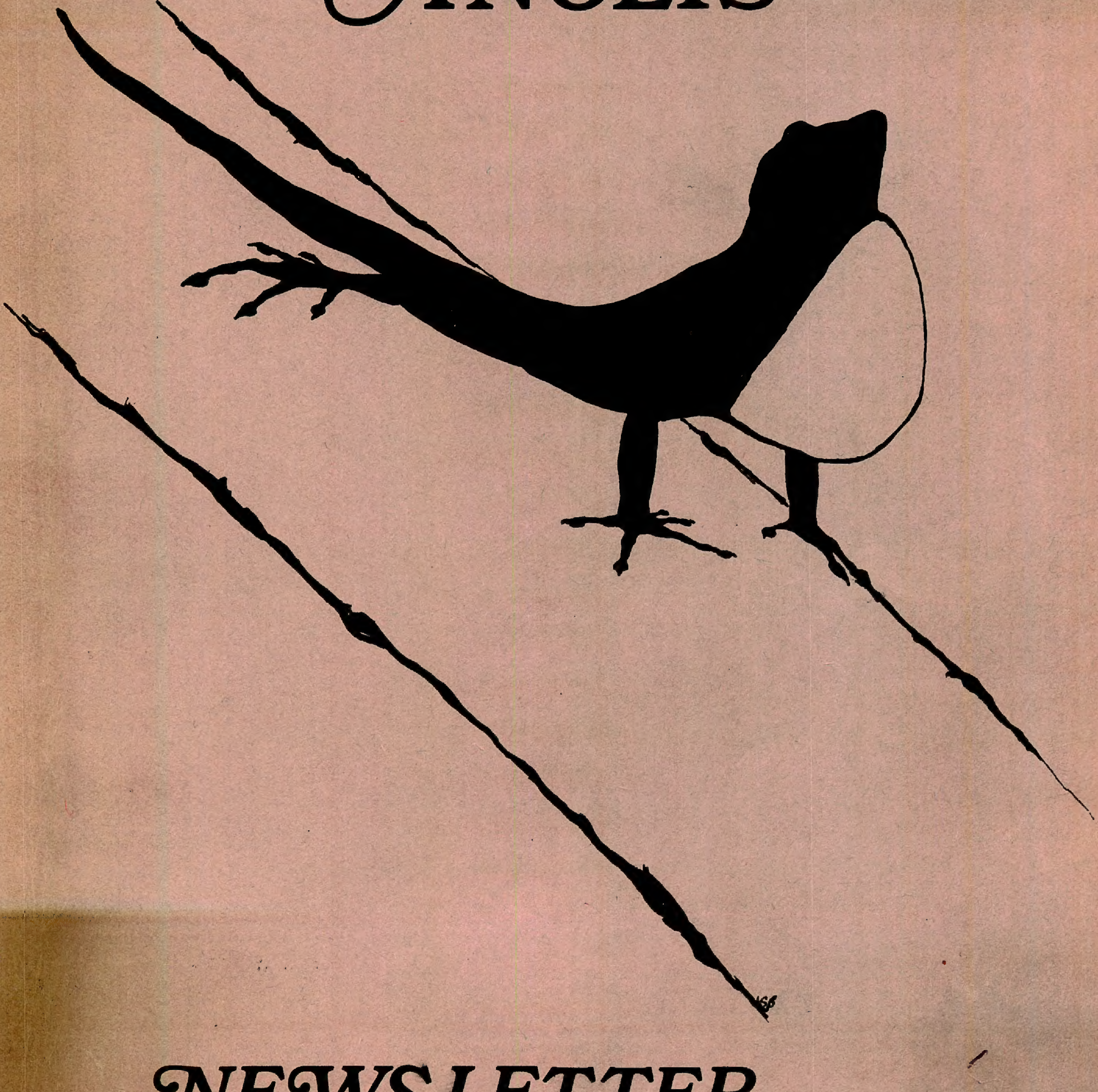
The Second

ANOLIS



NEWSLETTER

THE SECOND *ANOLIS* NEWSLETTER

The first *Anolis* Newsletter was never so labelled. It was only an elaborate - over elaborate - report to the National Science Foundation which I secondarily made an in-house information bulletin.

The informational success of the first bulletin/newsletter led me to believe that second and succeeding newsletters might be welcome, since they succeeded - for me as well as the rest of the group - in giving a sense of what was being done, why and with what results. I orally promised such a newsletter to many people but not until now, when once again NSF has compelled me to write a report, have I got around to actually editing and sending out the long awaited SAN.

