toxin. Howlers may have to use a variety of leaf sources at any one time to avoid ingesting and accumulating too much of the toxins contained in the leaves of any particular species. They may have to combine different foods each day, selecting from what is available and accessible to them, in such a way as to maximize the energetic and nutritional benefits while minimizing the costs of detoxification. It has been suggested that Barro Colorado howlers use a relatively limited number of food species (Hladik and Hladik, 1969; C. M. Hladik, 1978). The fact that howlers in the Lutz Ravine spent 80 percent of feeding time on 14 plant species may indicate the degree of concentration on food species, but it does not define the number of food species required; a further 56 species were evidently required by howlers in this area to meet their dietary needs.

Both the diversity of food species and their high rate of turnover must at least in part be related to the highly heterogeneous composition of the forest on Barro Colorado and the various phenological strategies of the tree species. For a relatively large animal such as a howler monkey, the great diversity of plant species would make it difficult to specialize on only a few species, since the probabilities of encountering them in any given area would be very low. Further, there might not be any new leaves, fruit, or flowers available in such species at a given time, since most species are discontinuous producers of those items. By diversifying and changing the species used as food sources, howlers are able to take advantage of the different phenological cycles of plant species on Barro Colorado and maintain a diet based on seasonal foods throughout the year.

As noted, howler monkeys avoid eating leaves from some relatively common tree species. They seem to have strong preferences for certain species and even for certain individuals within some species. Each plant species and plant population produces a diverse set of secondary compounds (Freeland and Janzen, 1974). It is unlikely that any one herbivore species would have a detoxification system complex enough to deal with the full spectrum of secondary compounds. The food preferences of howler monkeys may indicate that during their evolutionary history and/or life span, they have developed mechanisms (physiological and/or behavioral) that cope more efficiently with the secondary compounds of certain plant groups. The families for which howlers show strong preferences, Moraceae and Leguminoseae, are widely distributed throughout the Neotropics. Asynchronous intraspecific fruiting and flushing cycles and/or frequent fruit and leaf production in some members of the Moraceae and the relatively high nitrogen content and low toxicity of some young leaves in the Leguminoseae may partially explain the preference shown for these 2 families (Orians and Janzen, 1974; Smith, 1977).

Many elements in the foraging behavior of howler monkeys are very similar to what Freeland and Janzen (1974) have predicted for "generalist" herbivores. They have suggested that because of the danger and metabolic cost of consuming plant secondary compounds, we can expect that body size and hunting strategy of many herbivores have been selectively adapted to diversify the number of chemical types of foods available rather than to maximize the quantity eaten of any particular food at any one time. Among their list of predictions for a generalist herbivore are: (1) a number of different staple foods over a short period of time; (2) a continuous food sampling program; (3) preferential feeding on foods with which they are familiar; (4) preference for foods containing only minor amounts of toxic plant compounds; and (5) the capacity to seek out and eat plants containing highly specific classes of nutrients. These predictions appear to have been fulfilled by the preliminary results of my fieldwork on the howler monkey.

Earlier in the paper, I made the distinction between anatomical folivores, which have highly specialized features in their digestive tracts associated with leaf-eating, and behavioral folivores, which apparently lack specializations of this type and/or magnitude. Given a choice, both anatomical and behavioral folivores should select foods that give the highest net yield of energy and nutrients. Thus, whenever possible, they should prefer to eat young leaves, fruits and flowers rather than mature leaves. Anatomical folivores, however, have been observed to eat relatively high proportions of mature foliage, often from only 1 or 2 tree species (Ripley, 1970; Hladik and Hladik, 1972; Richard, 1973; Clutton-Brock, 1974, 1975; Curtin and Chivers, 1978). Their specialized digestive tracts presumably enable them to utilize such foods efficiently; the activities of their extensive gut flora could make an important contribution to the energy metabolism of such animals, as well as providing additional protein and vitamins and performing detoxificatory functions (Bauchop and Martucci, 1968; Bauchop, 1971; Scheline, 1968; and others).

Though behavioral folivores may also benefit from the activities of gut flora, the morphological differences suggest that they are less efficient than anatomical folivores at utilizing foods that are high in structural materials. In particular, behavioral folivores may be under greater pressure to get soluble carbohydrates from other types of foods, such as fruits. They may depend more on fruit (and/or flowers) to provide the ready energy they require not only for maintenance and daily activities, but also to help defray the costs of detoxification. As noted, howler monkeys do prefer to eat both leaves and fruit each day and further show a daily pattern of first eating fruit and then eating leaves.

Howler monkeys in some habitats spend as much as 62 percent of their annual feeding time on leaves (Glander, personal communication), and in some months on Barro Colorado howlers spent as much as 65 to 80 percent of their overall feeding time eating leaves. In other habitats (Schlichte, 1978) and in other months on Barro Colorado, the proportion of fruit was more than 80 percent of feeding time. Yet, my data show that howlers were no more active when they were eating a high proportion of fruit. This suggests that the howler's daily level of activity may in part be programmed for periods of low fruit availability. At such times, all of the howler's daily energy intake and even some energy reserves may be utilized for maintenance activities and the detoxification of secondary compounds in its foods.

Though many Neotropical primates eat some leaves (Hladik and Hladik, 1969; Kavanagh and Dresdale, 1975; C. M. Hladik, 1978; W. Kinsey, personal communication), the howler is the only Neotropical primate thus far studied that spends more than 40 percent of its annual feeding time on foliage. In the Old World, leaf-eating monkeys comprise the highest percent of the arboreal mammalian biomass (Eisenberg et al, 1972). Though howler monkey populations do have a considerably higher biomass than other Neotropical primates, they have not reached densities equal to those observed for folivorous primates in the Old World (Eisenberg and Thorington, 1973). Eisenberg and Thorington (1973) suggest that this may be because ancient and highly specialized primary consumers, the sloths, have pre-empted the role of folivore specialist in the New World. It would seem that the relatively low density of folivorous primates in the New World may be due to the lack of highly developed anatomical specializations for leaf-eating. Without such specializations, howlers cannot utilize large amounts of mature leaves (at least from most species) as a food resource. Thus, their ability to penetrate the leaf-eating niche would have been limited. In the Old World, on the other hand, the development of ruminant-like specializations led to an adaptive radiation and higher densities of leaf-eating primates. Whereas sympatry between different species of Colobinae and Indriidae is common, there is as yet no evidence of sympatry between different species of *Alouatta*, which suggests that they all occupy the same dietary niche. It further suggests that food in this niche may be limited.

Summary

The data I have presented and discussed suggests the following view of the howler monkey.

1. Howler monkeys are generalist primary consumers of the type that I would call *behavioral folivores*. They appear to lack highly specialized features in the digestive tract associated with leaf-eating such as those of colobines and indriids, which I would call *anatomical folivores*. Lacking such specializations, howlers are presumably less efficient than the latter at utilizing abundant perennial foods such as mature leaves that have relatively high contents of structural materials and secondary compounds.

2. Howler monkeys on Barro Colorado regularly eat a substantial proportion of leaves, but they show a strong preference for immature leaves, which are less abundant than mature leaves and, for most plant species, are only seasonally available.

3. Fruit is very important in the howler diet and is also a seasonal food source. Howlers apparently prefer to eat both leaves and fruit daily (supplemented at times by flowers and flower buds).

4. The howler diet does not appear to consist of foods from a limited number of common plant species. There is great diversity overall and a certain amount of diversity each day in the food species used. There is also a high turnover of food species over a period of time.

5. The food species used are not necessarily the most common species within the howler's home range, which suggests that there are preferences for certain tree species and families.

6. Food may always be available somewhere within the howler's home range, but it is not always readily available nor easily obtained. The howler must constantly change the species used for food and monitor its home range for food sources. It may get the same basic diet each day, but only by using different species.

7. Howler troops have a ranging pattern of traveling a certain distance each day, often traveling in loops over several days. This may be a strategy that enables them to continuously sample and monitor potential food sources while keeping a number of known food sources within a short distance.

8. The daily activity patterns of howlers, as measured in time, are remarkably even from day to day and month to month, and howlers spend a relatively high proportion of their time resting. The regularity of their behavior suggest that howlers are able to avoid extreme fluctuations in their voluntary expenditure of energy, and the low level of activity may enable them to maintain reserves of energy for times when fruits are in short supply.

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A Preliminary Report on the Habitat Utilization of a Group of Howler Monkeys (*Alouatta villosa pigra*) in the National Park of Tikal, Guatemala

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Introduction

In their influence on the vegetation, primates play an important role in the ecosystem of the tropical forest (Hladik and Hladik, 1969). Several authors have tried to describe this role for the howler monkey, *Alouatta villosa* (Altmann, 1959; Carpenter, 1934; Chivers, 1969; Richard, 1970). Most of the work was done on Barro Colorado Island, Panama Canal Zone; others worked in Venezuela and Peru. Only recently have investigations been conducted by Glander (1975) in Costa Rica. More field investigations in different biotopes are necessary to clarify the actual and potential influence of the howler in the ecosystem. Since Guatemala is one of the most northern countries in which howlers are found (Hall and Kelson, 1959), investigations of the feeding behavior and habitat utilization are of interest for obtaining comparable data on the ecology of the howler monkey.

The area of investigation was situated in the mountain forest of Guatemala, 25 km north of Coban, the capitol of the District of Alta Vera Paz. Because of severe observational difficulties encountered on the terrain, only a few observations between March and August 1974 could be made. A more suitable place was found in the lowland of the Peten District, 400 km north of Coban, at the National Park of Tikal. A study of the energy budget of the same primate population in Tikal was carried out by Coelho (1974). This provides us with the added advantage of reliable data on repeated observations by independent observers. Unfortunately my study, like Coelho's (June to August, 1973), was of short duration and had to be finished in 4 months (October 1974 to January 1975).

Study area

The National Park of Tikal was erected to protect the famous archeological site of Mesoamerica, the ruins of the old Maya capitol. Over an area of 567 km^2, numerous ruins—mostly located on small elevations up to 250 m—are scattered throughout the mainly level park. The center, situated on a small hill (225 m), is covered by palaces and temples which are approximately 70 m high. It is surrounded by so-called "bajos" or flat broad areas in which water accumulates during the rainy season from June to October. The *bajos* dry out during the hottest period of the year from December to May. Because of the limestone substrate, no streams or permanent pools occur. A map of the archeological site was used for planning the grid system.