NO AUTHOR SHOULD BE QUOTED WITHOUT HIS CONSENT.

Distribution is free to contributors and to selected institutions. If other copies are requested, there will be a xerox charge. This and successive Newsletters will, like University Microfilm Dissertations, be "PUBLISHED ON DEMAND."

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ROBIN ANDREWS (Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80521), in collaboration with A. S. Rand and working with anole populations on Barro Colorado Island and in the anole facility at Balboa, has summarized the major characteristics on the reproductive biology of anoline lizards as follows:

1. Reproductive effort in *Anolis* is a function of rate of reproduction (*one* egg every one to two weeks in small Central American anoles) and hatchling size (proportional to species size).

2. Differences in reproductive effort, whether seasonal or spatial, involve alterations in rate. Thus *A. limifrons* hatchlings are larger in the dry season, apparently as a result of longer retention of the eggs before laying.

3. The small clutch size and frequent ovipositions characteristic of anoles seem true also for other small lizards of relatively equable tropical habitats. This reproductive strategy contrasts strongly with that found in lizards of temperate and strongly seasonal habitats (large numbers of eggs laid in one or few clutches).

4. One important contributing factor to these contrasting reproductive strategies is postulated to be differences in predation pressure.

High predation pressure on anoles and other small lizards in the tropics results in relatively r—selected reproductive strategies: small clutches can be laid at frequent intervals at low cost to the female; at the same time the early maturity of the female increases the probability that she will reproduce before death.

On the other hand, predation pressure on temperate lizards is relatively low. Hence their reproductive strategy is determined by the environmental restraints of the limited periods suitable for the incubation and development of the young. For them, therefore, large and few clutches are optimal because they can be timed for the critical periods.

Robin Andrews has also collected data on the contrasting characteristics of island (Dominica) and mainland (Panama, Costa Rica) anoles: island anoles appear to be food-limited while mainland anoles are probably controlled by predation. Thus island anoles have relatively low growth rates which can, however, be increased markedly with increase in food. Mainland species, on the other hand, have high growth rates that are not (in one species) increased by greater supplies of food. They differ also in their trophic position. Island anoles are the dominant insectivores (few higher order predators) in their depauperate insular faunas, while mainland anoles are relatively unimportant insectivores (many higher order predators) in the complex habitats of the mainland tropics. Some other contrasting features follow from these.

1. The size classes within island species appear to be dividing food resources more finely, i.e. show lower within phenotype variance in the sense of Roughgarden, hence are greater specialists than the size classes of the mainland species which show higher within phenotype variance, hence are greater generalists.

2. Lower growth rates in insular populations result from greater pressure from these populations on the total food supply.

3. Survival rates are higher on islands and individuals are more abundant. Predation keeps the survival and abundance of mainland populations low.

4. Sexual dimorphism in size is greater in insular populations. Presumably several factors are involved, including specialization by the sexes on different size prey as well as dominance relationships, both more important in the resource-limited, relatively predator free ecology of the islands than in the contrasting ecology of the mainland.

A parallel manuscript by Andrews on growth rates in 15 populations of 13 species of *Anolis* finds comparable differences between mainland and island lizards. The rate constant G of the logistic equation for the fastest growing species is almost five times that of the slowest growing species. Males and females of a given species have very similar rate constants with those of females generally higher.

Differences in food availability had a marked effect on the growth of juveniles of an island species, *A. oculatus*, both in the field and especially in the laboratory (.10 mm and .17 mm/day under moderate and excellent field food availability respectively, and .27 mm/day with food *ad libitum* in the laboratory). In contrast, a mainland species, *A. limifrons*, did not increase growth under conditions of high food availability. The rate of growth was the same in field and laboratory (.17 mm/day).

When comparable species of the lowland tropics are considered, West Indian *Anolis* are characterized by relatively low growth rates ($G = .005-.011$) and Central American species by relatively high rates ($G = .016-.023$). As a group the mainland populations grow 2-3 times faster than island populations. Andrews interprets these contrasting data as implying that island anoles are food limited and that mainland anoles are not.

Two giant species - one mainland (*A. frenatus*) and one insular (*A. garmani*) - have similar rate constants intermediate between those of the smaller mainland and smaller island species. (Actually, *A. frenatus* females have a daily growth rate of .3 mm - larger than any rate cited above - but *A. frenatus* has to grow more to achieve the same proportional change in length as a smaller species, and this requires more time, reducing the value of G.)