In contrast to the easily accessible area in Tikal is the topography of the area near Coban. The latter site is situated on the slope of a 2000 m high mountain (rocky limestone). The study and searching were conducted at an altitude of about 1000 m (ranging from 800 to 1500 m). No trails existed and steep canyons, bottomless holes, and huge rock barriers made searching and following nearly impossible. The attempt to use biotelemetric techniques failed because of my inexperience in catching the animals by means of a narcotic gun. All of these difficulties forced me to change to Tikal.

Vegetation

The vegetation of Tikal was described by Lundel (1934, 1937). I took my own vegetation census by placing a grid on that part of the map which covers most of the howler group's range. In this way, marked quadrats of 250 × 250 m were established. In the middle of each of these quadrats in an area of 25 × 25 m, I recorded the number of trees with a diameter of more than 10 cm above the buttress.

The scientific names were obtained with the help of identification books, based on the local names. The *ramôn* (*Brosimum alicastrum*) is the most common tree, followed by *zapotillo* (*Sideroxylon* sp. and *Lucuma durlandii*), and the *tzol* (*Tikalia prisca*) (Table 1). The first 10 most common tree species made up 78 percent of 301 trees counted. I studied the distribution of *ramôn* trees, which turned out to be the main food sources for the howlers (Coelho, 1974). In the area inhabited by the group observed, I selected 3 quadrats each 250 × 250 m; 2 were located at the hill site and 1 in the *bajos*. Here, I counted the frequency of *ramôn* trees with a diameter over 10 cm. In the *bajos* remarkably fewer *ramôn* are found than at the hill site. The trees seem to grow mainly on rocks or ruins, a fact which has implications for the interpretation of the spatial utilization by the group.

The fruiting period for *ramôn* was described in a nonquantitative way. Upon arrival in Tikal on September 18, 1974, I found ripe, orange *ramôn* fruits; the next time, on October 15, *ramôn* had small fruits 2-3 mm in diameter. In November, the fruits ripen gradually and a few male flowers could be seen; in December, the fruits have a diameter of about 0.5-1 cm. Most of the male flowers have dropped off by the end of December. In January, the fruits thicken to 1-3 cm. By mid-January, within four days, these fruits turn orange and have a sweet pulp. Beginning in February most fruits fall off and the first immature fruits begin to appear.

The vegetation of the Coban study area was not identified. It is expected to be very different from that in Tikal and certainly *Brosimum* is not so important.

Methods

Various observation techniques have been applied by investigators on arboreal primates (Carpenter, 1965; Coelho, 1974). I followed a group continuously for one week and observed their daily activities from 6 A.M. to 6 P.M. While following the group, I collected information on the quality of foraging and feeding, play, social contacts, and other behavior. I found it reasonable to collect samples in terms of 5-minute blocks. Data were recorded every 5 minutes on a tape recorder. For the most part, the group members acted synchronously and the activity of the group as a whole was recorded. If a member acted differently from the group, this was recorded, but the activity of the majority was also recorded as the group activity for the interval.

Table 1.—Tree species occurring in the study area at Tikal expressed as frequency of occurrence and percentage of total

No.	F_1	*%*	*Local name*	*Scientific name*	*Family*
1.	50	17	Ramón	Brosimum alicastrum	Moraceae
2.	49	16	Zapotillo	Syderoxylon sp.	Sapotaceae
				Lucuma durlandii	Sapotaceae
3.	32	11	Tzol	Tikalia prisca	Sapindaceae
4.	31	10	Cedrillo	Trichilia hirta	Meliaceae
5.	17	6	Jobo	Spondias mombin	Anacardiaceae
6.	14	5	Sesmóo	?	?
7.	12	4	Huevos de caballo	Stemmadenia mombin	Apocynaceae
8.	11	4	Malerio blanco	Aspidosperma megalocapon	Apocynaceae
9.	10	3	Pimenta	Pimenta dioica	Myrtaceae
10.	10	3	Chintiok	Wimmeria bartlettii	Celastraceae
		79%			
11.	7		Palo de limon	?	?
12.	5		Chico zapote	Archas zapota	Sapotaceae
13.	5		Copal	Protium copal	Bureraceae
14.	5		Yaxnic	Vitex gaumeri	Verbenaceae
15.	4		Chacaj	Bursera simaruba	Burseraceae
16.	4		Botán	Sabal sp.	Palmaceae
17.	4		Pellejo	?	?
18.	3		Subin	Honchocarpus guatemalensis	Leguminosae
19.	3		Mano de leon	Sterculia apetala	Sterculiaceae
20.	3		Testáp	?	?
21.	2		Quebracho	Krugiodendron ferreum	Myrtaceae
22.	2		Chile chachalaca	Allophylas cominia	Sapindaceae
23.	2		Anonilla	Annona sclerodema	Anonaceae
24	2		Guaya	Talisia olivaefermis	Sapindaceae
25.	2		Higo	Ficus sp.	Moraceae
26.	2		Zoplillo	?	?
27.	1		Manchiche	Lonchocarpus castilloi	Leguminosae
28.	1		Aguacatillo	Phoebe sp.	Lauraceae
29.	1		Silion	Pouteria (?) amygdalina	Sapotaceae
30.	1		Guarumo	Cercropia sp.	Moraceae
31.	1		Luin	Ampelocera hottlei	Ulmaceae
32.	1		Capulin silvestre	Xylopia frutescens	Anonaceae
33.	1		Amaté	Ficus sp.	Moraceae
34.	1		Cedro	Cedrela odorata	Meliaceae
35.	1		Caoba	Swietenia macrophylla	Meliaceae
36.	1		Ceiba	Ceiba pentandra	Bombacaceae
	301				

Because of the group's cohesion, I could easily define which tree was visited during daily movements. The trees were then marked with spray paint. Later, the species were identified; the distance between the trees measured; and their positions marked on a map. This method showed the exact traveling route of the group, and the distance which they traveled could be measured.

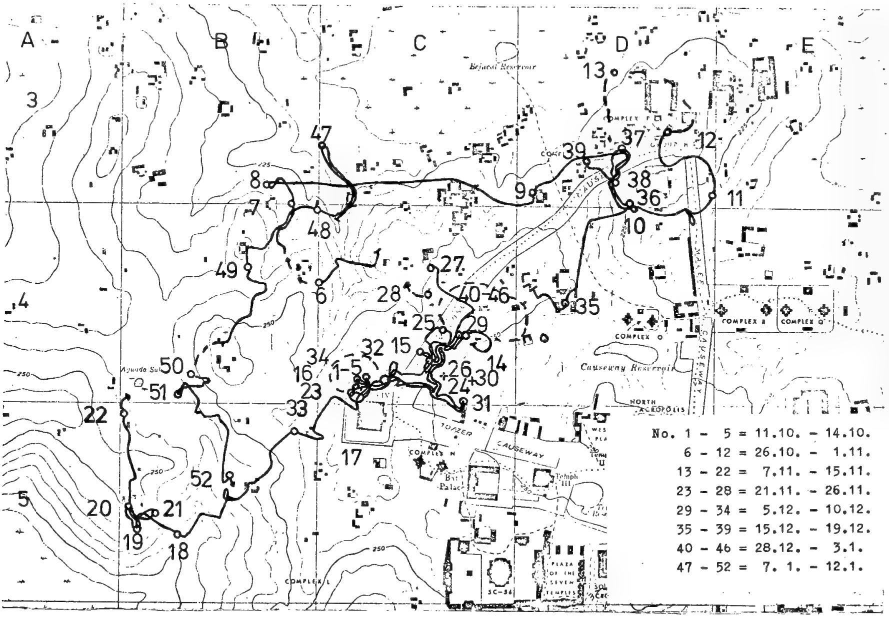

Figure 1. Routes traveled by the group. Numbers are attached to the sleeping trees (circles) for different observation days. The exact dates are tabulated in the right corner.

Results

Group composition, neighboring groups, and home range

The group observed (Group A) consisted of one old male (characterized by very sparse fur and a large subcutaneous swelling caused by botfly larvae on the right side of the thorax); a smaller, younger male; a female (characterized by a swollen vulva which remained in that state even when she gave birth to a male baby between November 27 and December 4, 1974); a younger female (with thick black fur and a small vulva); a juvenile (with a swelling on the neck); and a smaller juvenile. Because of the characteristically marked old male, I could identify the group easily.

The route Group A traveled during the period from October 11 to January 12 (shown in Figure 1) gave a rough estimate of the range the group occupied at that time. The home range covered about 125 ha, much higher than values previously recorded (Coelho, 1974). No other groups were seen within this range.

One other group (quadrat C/2) consisting of one male, two females, and one juvenile female, was detected to the north. I heard roaring north of the airfield in quadrat F/3 and south in D/7, but could not locate the animals. I found one solitary male in E/8, south of the home range of Group A. Near the "Bat Palace," I met a single female with her juvenile (female). I followed her for 2 days without meeting other howlers as she traveled toward Complex L. This lack of other howler groups in the vicinity of Group A is in sharp contrast to the findings of Coelho (1974), who found 4 groups, 2 exactly in the range of Group A and 2 southward also occupying wide areas of that range.

At the Coban study site, I found 4 groups within a 200 ha area. These included a total of 21 adults and 2 infants; 1 2-male group, and 1 solitary male. This gives a population density (13/100 ha) twice as high as that recorded for Tikal by Coelho (5 monkeys/100 ha). The composition of 2 of the 4 Coban groups was as follows:

Group A: 1 male, 1 female, 1 female with baby (male), 1 female juvenile.
Group B: 1 male, 2 females, 1 female with baby (female), 1 female juvenile.

Feeding

Of the 36 tree species which are most common in the area inhabited by the group, only 7 were seen to be eaten by the howlers (Table 3). The picture becomes even more extreme if the time (in 5-minute units) that the group spent feeding in these 7 tree species is considered. Most of the time (87.5 percent), the group was occupied with eating *ramón*. Thus, the howlers observed are extreme food specialists, depending almost totally on 1 food tree. This does not mean that they need to depend on that tree. Indeed, it is hard to understand why they do not utilize other food sources, for example, as the spider monkey (*Ateles*) does. During November and December, spider monkeys were seen very often eating the fruit of *Jobo* (*Spondias mombin*) which is also eaten by various other animals, such as agoutis (*Dasyprocta*), or peccaries (*Tayassu*).

From the *ramón* tree, the leaves and fruits, and in some cases even the male flowers are eaten. The fruits are consumed at all stages of ripeness: in the first stage (up to 2 mm), the whole fruit with adjacent sprouts and leaves; in the second stage (1–2 cm), the entire fruit with seeds and pulp; in the next stage, mainly the seed is preferred and the pulp spat out. In the ripe, orange state, both seed and pulp are eaten. *Ramón* seems to be a main food source for all kinds of animals in this area. That Coelho reported 74 percent *ramón* fruit pulp and only 2 percent *ramón* seeds were eaten may be due to the fact that he observed the feeding behavior during a period when the *ramón* fruit was ripe. It was my impression that howler monkeys were mainly eating seeds, but it was difficult to distinguish whether they were eating fruit or pulp.

The leaves from *amate* (*Ficus* sp.), *higo* (*Ficus* sp.), and *malerio* (*Aspidosperma megalocapon*) contain a large amount of latex, as do the fruits of *amate*. The pulp of these fruits is preferred.

In general, howlers are not very refined in eating various parts of a plant; for instance, the entire leaf is eaten and no distinction is made between the stem and the other parts.

Home-range utilization

The general pattern of traveling described by Carpenter (1965) was confirmed by my observations (Figure 1): "Several days limited travel were periodically followed by unusually long and fairly continuous marches." The distance covered varied from about 40 m to 700 m per day with an average of 250 m. The tracks were concentrated near Temple IV, since the group spent 27 out of 52 observation days there. It is in this area that Coelho had seen 3 of his 4 groups. Another concentration was near Complex P (D/3); the group was seen there 9 times. It was seen 5 times near a ruin in quadrat B/5. The group concentration could be explained by the abundance of fruit-bearing *ramón* trees found there. As mentioned above, *ramón* usually grows on rocky limestone, the material commonly used for the now-ruined structures.

The tendency of the group to actively seek out the food trees can be seen by comparison of the frequency of tree species visited with the frequency of occurrence of tree species (Tables 1 and 2). If the

Table 2.—Percentage of time fed on different food plants by Alouatta.

No.	*Local name*	*Scientific name*	*Observed 5-min units*	*%*	*Comments*
1.	Ramón	Brosimum alicastrum	794	87.5	fruits, leaves, buds
2.	Higo	Ficus sp.	28	3.0	leaves, buds
3.	Amaté	Ficus sp.	25	3.0	fruits, pulp, leaves
4.	Chacaj	Bursera simaruba	17	2.0	leaves
5.	Malerio blanco	Aspidosperma megalocapon	11	1.0	leaves
6.	Cola de garobo	Ximenia americana	9	1.0	leaves
7.	Chico zapote	Archas zapota	3	0.3	fruits
8.	Lianas		13	1.5	leaves, fruits
9.	rest		7	0.7	
			907		

Table 3.—The tree species of Tikal which were visited by Troop A from October 1974 to January 1975. (See text for explanation of calculations.)

No.	F_2	*%*	F_2/F_1	*Local name*	*Scientific name*
1.	423	64	4	Ramón	Brosimum alicastrum
2.	24	3.6	1.8	Chico zapote	Archas zapota
3.	23	3.5	0.3	Tzol	Tikalia prisca
4.	17	2.6	7.8	Amaté	Ficus sp.
5.	14	2.1	0.5	Huevos de caballo	Stemmadenia mombin
6.	14	2.1	3.2	Higo	Ficus sp.
7.	14	2.1	2.1	Mano de Leon	Sterculia apetala
8	13	2.0	0.5	Malerio blanco	Aspidosperma megalocapon
9.	13	2.0	1.5	Chacaj	Bursera simaruba
10.	12	1.8	0.3	Jobo	Spondias mombin
11.	12			Cedro	Cedrela odorata
12.	9			Yaxnic	Vitex gaumeri
13.	8			Silión	Pouteria amygdalina (?)
14.	8			Chimón	Ficus sp.
15.	7			Manchiche	Lonchocarpus castilloi
16.	6			Cedrillo	Trichilia birta
17.	5			Caoba	Swietenia macrophylla
18.	5			Chilechachalaca	Allophylas cominia
19.	5			Pimenta	Pimenta dioica
20.	5			Salte mucho	Sickingia salvadorensis
21.	3			Chintoc	Wimmeria bartletii
22.	3			Sackiché	?
23.	3			Cola de garabo	Ximenia americana
24.	3			Copál	Protium copal
25.	2			Quebracho	Krugiodendron ferreum
26.	2			Botán	Sabal sp.
27.	2			Capulin silvestre	Xylopia frutescens
28.	2			Sesmóo	?
29.	2			Guaya	Talisia olivaefermis
30.	2			Ceiba	Ceiba pentandra

group located its food trees by chance, one would predict the same frequency distribution of visiting as of occurrence. Six of the food trees, however, are in the group of the 10 most frequently visited, but do not occur most frequently in that area. This tendency can also be seen by comparing the quotients of the relative frequency of visits (F_2) and relative frequency of occurrence (F_1) of a specific tree species (Table 3). The group seemed to know the topography of its home range very well. As reported by most of the investigators (Bernstein, 1964; Richard, 1970), certain pathways were used. In 4 instances the group used the same tree path, sometimes for a distance of 250 m and often after longer lapses in time.

Activities

The picture of the howler as a very inactive animal, as described by several authors, is also confirmed by this study. Out of a total of 3980 5-minute observation periods on 28 observation days, 1629 periods are spent resting (66 percent), 471 periods moving and shifting (12 percent), and 890 periods feeding and foraging (22 percent). These figures differ slightly from those found by Richard which were 80, 9 and 10 percentage points respectively. The diurnal pattern of activity is in good agreement with the findings of Coelho (1974) and Altmann (1959). By measuring the distances traveled and time spent moving and shifting, a sharp peak for movement occurs between 1:30 P.M. and 3:00 P.M., a small maximum activity peak at 10:00 A.M. to 11:00 A.M. was also obtained (Figures 2 and 3). An additional resting period occurred between 12 noon and 1:00 P.M. An afternoon movement period just before reaching the sleeping places seems to be characteristic of African as well as American primates. This pattern gives only a general picture of the diurnal activity cycle of the group, since the data were obtained by superimposing the day-to-day activity patterns (here a total of 28 days). Activity on any day depended on such variables as climate and food distribution. More information should be obtained when the actual group rhythm is taken into account instead of summing data for the more or less artificial coordinates of time of day. It seems to me that the group had a regular sequence of moving and resting periods as reported by Richard (1970) and Altmann (1959).

Discussion

The general appearance of the howler monkey described in this study is in agreement with the findings of several authors. The howler is a lethargic animal, which "moves slowly between food sources" (Richard, 1970) and has a "very low level of activity" (Richard, 1970). In this study, two-thirds of its daylight activity is resting. Richard (1970) even found about 80 percent resting and Coelho (1974), 60–70 percent for the adult-age class. The howlers know their range well and use pathways, looking actively for food trees. They concentrate for periods of time at such places where food is easily found in abundance.

The striking difference with respect to the findings of Coelho is in the actual habitat-utilization pattern. Coelho found in this same study area 4 groups with a total of 25 animals; I found only 2 with 11 animals. In the quadrat (C/4) where the group observed was concentrating its activities, he saw 3 of the 4 groups. I found only 1 group, although I was informed that there "should be" 3 or 4. In spite of all efforts to find more groups in that area, we only met a single female with her juvenile. Perhaps Coelho with his 8 observers had a better chance to find groups than I who had only 1 assistant. A more likely explanation is that indeed at the time of my observations, only 1 group occupied the area of study. Perhaps in another season, more groups are concentrated in this place. A very reasonable interpretation of differences in habitat utilization could be the influence of a seasonally and spatially dependent food supply.

If shortage of food forced the howlers to concen-

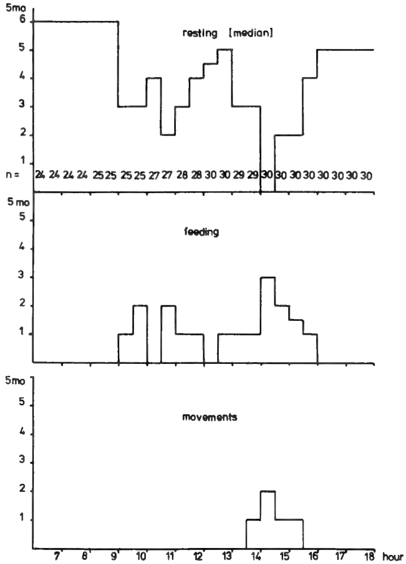

Figure 2. Activity patterns (diurnal cycle) measured in 5-minute units (5 mo) or in traveled distance (paces; one pace, about 0.8 m).

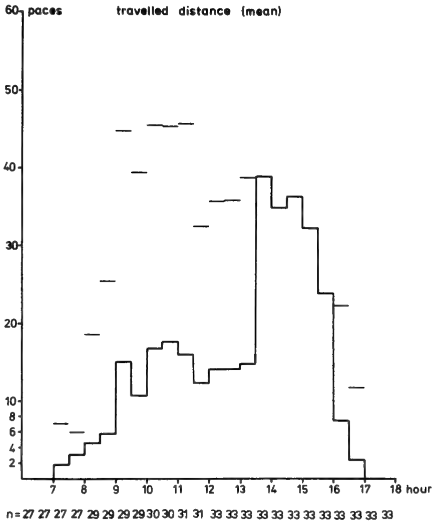

Figure 3. Travel distance as a function of time of day. The small lines above means give the standard deviations; n is the number

trate in certain areas from June to August, then Coelho's statements "that in Tikal food resources available to animals (here, primates) are not limiting population size to its present level" or "the concept of food resource limitation is largely a myth among primatologists" must be rethought. First, it is questionable whether a 3- or 4-month observation period is sufficient to provide an answer to the question of whether food availability or other factors are responsible for the limitation of a given animal population. At least 2 main factors directly influence the population size, as Denham formulates it: "In considering primates in their habitats, those parts of the environment with which we must deal directly are food and predators" (Denham, 1971). On the "predator" side, the microscopic fauna is the most important regulator of howler population as are diseases and ecto- as well as endo-parasites. Probably this could be the main factor determining the howler population in Tikal at its present level: 10 years ago a large yellow-fever epidemic was reported in Guatemala. While this virus affects spider monkeys as well as howlers, an interesting question would be why the spider monkey has recovered fairly well and shows a higher density now than the howler (Coelho, 1974).