Age at maturity differs considerably between the relatively slow-growing island species and the relatively fast-growing mainland species, 5-9 months as opposed to 3-4 months. Andrews interprets this as an indication that, as a group, island anoles are relatively K-selected as compared with their mainland counterparts.

There is wide individual variation in growth rate in anoles, presumably with both genetic and nutritional components. Andrews predicts that the genetic component is greatest in unpredictable environments where populations are limited by density independent factors and least where populations are limited by density dependent factors.

An interesting point is that there is in Anolis a relatively long period between sexual maturity and maximum size; it may in fact equal or exceed the period between hatching and sexual maturity. Andrews calls attention to the probability that, as long as energy is put into growth, reproductive effort must be somewhat lowered and that maximal reproductive effort may be possible only as size approaches an asymptote. On the other hand, benefits are accrued by attaining sizes larger than those at which reproduction is first possible. Large size is selectively advantageous if it is related to greater survivorship, enhances ability to obtain resources, or if reproductive effort is positively correlated with size. Hence, optimally, each individual lizard may have an r-oriented strategy when young and K-selected strategy when old. In other words, in a single population lizards may be able to reap the benefits of both early maturity and, for those that survive, the benefits of greater reproductive effort associated with relatively large size.

DAVID CREWS (Department of Zoology, University of California, Berkeley, California 94720) continues to study the psychobiology of reproduction in *Anolis carolinensis*

His findings to date have been:

1. Female receptivity correlates with stages of follicular maturation, sexual receptivity being restricted to a period preceding ovulation and dependent on hormonal conditions arising during the course of follicular maturation. Thus during the breeding season, receptivity, like the follicular cycles, is rhythmic.

2. In more recent investigations of the relationship between female sexual receptivity and the pattern of secretion of ovarian hormones during the follicular cycle, Paul Licht and Crews have developed a radioimmunoassay for measuring concentrations of estradiol and progesterone in the peripheral plasma. Although sample sizes are to date small, it appears that estradiol titer increases as the follicle matures while progesterone is highest after ovulation.

3. In related experiments, Michael Budin and Crews have been trying to determine the minimum effective dosage of estradiol benzoate (EB) necessary for reinstating sexual receptivity in ovariectomized females. They find that a single injection of .8 micrograms of EB will make at least 50% of the females receptive to male courtship while as little as .1 microgram/day will rapidly induce (in three days) and maintain receptivity.

4. Mating abolishes receptivity until the preovulatory stage of the next follicular cycle. Mating must be completed to affect receptivity.

5. Male courtship acts along with environmental stimuli to induce ovarian recrudescence in winter-dormant females.

6. Male-male aggression inhibits the environmental induction of ovarian recrudescence. Non-specific stress, e.g. handling by the experimenter, does not.

7. Castration abolishes male courtship behavior, hence preventing male courtship facilitation of ovarian recrudescence. Androgen replacement therapy restores male courtship behavior in castrated males and consequently courtship facilitation of ovarian recrudescence.

8. The critical cue for both long-term courtship facilitation of ovarian recrudescence and short-term behavioral responsiveness of receptive females to male courtship is the ability of the male to extend the dewlap, thus changing the body profile, and not dewlap color.

9. Paul Licht and Crews have found that the corpora atretica render the female insensitive to both environmental and hormonal stimulation and probably function to maintain the refractory period following the breeding season.

Crews is well aware that some aspects of this story may be species-specific and others (e.g. the absence of any importance for dewlap color) probably depend upon the fact that carolinensis in the United States is a "solitary" anole over most of its range. (In fact, its contacts are only with local populations of recently introduced species.) Hence Crews would like to extend his studies to other species and to systems of two and more species.

Crews' concern with the importance of a functional dewlap for courtship and hence for female receptivity has led him to make a detailed analysis of the display repertoire in Anolis carolinensis (a species, oddly enough, not previously studied).

He recognizes four display types: challenge, courtship, submission and assertion. Each of these has a characteristic sequence of motor patterns common to all observed individuals, but shows variation in patterning between or also within the behavior of individual lizards.

Thus, in the challenge display variation occurred between individuals but each individual had his own distinct display pattern which he performed consistently. Courtship and assertion displays both varied within individuals, but the courtship display more so. Most of the variation in both was in the number of head bobs performed before, during and after dewlap extension. In the submission display no patterning was evident; submissive head nodding was rhythmical, with the number of head nods being highly correlated with the mean duration of the display.