In addition to the above speculation, a further question concerns whether the analysis of population density and food limitation based solely on the main energy input could bring us closer to an answer of whether a population is dependent on food supply. Ecologists agree mainly that "as a rule animals consume a very low percentage of the food available" (Remmert, 1974). But need the inversion of this statement that food is always plentiful in the habitat and is not a limiting factor be true? Remmert (1974) reports cases in which food can be a limiting factor although it is plentiful in the habitat. He explains this by (1) the lack of co-factors in the diet, (2) the lack of a certain balance in the diet at certain times, and (3) by the occurrence of poisonous compounds (alkaloids) in the food.

Another question is whether Coelho, in estimating the energy budget of the primates in Tikal, took into consideration the errors which could occur. The energy budget of an animal population is balanced between the energy production on the one hand and the energy expenditure on the other. The energy production is simply computed out of the *ramôn* productivity brought into the formula: $E = D \times P \times C \times A/56$ kcal/24 hours for the 8-week (56 days) fruiting period, where E is the energy available ($50.1375 \cdot 10^6$ kcal/24 hours).

D is the number of fruit-bearing *ramon* trees/ha (38.2)
P is the production of fruits/tree (56.4 kg)
C is the weighted kcal value of the fruit/kg (2606 kcal)
A is the area in ha inhabited by the group (500 ha).

The factors D, P, and C were estimated by Coelho and could be subject to error. Of major importance is the number of fruit-bearing trees (D). According to Coelho, *ramôn* has 3 fruiting periods: February to March, June to July, and October to November. During these periods not all *ramôn* trees bear fruits. In addition the amount of fruit is certainly not distributed evenly throughout the periods. Near the end on January 24, I noted that only 20 percent of the trees had fruits; one week later (February 5), 15 percent had fruits. At the end of the period, the fruits fall rapidly and perhaps only 1 percent had fruit. If at any time of the fruiting period only 10 percent of the *ramôn* would bear fruits, then the number of primates supported by the area, for which Coelho gave the value 42,500, would be less by a factor of 10. Three times in the year, the fruiting period lasts 8 weeks. If the primates were totally dependent on *ramôn*, it would be difficult for them to find food between the periods. I found, however, that the periods lasted longer than Coelho has assumed and that no abrupt break occurred between the beginning and end of the periods. At the beginning of the fruiting period, the monkeys must feed on immature fruits, which differ in their caloric value from the mature fruits on which Coelho's calculations are based.

Ramôn occurs in a much smaller area than assumed by Coelho (500 ha). I estimated that *ramôn* grows only in 15 out of 20 quadrats; 5 of these are "bajos" or human habitations. On the other hand, the productivity of a *ramôn* tree might be underestimated; however, I consider Coelho's assumption to be correct: that is one-fourth of the available fruits are actually eaten and the other part is eaten by other animals or falls down and is unavailable.

The crucial question as to whether plenty of food is always available remains of major importance and must be answered by further investigation in Tikal. One must keep in mind that "prediction concerning the energy flow in ecosystems is only possible, if the mechanisms of population control have been studied" (Remmert, 1974).

Summary

The study was carried out between October 1974 and January 1975 on a population of howler monkeys, which was observed 1 year before by A. M. Coelho

and C. A. Bramblett during a 2-month study on energy budget of howler and spider monkeys. Additional observations for comparison were taken in the highlands of Guatemala. In Tikal, 1 group of howlers was followed daily over a period of 5 to 7 days at 1-week intervals. The group could be recognized, especially on the basis of a characteristically marked adult male. The exact route and the trees visited by the group were identified and plotted on a map, giving an accurate picture of how the home range was utilized. In an area of 130 ha, certain locations were preferred which could relate to an abundance of the main food source. The same route was used repeatedly over long distances. Using 5-minute intervals, various data were gathered from 6:00 A.M. to 6:00 P.M. The amounts of time spent feeding, resting, and in motion were recorded. The main food source was *Brosimum alicastrum,* as Coelho and others have stated. About 70 percent of feeding time was spent on the fruits of this tree, which were eaten at all stages of growth. The group actively sought out trees which bore their favorite fruits. Group size, population density, and home range seemed to be similar to that of a howler population studied in the highlands of Guatemala. The data were discussed in view of the results of Coelho (1974) and others.

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Howling Monkey Feeding Behavior and Plant Secondary Compounds: A Study of Strategies

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Introduction

A long-term investigation of the relationship between the habitat and social organization of mantled howling monkeys (*Alouatta palliata* Gray) in Costa Rica was begun in June 1972. The data reported here are the result of a 14-month period between June 1972 and August 1973. During this time, 2071 hours of direct animal observation were accumulated on 172 days. The study group's composition (Group 1, herein) and the observation time for each animal is given in Table 1.

The study site was situated on Hacienda La Pacifica, Guanacaste Province, Costa Rica, at latitude 10°28'N, longitude 85°07'W. Hacienda La Pacifica is a 1330 ha cattle ranch located at the base of the Cordillera de Tilaran, 5 km northwest of Cañas. It is 45 m above sea level and lies within the lowland tropical dry-forest life zone (Holdridge, 1967). Approximately one-fourth of the ranch remains forested; the remainder has been cleared for farming. Total deforestation is not practiced. Instead, windbreak strips and riparian forests are left to protect the soil against wind and water erosion.

Table 1.—Name and age/sex class of each member of Group 1 at the beginning of the study, September 1, 1972. Also, the number of days each animal was the focal animal and the number of minutes each animal was observed.

Animal	*Age/Sex*	*Focal days*	*Time of observation minutes*
Scar	adult male	18	13218
Baker	adult male	19	13563
White/red	adult female	19	13631
Blue	adult female	18	13614
Yellow	adult female	19	13806
Green/red	adult female	19	14271
Dogcollar	adult female	20	14142
Green *	juvenile female	20	14917
Charlie	juvenile male	6	4021
Able	juvenile male	4	2423
Bonnie	juvenile female	5	3128
Shadow	infant male	3	2236
Blue's infant	infant male	2	1325

* Green was classified as an adult after she gave birth on 1/11/73.

The idea of viewing feeding strategies in terms of plant secondary compounds presented in this paper is not original nor of recent vintage (see McKey, 1978, for a similar study). The possible significance of plant produced chemicals was recognized as early as the late 19th-century (Stahl, 1888). For a long time, investigators working with nonprimate organisms—especially insects—have been concerned with the impact of plant secondary compounds (Fraenkel, 1959; Ehrlich and Raven, 1965; Whittaker, 1970; Feeny, 1970; Freeland and Janzen, 1974; and many others). On the other hand, primatologists have been derelict in considering the ramafications of these plant chemicals, especially since the expanding literature indicates that secondary compounds are widely distributed throughout the plant world (Willaman and Schubert, 1961; Watt and Breyer-Brandwijk, 1962; Kjaer, 1963; Shorland, 1963; Hegnauer, 1964; Moir, 1968; Feeny, 1970; Raffauf, 1970; Whittaker, 1970; Janzen, 1971; Whittaker and Feeny, 1971).

The presence of these chemicals does not mean that all secondary compounds are toxic to all organisms; even the very toxic ones can be and are ingested by some organisms (Janzen, 1978). However, the early work of Stahl (1888) in which he suggests that not everything that is green is palatable and the large volume of data since his time contain significant implications for investigators working with herbivorous primates, especially so since many investigators seem to feel that leaf-eating monkeys have an unlimited food resource.

Do leaf-eating monkeys utilize all of the available resources (leaves)? If not, which specific resources do they use and why? The objectives of this paper are to view the strategies of 1 group of folivorous primates for dealing with seasonal food availability and the chemical defenses of plants.

Methods

Details of the methods used to obtain a detailed description of the habitat and the capture and marking of the animals can be found elsewhere (Glander, 1975), but I will provide a brief résumé here in order to place the following data in perspective. Every tree in the home range of the study group was marked with a bright orange ordinal. The tree height, canopy depth, and distance between trees was measured. A map was constructed. Whenever possible the tree was identified as to species (Opler, personal communication). A weekly phenological record of the numbered trees was obtained. Climatological data were recorded at a government weather station located 600 m from the study area.

To collect durational data and overcome many of the problems unique to the study of arboreal primates, I employed the technique of focal animal observation (Altmann, 1974) plus a random method of preselecting the focal animal (Glander, 1975). This method provided a comprehensive record (durational) for all daily activities of a focal animal without sacrificing group dynamics. *Ad lib.* sampling (Altman, 1974) of nonfocal animals was done opportunistically. Durational information is necessary for determining energy budgets (Coelho, 1974), and energy budgets link the animal's social behavior with its environment; an explicit example of possible environmental impact on social structure (in preparation).

In order to insure unambiguoius individual recognition, individualized leather collars with colored metal tags were placed around the necks of all but 1 of the females in the study group. The uncollared female served as a behavioral control for the collared animals. The adult males were readily distinguished by physical markings and the infants and juveniles could be differentiated by their regular close association with particular tagged females. The capture of all animals (except infants) was effected by a CO_2 dart-gun. A large piece of canvas rigged with handles was used to catch the animals as they fell from the trees.

There were several other groups in areas around the study site but only one group (Group 2) had any contact with Group 1. Group 2 spent 69 of the 172 days of observation in the study area. At the beginning of the study, Group 2 contained 6 adult males, 15 adult females, 12 juveniles, and 2 infants. This group frequently split into subgroups of 27 and 8.