The greater variation between individuals than within individuals suggests that the challenge display, and possibly the assertion display, may aid in individual recognition. Crews has noticed that, while newly introduced females will submissively head nod in response to the initial challenge display of the resident male, regardless of their physiological state, females that have been previously housed with that male often will not. The familiarity of the cage does not seem to be an important factor in this response, since females already familiar with a particular male will not usually head nod to the male's challenge display even when placed in an otherwise strange cage. Similarly, males that have fought with another male and lost will immediately exhibit the subordination display when challenged by the same male in the same or a different cage. This recognition appears to persist, since both males and females will continue to respond appropriately after having been separated from one another for as long as 14 weeks.

Crews would infer, therefore, that the part of at least certain display patterns common to all members of a species may aid in species recognition while each animal's unique variation on this theme may serve for individual recognition.

A word of advice to all those trying to raise and/or maintain anoles in the laboratory. Try to simulate (as closely as possible) the environmental (physical as well as climatic) conditions the species normally experiences during the breeding season. Everything may hinge on a single variable. For example, Crews has found that female carolinensis will not become reproductively active if the relative humidity is less than 50%.

GEORGE GORMAN (Department of Biology, University of California, Los Angeles, California 90024) and collaborators have recently completed a number of studies in diverse areas of anolology:

1. *New karyotypes*. Gorman has collected on Mona, Redonda and Blanquilla islands material of three *Anolis* which had not been previously karyotyped. He is reporting on these with Brad Stamm who did the actual chromosome preparations. The most interesting result is for the Mona anole, *A. monensis*. Though it has sometimes been regarded as a subspecies of *A. cristatellus*, its karyotype resembles in detail that of *A. cooki*, the arid area sibling of *cristatellus*. *A. nubilus* of Redonda has a karyotype identical to that of neighboring members of the *bimaculatus* group. Chromosomes thus confirm its membership in the group but add no new information. *A. blanquillanus* of Blanquilla has a 2n=36 karyotype and this fits as it should in the *roquet* group with which it had been placed on external characters.

Gorman utilized the opportunity of the collecting visits to study the natural history of the three species.

These are most detailed for the structural habitat of *monensis* and the behavior of *blanquillanus*. *A. nubilus* was not abundant.

Despite the fact that it is a "solitary" anole, Gorman found no evidence of ecological release in *A. monensis* - "a typical trunk-ground lizard that does not seem to choose a broader variety of perch types than *cristatellus*. There is also no evident thermal niche expansion."

The behavior of *A. blanquillanus* fitted its geographic and postulated phyletic position: intermediate between *luciae* of St. Lucia and *bonairensis*. The greater resemblance was to *bonairensis*: much tail-lashing before bobbing, few pauses in any display sequence, shorter total time for a display sequence and more peaks in a bobbing series. However, there was resemblance to *luciae* in a greater tendency to pause than in *bonairensis* and in the occasional partial retraction of the dewlap during the pause.

2. *A new interpretation of the roquet group*. With Michael Soulé, Gorman, using new information from electrophoresis, scoring 26 genetic loci, has reinterpreted the relationships and colonization sequence in the *roquet* group. The new data emphasize the distinctness of *griseus* and *richardi*, formerly considered conspecific. *A. luciae* is markedly distinct from other species and has strong similarities only to *A. bonairensis* and *A. blanquillanus*. The relative lack of similarity of *luciae* to *griseus* and *trinitatis* on St. Vincent and the relative similarity of these two to each other has brought Gorman and Soulé to the view that the former hypothesis that *griseus* and *trinitatis* are separate invasions of a *luciae* stock into St. Vincent is wrong and that *griseus* and *trinitatis* differentiated on the St. Vincent bank from a single invasion from the south. (As

they comment, St. Vincent is "one of the least suitable Lesser Antillean banks for such an event, as it is small and not fringed with many islands.")

On the basis of the new electrophoretic evidence and re-evaluation of older data (behavioral and ecological), a totally revised colonization sequence is proposed: continent to Grenada → protorichardi; Grenada to St. Vincent → by intra-island radiation *trinitatis* and *griseus*; St. Vincent to St. Lucia → *luciae* (before differentiation of *trinitatis* and *griseus*); St. Lucia to Blanquilla and Bonaire → *blanquillanus* and *bonairensis*; St. Vincent to Martinique → *roquet*; Martinique to Barbados and Grenada independently → *extremus* and *aeneus*. The new argument depends not only on genetic similarity as estimated from electrophoresis, behavior and other characters but on the hypothesis of strict time-dependence for differentiation (e.g. Martinique *roquet* has six subspecies, so is older than Barbados *extremus* which has none).