Results

Rainfall and temperature

On the basis of rainfall, the study site experienced 2 distinct and separate seasons, a 5-month dry season (December–April) and a 7-month wet season (May–November) (Figure 1). The total rainfall for the study period was 1431 mm.

The pattern of rainfall was somewhat unusual during the study period. Normally, a small dry season (*el veranillo*) occurs in June or July with most of the rain falling before and after the *veranillo*; however, June, July, and August were the wettest months with October being relatively drier (Figure 1).

The long dry season began in late December 1972 and continued until April 27, 1973. The onset of the dry season was gradual with very small amounts of rainfall after November 15, 1972 (ranging from 0.3 mm to 3.2 mm).The last rain fell on December 21, 1972 (3.2 mm). Following that day, no rain fell for 126 days. The first rain of the wet season fell on April 27, 1973 (110 mm). This was not only the beginning of the wet season, but also the day with the greatest amount of rainfall during the study. The sudden onset of the wet season is typical of the seasonal transition from dry to wet and contrasts with the gradual onset of the dry season.

It rained 108 of 358 days during the study. There was an average of 9 days of rain per month. The months of January, February, and March were without rain (Figure 1).

The maximum daily temperature experienced during the study was 37.0° C (Figure 2). The minimum daily temperature was 19.0° C. The mean monthly temperature for the study period was 27.7° C (range 26.1° C to 30.8° C) and the variation in the mean from month to month ranged from 0° C to 2.9° C. Both the hottest and coolest weather occurred during the dry season: April 1973 was the hottest month; December 1972 was the coolest. Strong winds contribute to the desiccation during the dry season.

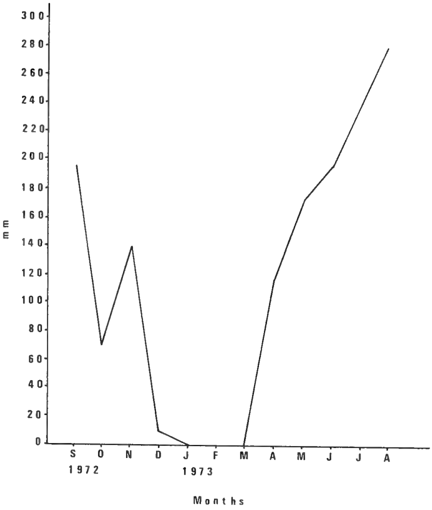

Figure 1. Rainfall for the study site.

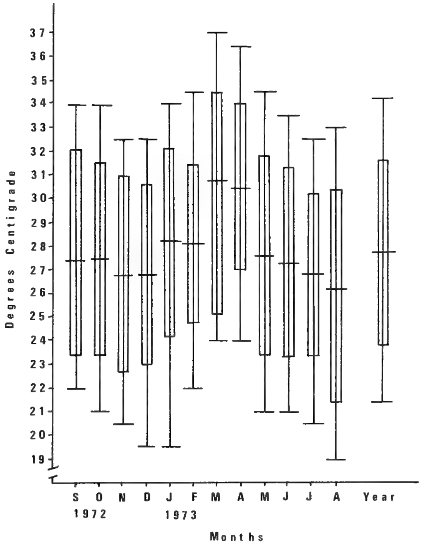

Figure 2. Monthly temperature averages and extremes. Single line represents the maximum-minimum temperature. Double lines represent the average maximum and average minimum temperatures. Mid-line represents the monthly average temperature.

Habitat description

The study site is a strip of remnant forest along the

Río Corobici. Utilizing naturally occurring lines of demarcation—tree phenophases—I conceived the study area as subdivided into 4 areas (Figure 3). Area 2 and Area 3 consisted of riparian forest on the left and right banks of the river, respectively; Area 1 and Area 4 were upland forest extensions connecting with the riparian forest of Areas 2 and 3, respectively. The distinction between riparian and upland forest was based on the phenology of the trees present in the areas. Most of the trees in the upland regions dropped their leaves and remained bare for much of the 5-month dry season. Trees in the riparian areas also were deciduous, but a majority flushed new leaves whenever leaf-fall occurred and maintained their leaves throughout the dry season. Only a few remained bare. The upland and riparian forest areas were markedly distinct during the dry season.

FIGURE 3

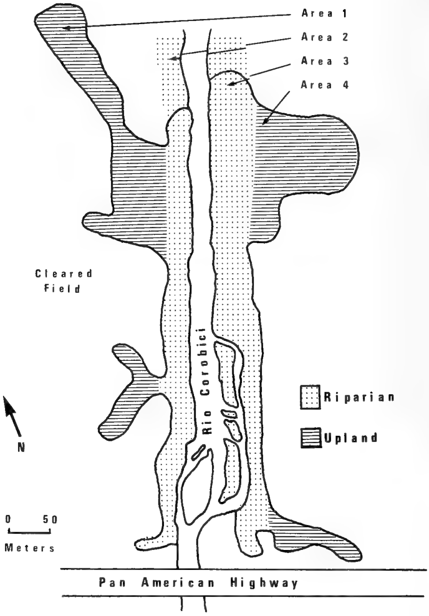

Figure 3. Diagrammatic representation of the study site. The study area was surrounded on all sides by cleared fields except up-river where the riparian forest was continuous.

The riparian forest was composed of trees that formed a general canopy 15 to 20 m high. Emergents reached 33 to 37 m. The average tree height was 11.4 m (S.D. 5.6, N = 981); the average canopy depth was 7.3 m (S.D 4.8; N = 981). Stratification was apparent along the river. The understory in the riparian forest was variable due to browsing by cattle. Epiphytes were sparse with a few orchids and bromeliads present. Ten percent of the tree crowns contained lianas and vines.

The upland forest was composed of shorter trees that formed a canopy 10 to 15 m high. Emergents were rare. The average tree height was 8.3 m (S.D. 3.1, N = 696). The average canopy depth was 4.6 m (S.D. 2.2, N = 969). Stratification was not apparent in the upland forest. Epiphytes and lianas were rare. Vines were present in about 10 percent of the tree crowns in Area 1, but absent in Area 4.

The home range for Group 1 during the 12 months of the study contained 1699 trees, representing 96 species (Glander, 1975). Of these, 992 were tallied in the riparian forest, and 707 were found in the upland forest. The stand for the total area had a density of 172 trees/ha (69 trees/acre). The stand density was 207 trees/ha (84 trees/acre) for the riparian forest and 139 trees/ha (56 trees/acre) for the upland forest. The 96 species represented 79 genera and 37 families. Eight families (22 percent), Anacardiaceae, Bignoniaceae, Borginaceae, Caesalpinaceae, Mimosaceae, Myrtaceae, Papilionaceae, and Sterculiaceae, contained 76 percent of the trees. The family, Leguminosae, which is often divided into 3 families—Caesalpinaceae, Mimosaceae, and Papilionaceae—contained 29 percent (487) of the trees present. The family with the most representatives was Papilionaceae (341) although the 2 most common species were *Guazuma ulmifolia* (Sterculiaceae) and *Cordia dentata* (Boraginaceae). Thirteen families were represented by a single species and 4 by a single tree.

There were 20 dioecious tree species comprising 10 percent (170) of the total trees in the area. An attempt was made to determine the sex of each dioecious tree. Group 1 fed on the fruit of the following dioecious species: *Chlorophora tinctoria, Cecropia peltata, Coccoloba caracasana, Simarouba glauca, Spondias mombin, S. nigrescens.* The individuals of *C. tinctoria* (3 of 6) were equally divided between males and females, but *C. peltata* (1 of 3), *C. caracasana* (1 of 9), and *S. glauca* (1 of 4) had only 1 female each. *S. mombin* (9 of 12) and *S. nigrescens* (7 of 9) had more females than males.

Habitat utilization and day range

In two-dimensional terms the home range of Group 1 consisted of 98,850 sq m (9.9 ha). The upland forest

Table 2.—All tree species used as food sources by Group I listed by family (alphabetical order). The number of individuals of each species and family is indicated.

75	ANACARDIACEAE		
		48	*Anacardium excelsum*
		10	*Astronium graveolens*
		8	*Spondias mombin*
		7	*S. nigrescens*
		2	*S. purpurea*
12	BIGNONIACEAE		
		6	*Tabebuia neochrysantha*
		6	*T. rosea*
1	BOMBACACEAE		
		1	*Ceiba pentandra*
9	BORGINACEAE		
		1	*Bourreria quirosii*
		1	*Cordia alliodora*
		1	*C. collococca*
		5	*C. dentata*
		1	*C. panamensis*
8	BURSERACEAE		
		8	*Bursera simaruba*
16	CAESALPINACEAE		
		11	*Hymenaea courbarill*
		5	*Schizolobium parahybum*
1	CARICACEAE		
		1	*Cariaca papaya*
2	COCHLOSPERMACEAE		
		2	*Cochlospermum vitifolium*
2	EBENACEAE		
		2	*Diospyros nicaraguensis*
8	ELAEOCARPACEAE		
		4	*Muntingia calabura*
		4	*Sloanea terniflora*
1	FLACOURTIACEAE		
		1	*Casearia arborea*
2	MALPIGHIACEAE		
		2	*Byrsonima crassifolia*
8	MELIACEAE		
		1	*Cedrela mexicana*
		2	*Trichilia cuneata*
		5	*Trichilia* sp.
40	MIMOSACEAE		
		1	*Albizzia adinocephala*
		6	*Enterolobium cyclocarpum*
		2	*Inga vera* var. *spuria*
		7	*Lysiloma seemannii*
		14	*Pithecolobium longifolium*
		10	*P. saman*
8	MORACEAE		
		3	*Cecropia peltata*
		2	*Chlorophora tinctoria*
		2	*Ficus glabrata*
		1	*F. ovalis*
2	MYRTACEAE		
		2	*Eugenia salamensis*
76	PAPILIONACEAE		
		22	*Andira inermis*
		6	*Dalbergia retusa*
		15	*Gliricidia sepium*
		1	*Lonchocarpus costaricensis*
		2	*L. hondurensis*
		24	*L. minimiflorus*
		1	*Myrospermum frutescens*
		4	*Pterocarpus hayesii*
		1	*Sweetia panamensis*
2	POLYGONACEAE		
		2	*Coccoloba caracasana*
16	ROSACEAE		
		16	*Licania arborea*
5	RUBIACEAE		
		2	*Calycophyllum candidissimum*
		1	*Chomelia spinosa*
		1	*Genipa caruto*
		1	*Guettarda macrosperma*
2	RUTACEAE		
		2	*Zanthoxylum procerum*
1	SAPINDACEAE		
		1	*Thouinidium decandrum*
11	SAPOTACEAE		
		6	*Manilkara achras*
		5	*Mastichodendron tempisque*
2	SIMAROUBACEAE		
		2	*Simarouba glauca*
5	STERCULIACEAE		
		2	*Guazuma tomentosa*
		3	*Sterculia apetala*
16	TILIACEAE		
		15	*Luehea candida*
		1	*L. speciosa*

contained 50,900 sq m (5.1 ha) and the riparian forest, 47,950 sq m (4.8 ha). However, since Group 1 came to the ground only 3 times, all in the same place, I believe a more realistic estimation of the area used by Group 1 can be obtained by using the average canopy depth for the trees in the study site. Thus, the 3-dimensional area—tree crowns—utilized by Group 1 was 234,140 cu m of upland forest and 350,035 cu m of riparian forest. Further, they spent 160 of the 172 observation days (93 percent) in the riparian forest. Therefore, 93 percent of their time was spent in 60 percent of their home range.

There was considerable variability in the distance covered each day, ranging from 207 to 1261 meters. The average day range for the year was 596 meters, but based on the extreme daily variability the yearly average is all but meaningless. The average daily difference (distance covered on 1 day compared to distance covered on the day immediately before or after the focal day, 76 such records) was 234 meters (range 0 to 742 m). There were only 19 days when the difference between daily distances traveled was less than 100 m; only 1 record where the distance covered was identical. There was a seasonal difference in the average daily distance covered, i.e., 592 m during the wet season and 552 m during the dry season. The seasonal average difference was 246 m for the wet season and 227 m for the dry season.

Resource use

A total of 331 trees, 51 vines, and the mistletoe in 2 trees were utilized as food sources by Group 1 (Table 2). Only the trees will be considered here. Many of the individual trees were used very few times, i.e., 104 were used only once. Based on the time spent feeding in the various trees, Group 1 obtained a majority of their food from only 5.2 percent of the trees available (88 of 1699). They spent 20,074 minutes of their feeding time (75.7 percent) in those 88 trees and only 6461 minutes feeding in the other 243 resource trees.

Additional information about the howlers' feeding pattern can be garnered by returning to the 104 trees used only once. The howlers fed in the 104 trees for 719 minutes. Of the 104, 78 are of the same species as the 88 used for a major part of the food. Those 78 trees were utilized for a total of 569 minutes (7.3 minutes/tree) as compared to 20,074 minutes (288 minutes/tree) for the 88 trees. Apparently sampling of new individuals of a major resource species was occurring as well as sampling of new tree species, e.g., 26 of the 104 trees utilized once represented 18 new species not previously utilized. These trees were used by Group 1 for 150 minutes (5.8 minutes/tree). The 18 sampled species represented 12 families. As further evidence for sampling of new tree species, eight species were used for only 82 minutes (Table 3). In 2 cases, Rubiaceae and Sterculiaceae, Group 1 members sampled at least 1 tree of each species in the family. The sampling was always done by an adult and only 1 animal at a time.

The 331 individual food trees represent 61 species from 26 families. The food species were not utilized with equal frequency. Twenty-four species were visited 5 times or less. There were 8 species that were visited 100 or more times. In many cases, only a few trees from any 1 species were used for food (Table 3). For example, only 2 percent of the *Cordia alliodora*, 3 percent of *C. dentata*, 1 percent of the *Guazuma ulmifolia*, and 4 percent of the *Myrospermum frutescens* individuals were utilized for food. Also, many of the higher percentages of utilization occurred

Table 3.—Alphabetical listing of every tree species used as a food source by Group I.

Species	*Number of trees present*	*Number of trees used*	*% used*	*Total time species used min*	*Number of visits*	*Average length of visit min*	*Part eaten*
Albizzia adenocephala	1	1	100	173	17	10	Nl,Fl
Anacardium excelsum	68	48	71	1855	302	6	NlPe,Nl,Pe,FlPe
Andira inermis	28	22	79	3118	217	14	Nl
Astronium graveolens	18	10	56	1401	113	12	Le,Nl,NlPe,Pe
Bourreria quirosii	2	1	50	2	1	—	Fl
Bursera simaruba	19	8	42	694	66	10.5	Le,Nl,Fl
Byrsonima crassifolia	2	2	100	83	5	17	Fr
Calycophyllum candidissimum	17	2	12	15	4	4	Le
Carica papaya	1	1	100	7	2	3.5	Le
Casearia arborea	7	1	14	1	1	—	Nl
Cecropia peltata	4	3	75	286	30	9.5	NlPe,Nl,Fr
Cedrela mexicana	8	1	13	1	1	—	NlPe
Ceiba pentandra	6	1	17	9	2	4.5	Nl,NlPe
Chlorophora tinctoria	7	2	29	24	4	6	Le,Fl,Fr
Chomelia spinosa	5	1	20	6	1	—	Le
Coccoloba caracasana	9	2	22	92	3	30	Fr,Nl
Cochlospermum vitifolium	30	2	7	16	5	3	Fl,NlPe
Cordia alliodora	42	1	2	23	4	6	Le
Cordia collococca	23	1	4	3	2	1.5	Nl
Cordia dentata	197	5	3	107	12	9	Fr
Cordia panamensis	6	1	17	10	3	3	Nl,Fl,Le
Dalbergia retusa	20	6	30	224	13	17	Fl
Diospyros nicaraguensis	2	2	100	35	3	12	Le,Nl,Fl

Table 3.—Alphabetical listing of every tree species used as a food source by Group I.

Species	*Number of trees present*	*Number of trees used*	*% used*	*Total time species used min*	*Number of visits*	*Average length of visit min*	*Part eaten*
Enterolobium cyclocarpum	13	6	46	389	59	6.5	Fl,Le,Nl
Eugenia salamensis	75	2	3	167	13	13	Fr
Ficus glabrata	2	2	100	910	74	12	Nl
Ficus ovalis	1	1	100	28	1	—	Nl
Genipa caruto	5	1	20	1	1	—	Nl
Gliricidia sepium	149	15	10	336	60	5.5	Le,Nl,Fl
Guazuma ulmifolia	201	2	1	13	2	6.5	Le
Guettarda macrosperma	2	1	50	9	2	4.5	Le
Hymenaea courbarill	64	11	17	139	23	6	Nl,Fl
Inga vera var. *spuria*	5	2	40	168	24	7	Nl,Fl,Le
Licania arborea	29	16	55	1812	186	9	Nl,Le
Lonchocarpus costaricensis	7	1	14	26	1	—	Fl
Lonchocarpus hondurensis	2	2	100	118	12	10	Fl,Nl
Lonchocarpus minimiflorus	97	24	25	821	59	15	Nl,Fl
Luehea candida	54	17	31	423	69	6	Fl
Luehea speciosa	2	1	50	231	24	9.5	Fl
Lysiloma seemannii	24	7	29	69	15	4.5	Nl,Tw,Fl
Manilkara achras	7	6	86	1587	103	15	Fr,Nl
Mastichodendron tempisque	6	5	83	523	40	13	LePe,Fr,NlPe,Fl
Mungingia calabura	9	4	44	967	87	11	Fr,Nl,Fl,Le
Myrospermum frutescens	24	1	4	311	21	15	Le,Nl,Fl
Pithecolobium longifolium	16	13	81	2033	169	11	Nl,Fl
Pithecolobium saman	11	10	91	2577	260	10	Le,Nl,Fl,Fr
Pterocarpus hayesii	4	4	100	1209	117	10	Nl
Schizolobium parahybum	6	5	83	370	42	8.5	Fl,Fr
Simarouba glauca	6	2	33	2	2	1	Fr,Le
Sloanea terniflora	16	4	25	23	4	5.5	NlPe
Spondias mombin	20	8	40	843	76	11	Fr,Nl,Fl,Le,Pu
Spondias nigrescens	10	7	70	428	56	8	Pu,Fl,Nl,Fl
Spondias purpurea	31	2	6	112	15	7	Nl,Le,Fr
Sterculia apetala	4	3	75	18	3	6	Nl,Pu,Pe
Sweetia panamensis	5	1	20	33	6	5.5	Le,Nl
Tabebuia neochrysantha	32	6	19	240	23	10	Fl
Tabebuia rosea	34	6	19	115	23	5	Nl,Fl,Fr
Thouinidium decandrum	26	1	4	5	1	—	NlPe
Trichilia cuneata	3	2	67	124	17	7	Le
Trichilia sp.	12	5	42	69	9	7.5	Fl,NlPe,Nl,Le
Zanthoxylum procerum	4	2	50	73	9	8	Nl,Fl,Le

Pu = pulvinus, Pe = pedicel, Tw= twig, N1Pe = new leaf petiole, F1Pe = flower petiole, LePe= leaf petiole because only 1 or 2 trees of that species were present in the range.

In fact, the most common tree species were utilized very little. The 5 most common trees were used for only 5.1 percent of the feeding time and more than 50 percent of that was the ingestion of the flowers of *Lonchocarpus minimiflorus*, the fourth most common tree (Table 4). Of the 15 most important food species (based on feeding time), only 4 rank in the top 15 most common trees, with 2 of those being fourteenth and fifteenth (Table 5). The second most important food species rank thirty-second in frequency of occurrence in the study area. The tenth most important food species ranks seventy-second. The 15 most common tree species were utilized for 35.6 percent of the total feeding time and three-quarters of that time was spent in the sixth, fourteenth, and fifteenth ranked tree species (Table 4).

The species utilized most for food (in terms of time) was *Andira inermis*, 3118 minutes. An individual *A. inermis* (tree 38) also was the tree in which the howlers spent the most time feeding, 924 minutes. The species used most on a per tree basis was *Lonchocarpus hondurensis*: 118 minutes for 2 trees. Many species were utilized for less than 10 minutes and 3 for only 1 minute (Table 3).

The longest average feeding bout of 30 minutes occurred in *Coccoloba caracasana* (Table 3). The average length of feeding bouts in *A. inermis*, the species utilized most, was 14 minutes. *Byrsonima crassifolia* and *Dalbergia retusa* each were used for an average of 17 minutes per feeding visit.

The species with the most feeding visits was *Anacardium excelsum* (Table 3). It was also the species with the most individuals (48 trees) visited for food.

Several species, *Muntingia calabura*, *Ficus glabrata*, and *Gliricidia sepium*, merit special comment. *M. calabura* was the only species to produce flowers, fruit, and new leaves throughout the year. It ranked thirty-fourth in frequency of occurrence and ninth in minutes of utilization (Table 5). The howlers spent 967 minutes feeding, primarily on fruit, in trees of this species.

The 2 individuals of *F. glabrata* produced new leaves during all months of the year with a large burst of new leaves at the beginning of the wet season. These 2 trees were utilized for 910 minutes of feeding.

There were 149 *G. sepium* trees present in the range of Group 1. Although Table 4 shows that 15 trees were used as food sources, new leaves were ingested from only 5 trees (#49, 50, 593, 599, 659) and mature leaves from only 3 trees (#49, 50, 593). Flowers were the only part eaten from the other 10 and nothing was taken from the remaining 134 trees. Phenophase for all 149 individuals was identical. The total feeding time of Group 1 for *G. sepium* was 343 minutes. Group 2 utilized the same tree parts from the same *G. sepium* individuals.

The families Anacardiaceae, Mimosaceae, and Papilionaceae are very important as food sources. Fifty-seven percent of the trees utilized as food sources by the howlers were members of these 3 families. In addition, the group fed in these families for 16,214 minutes or 61 percent of all feeding time (N = 26,535 minutes). All 3 families were utilized about equally—Papilionaceae was used for 6053 minutes. In each of these 3 families, 2 species received a majority of the feeding pressure.

Moraceae constituted another important food source. In fact, on a per tree comparison, Moraceae was more important than Anacardiaceae, Mimosaceae, or Papilionaceae. Individual trees of Moraceae were utilized for a total of 1230 minutes. There were 14 trees of this family in the range. Eight of them served as a food source during the study. The average feeding bout in these 8 trees was 154 minutes as compared to an average bout of 85 minutes for trees of Anacardiaceae, Mimosaceae, and Papilionaceae. Also, the group utilized more individuals of Moreceae (57 percent, 8 of 14 trees) than they did Anacardiaceae, Mimosaceae, and Papilionaceae (33 percent, 190 of 569 trees).

Two more families deserve mention: Rosaceae (1 species) and Tiliaceae (2 species). Group 1 utilized the 3 species in these families for a total of 2486 minutes (9 percent of 26,535 minutes total).

The importance of the 6 families profiled above—Anacardiaceae, Mimosaceae, Moraceae, Papilionaceae, Rosaceae, and Tiliaceae—can be further documented by noting that Group 1 spent 19,930 (75 percent) minutes feeding in species of these 6 families, while feeding for only 6605 minutes in all of the remaining 20 resource families.

Not all parts of an individual tree or tree species were utilized. The parts that were used varied with the time of year, the phenology of the tree, and the tree species. The average daily diet composition, based on the amount of time spent feeding on each tree part, consisted of 19.4 percent mature leaves, 44.2 percent new leaves, 12.5 percent fruit, 18.2 percent flowers, and 5.7 percent petioles and pulvinus (Figure 4). There was a distinct seasonal difference in the apportionment of feeding time for the various tree parts (Figure 5). The utilization of mature and new leaves was closely linked (Figure 6).

New leaves were the only part eaten from *Andira inermis*, *Casearia arborea*, *Ceiba pentandra*, *Ficus glabrata*, and *Hymenaea courbarill*. Mature leaves

Table 4.—The 15 most common tree species ranked by number of individuals present in the study area.

Rank	*Species*	*Number present*	*Percentage of total present*	*Feeding time minutes*
1.	Guazuma ulmifolia	201	11.8	13
2.	Cordia dentata	197	11.6	107
3.	Gliricidia sepium	149	8.8	336
4.	Lonchocarpus minimiflorus	97	5.7	725
5.	Eugenis salamensis	75	4.4	167
6.	Anacardium excelsum	68	4.0	2112
7.	Hymenaea courbarill	64	3.8	139
8.	Luehea candida	54	3.2	423
9.	Cordia alliodora	42	2.5	23
10.	Tabebuia rosea	34	2.0	115
11.	Tabebuia neochrysantha	32	1.9	240
12.	Spondias purpurea	31	1.8	112
13.	Cochlospermum vitifolium	30	1.8	16
14.	Licania arborea	29	1.7	1832
15.	Andira inermis	28	1.6	3077
	Totals	1131	66.6	9437

Table 5.—The 15 top resource tree species ranked by the amount of total time spent feeding in each species. The rank of each species by number present in the study site also is given.

Rank	*Species*	*Feeding time min.*	*Percentage of total feeding time*	*Rank by number present*
1.	Andira inermis	3077	11.6	15th
2.	Pithecolobium saman	2566	9.7	29th
3.	Anacardium excelsum	2112	8.0	6th
4.	Pithecolobium longifolium	1945	7.3	26th
5.	Licania arborea	1832	6.9	14th
6.	Manilkara achras	1584	6.0	34th
7.	Astronium graveolens	1379	5.2	23rd
8.	Pterocarpus hayesii	1203	4.5	48th
9.	Muntingia calabura	967	3.6	32th
10.	Ficus glabrata	910	3.4	55th
11.	Spondias mombin	814	3.1	21st
12.	Lonchocarpus minimiflorus	725	2.7	4th
13.	Burera simaruba	692	2.6	22nd
14.	Mastichodendron tempisque	523	2.0	40th
15.	Spondias nigrescens	434	1.6	30th
	Totals	20763	78.2	

were never eaten from these tree species. In fact, when the leaves reached a certain stage of development, signaled to me by a color change, the howlers stopped feeding from those tree species until new leaves were again produced.

Mature leaves of 24 species were eaten, but the quantity eaten from many of these species was very small. Relatively larger amounts of mature leaves, based on feeding time, were taken from *Bursera simaruba*, *Pithecolobium saman*, *Trichilia cuneata*, and *Myrospermum frutescens*.

On those occasions when Group 2 was observed in the study area, their feeding behavior was recorded. The feeding of a solitary young male and a solitary female were also noted. In all cases, these monkeys fed on the same kinds of food that Group 1 members ate. They utilized the same parts from the same trees as Group 1 used. Frequently, it appeared that they moved into the range expressly to utilize a particular food item such as the fruit of *Spondias mombin*, the new leaves of *Pithecolobium longifolium*, or the new leaves of *Andira inermis*.

Discussion

At first glance, the results reported here (i.e., a very small percentage of the available resources were used) seem to support the suggestion of other investigators that howlers have more food available than they could ever use (Carpenter, 1934; Altmann, 1959; Chivers, 1969). However, the resource utilization was not random as should be expected if all trees were equally valuable resources. In almost all cases, the resources selected were not the most abundant (Tables 4 and 5). Why did Group 1 avoid the leaves of almost all of the most common trees even though 63.6 percent of their feeding time was spent eating leaves? (See McKey, 1978, for similar results for another primate). On some days leaf-eating comprised as much as 99 percent of the feeding time. Group 1 demonstrated a high degree of selectivity between the parts of a tree, between individuals of a tree species, between tree species, and between tree families.

It might be argued that these feeding patterns are simply adventitious or fortuitous and once established have remained fixed in the group. If that were the case, then another group inhabiting an area with the same or similar tree composition should not have the same feeding pattern. As was mentioned above, when Group 2 came into the study area they utilized the same tree families, tree species, and tree parts for food. The duplication of food resources even went so far as the use of exactly the same 3 individual trees (widely separated) of *Gliricidia sepium* for mature leaves.

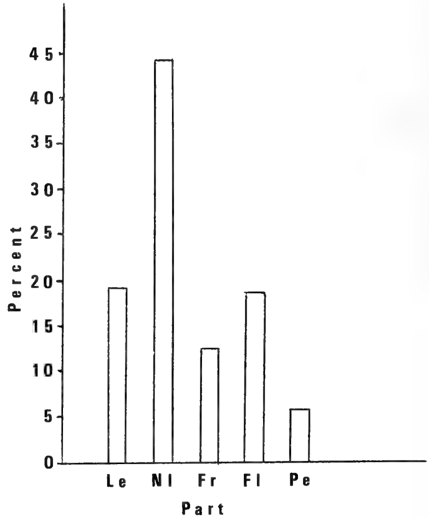

Figure 4. Diet composition. Based on the number of minutes spent feeding on each tree part. Results given as percent of total daily feeding time. Le = mature leaves; Nl = new leaves; Fr = fruit; Fl = flowers; Pe = petioles and pulvinus.

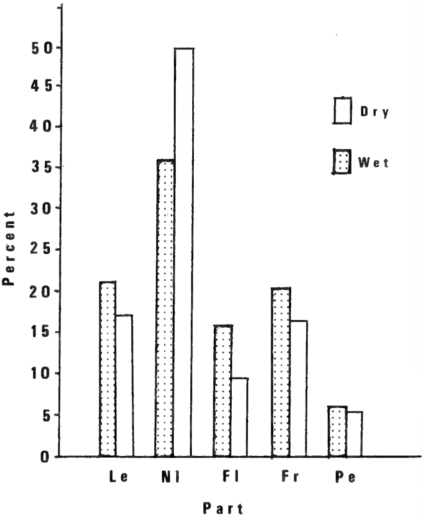

Figure 5. A comparison of wet-season and dry-season diet based on feeding time. Symbols and method of reporting results are the same as Figure 4.

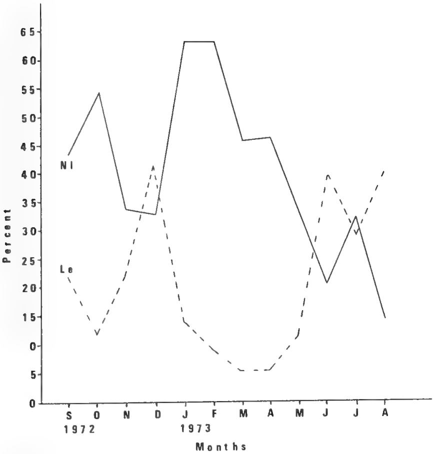

Figure 6. A monthly comparison of the percent of feeding time spent ingesting mature leaves and new leaves.

Another explanation for the selectivity demonstrated by Group 1 might be based on nutrition; however, as described below, plant secondary compounds may bind the nutrients. Even if they do not interfere with nutrition in this manner, secondary compounds are ubiquitous and must be dealt with by folivores.

I propose that the high degree of resource selectivity demonstrated by Group 1 is in response to the presence of secondary compounds in their food. The results reported here support Janzen's (1973) suggestion that animals do not feed on all of the plants available in their habitat, but do feed as though the plant's secondary compounds occur in definite and predictable patterns.

Secondary compounds do not have to kill to serve their purpose. They may serve as repellants (unpalatable or toxic), attractants (attracting pollinators), phytoncides (protecting against bacteria and fungi), or allelopathics (inhibiting other plant growth) (Whittaker, 1970). The ubiquitous presence of secondary compounds, produced by the plants as a chemical defense against predators (Stahl, 1888; Dethier, 1954; Fraenkel, 1959; Ehrlich and Raven, 1965; Whittaker, 1970; Freeland and Janzen, 1974), present folivores with a nonuniform food supply (Dethier, 1970). To counteract this defense certain folivores have evolved the capability of detoxifying ingested toxins but not all toxins can be detoxified by any one species (Whittaker and Feeny, 1971).

Plant secondary compounds directly and indirectly affect what is available as food. These compounds can prevent the animals from realizing the full nutritional benefits of a plant by binding some of the available nutrients (Feeny, 1970). In response, the animal must ingest more of the food to derive the same nutritional benefits from a similar food without the secondary compounds. However, the increased consumption results in the increased ingestion of associated toxins placing a heavier load on the animal's detoxification system. Thus the preference of new leaves by Group 1 is highly adaptive since plants concentrate nutrients in young leaves and stems (Fraenkel, 1953) and trees may have evolved the strategy of concentrating their toxins in mature leaves, leaving the new leaves relatively free of toxins (McKey, 1974).

Similarly, a knowledge of some of the selection pressures operating on plants can help to explain howler feeding strategies. Many investigators comment on the "wasteful" feeding habits of howlers, especially when feeding in *Cecropia* spp. Upon close inspection, I found Group 1 was eating the new leaves and the long petioles of the mature leaves and dropping the mature leaf blades of *Cecropia peltata*. This method of feeding also was used for *Sterculia apetala* and *Anacardium excelsum* leaves. Usually, only one part of a plant contains the secondary compound (Sim, 1965). Since the leaf blade is subjected to predator pressure first, it seems reasonable to assume that the trees concentrate the toxins in the leaf blades with very little in the petioles or pulvinus. As Freeland and Janzen (1974) suggest, herbivores should preferentially select that plant part with the least amount of toxin. The howlers are eating the petioles and new leaves, the parts with little or no toxins, and dropping the leaf blades, the part containing the concentrated toxins.

A similar feeding behavior was observed when the howlers fed on the fruit of *A. excelsum* and the pulvinus of *Spondias mombin* and *S. nigrescens*. An awareness of the location of the toxins can help to explain this feeding strategy. The howlers picked the *A. excelsum* fruit, but ate only the pedicel, a fleshy appendage which attaches the fruit to the tree. The fruit was dropped intact. The rind around the fruit of the closely related *A. occidentale* contains a poisonous oil: cardol oil (Little and Wadsworth, 1964), but the greatly enlarged pedicel is eaten by many humans (personal observation). Anacardiaceae is the poison ivy family. *S. mombin* and *S. nigrescens* are members of the family Anacardiaceae. The dropping of large amounts of *S. mombin* and *S. nigrescens* leaves occurs because the howlers ate only the pulvinus, the enlarged node at the base of the petiole.

These examples of dropping what appears to be food should be evaluated carefully in terms of feeding strategies. I do not consider this to be wasteful or careless feeding by the howlers. Rather, these are examples of highly selective feeding: a behavioral adaptation to counteract the tree's defensive strategy. From a cost-benefit point of view, the howlers may be maximizing their nutritional benefits while minimizing the amount of toxins being ingested. Ingestion of large amounts of toxins or certain toxins could be physiologically debilitating if not fatal. A physiological adaptation to the presence of these chemicals may be to reduce basal rates, thereby decreasing the intake of toxic substances (McNab, 1978). In terms of an energy budget, the functioning of a detoxification mechanism requires energy and specific nutrients at the expense of an animal's normal synthetic and maintenance processes (Williams, 1959).

Basically there are 2 feeding strategies that can be adapted by herbivores faced with the problems of secondary compounds, i.e., become a specialist (restricted diet) and feed on only one or two food species or become a generalist (broad diet) and feed on a wide variety of plant species (Cody, 1974). Cody further concludes that high resource abundance or renewal rate is favorable for specialists while a mixture of similar resources would favor a generalist. In terms of herbivory, a high resource abundance provides the specialist with a plentiful food supply. Howlers cannot be classified as specialists because, as pointed out by my data the home range of Group 1 does not contain the resource trees in sufficient density to permit adapting the strategy of a specialist. Not only are there not enough individuals of any 1 food species present in the home range, but the added factors of seasonality and secondary compounds further limit resource availability. Preferred food items such as new leaves are short-term occurrences. And, as the feeding behavior of Group 1 suggests, the diet must be diversified due to limited amounts of toxins which can be detoxified at any 1 time.

A specialist need only detoxify 1, or at most only a few toxins, thus diverting less energy and nutrients than the generalist who ingests a wide variety of toxic compounds. Even with a detoxification system, herbivores are limited in the amount of any food item they can safely ingest. The amount ingested is controlled by the concentration of the toxins in the food item and the quantity of that toxin the system is capable of processing.

The content and concentration of toxins present in a plant varies with environmental conditions. There are marked fluctuations of alkaloid content during the growing season as well as a circadian fluctuation (Huges and Genest, 1973). Many secondary compounds are increased when the plant is in full sunlight (Swain, 1972). Alkaloids are higher in actively growing tissue while slow growth enhances concentrations of hydrocyanic acid (Huges and Genest, 1973; Willaman and West, 1916). Also, geographical variations, edaphic conditions, and climatic factors affect secondary compounds (Swain, 1972).

Rainfall had little effect on the howler's activity, except during heavy downpours when they were inactive. In terms of food availability, however, rainfall is extremely important. As with most tropical forests, the distribution and not the amount of rainfall is the critical factor. Rainfall, in one way or another, appears to provide the trees with a cue as to when to begin leaf-drop, flower production, or new leaf production. A majority of the flower and new leaf production occurred during the dry season. There was almost no new leaf production during the wet season. As a result, there was more productivity, in terms of preferred food, during the dry season than during the wet season. Thus, even though the wet season appears to be a time of food abundance, it may actually be a time of stress since most of what is available are mature leaves, a tree part with large amounts of toxins. As pointed out, the consumption of mature leaves went down dramatically whenever new leaves were available (Figure 6).

The seasonal difference in average-day ranges can be explained in terms of food dispersion and toxin content. The consumption of new leaves (with little or no secondary compounds) does not require the animals to move very far (dry season). Most of the daily food intake can be obtained from one part of their home range, individual trees of *Pithecolobium longifolium* and *Andira inermis* on one side of the river had synchronous production of new leaves. Additionally, more flowers appear in the dry season and provide a localized resource. The consumption of mature leaves (with high toxin content) requires ingesting a small amount of leaves from many different tree species or several different trees of the same species which are widely dispersed (wet season). Also, fruit ingestion is high during the wet season and contributes to the increased day range since many tree species ripen only a few fruit each day. To harvest these, the howlers must travel greater distances.

The home range of any group of forest primate contains many trees, but, because of high tree-species diversity and low conspecific density, there may be very few individual trees of any one tree species available to the animals. Even though there may be several trees of a species present, utilization of all individuals may not occur because of different levels of toxin content within a tree species. This may help to explain why Group I moved through individuals of a species without feeding to feed in other members of the same tree species, e.g., they fed on mature leaves of only the same three *Gliricidia sepium* trees. [The mature leaves and fruit of *G. sepium* are crushed in water and used as an effective rat poison (Little and Wadsworth, 1964; Altschul, 1973)]. In some instances, the distance covered between feeding bouts in individuals of the same tree species exceeded 600 m, but there were individuals of that species much closer.

Any investigation of primate feeding behavior, especially folivorous primates, must consider the impact of plant produced secondary compounds. A few comparative studies of howlers and studies of other primate species have been done or are now in process (see McKey, 1978; Milton, 1978; and Rudran, 1978) but much work remains to be accomplished. Of immediate concern should be the biochemical and nutritional analysis of the food eaten by the animals. Equally important is the biochemical and nutritional analysis of the resources available but not consumed. Also needed are studies of the digestive mechanism of these leaf-eating monkeys.

These kinds of studies and continued quantitative investigations of free-ranging primates may provide an insight into the coevolutionary race between the predator (folivores such as howlers) and the prey (trees). The prey may react to predation by developing new secondary compounds or slightly altering old ones. The predator must either change to other resources or develop approximate detoxification mechanisms. That this is a dynamic system is of critical importance in the evaluation of the relationship between primate social structure and the environment.

Summary

Quantitative data collected during a 14-month field study of mantled howling monkeys (*Alouatta palliata* Gray) in Costa Rica indicates that the study group fed as though plant secondary compounds occur in a predictable manner. The study site was 9.9 ha of riparian forest containing 1699 trees over 4 m tall. The 13-member study group utilized 331 different trees, 51 vines, and the mistletoe in 2 trees. They spent 75.7 percent of their feeding time in only 88 trees and demonstrated a high degree of selectivity within and between tree species. Their daily diet consisted of 19.4 percent mature leaves, 44.2 percent new leaves, 12.5 percent fruit, 18.2 percent flowers, and 5.7 percent petioles and pulvinus.

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