Soulé and Gorman also have investigated "genetic variability" in the whole *roquet* group compared with certain Puerto Rican species. They stress "time-divergence" as better predictive of variability than niche width.

3. *The hybridizing anoles of Trinidad*. With Licht, Gorman has studied the annual reproductive cycles of *A. aeneus* and *A. trinitatis* from San Fernando, Trinidad. The two species differ markedly. *A. trinitatis* is essentially non-cyclical, *A. aeneus* ceases reproductive activity in the winter months (December-March). If Gorman is correct in assuming that Trinidad *trinitatis* were introduced from Kingstown, St. Vincent, where there is never a severe dry season, and *A. aeneus* comes from a seasonally dry part of the Grenada Bank, then on Trinidad the *aeneus* is preadapted to the pronounced dry season, whereas *trinitatis* probably wastes gametes during the winter months. This is the first evidence of an ecological difference between the species and may account, in part, for the apparent success of *aeneus*.

Gorman and Yang, working on the same two species, document a low level of introgression between the two species. Several electrophoretic markers were utilized that had not been studied previously. Whereas in their earlier study all animals were electrophoretically either "pure" *aeneus*, or *trinitatis*, or F_1 hybrids (heterozygous for all markers), they have now found evidence for backcrossing. One individual field-identified as a hybrid had several loci that were "pure" *aeneus*, and another individual field-identified as *aeneus* was heterozygous for several loci that implied *trinitatis* in its ancestry.

4. *Reproductive cycles of Puerto Rican anoles*. Gorman and Licht have a study on female cycles that will appear shortly in ECOLOGY, and a second paper by Licht and Gorman has been written dealing with the males.

Six species of anoles were studied for about 15 months of regular sampling from one locality on St. Thomas, and about a half-dozen localities on Puerto Rico.

Basically, all of them are cyclical breeders, but the decline in the uplands is much more dramatic than in the lowlands both within and between species. Thus, montane populations regress earlier than lowland forms (eliminating the possibility that they are responsive solely to photoperiod), and more completely.

Lowland populations of stratulus and cristatellus males were transplanted into a large outdoor cage in the mountains. The cristatellus did not survive, and when the first cohort was replaced with another, they too died. This implies that cristatellus may be absolutely limited from penetrating the rainforest for physiological reasons. The stratulus did well in the upland cage, and their decline was exactly in phase with the free-living montane animals, and not with that of stratulus from the lowlands.

Upland populations of krugi, cristatellus, stratulus and evermanni were brought to lowland cages. Reproductive decline did not occur in krugi, a result that was very different from the pattern of the upland populations in nature.

The upland cristatellus and stratulus brought to the lowlands showed a delayed and less drastic reproductive decline. Thus, in all cases so far discussed, there appears to be direct environmental control over seasonal reproductive cycling. However, A. evermanni proved to be an exception. Although typically an upland species, this form thrived in the lowland cages. Mortality was low; they grew very fat. However, the lowland sample showed as marked a reproductive decline as the wild upland forms, i.e. transplantation to a new climate did not influence reproductive cycling, implying thus a firmer genetic control of this phenomenon in this species.

5. Introduced populations. Gorman has new data on the distribution of A. extremus on St. Lucia. This species, introduced from Barbados, has a firm foothold and is sympatric with luciae. Contrary to the published observations of Lazell, who claimed that extremus did not seem to have any effect on luciae, Gorman found that the extremus often occurred in pure "enclaves" where luciae would be expected, but none were seen. Often, quite nearby, pure patches of luciae were found. This is very reminiscent of the situation on Trinidad, although in this case there are no known cases of hybridization.

Both species will defend territories against intruding males of either species.

Despite the seeming success of extremus, it is spreading very slowly. It appeared well established only between Castries and Vigie Beach. Occasional individuals were seen at scattered localities in the northern third of the island (including one at Forestiere, which is inland and in the mountains), but it was not possible to document that these were established populations. Human transport is likely.

It is not clear what advantage extremus might have over *luciae*, nor is it clear why it is so relatively restricted in distribution since it is clear that it can compete effectively against *luciae*.

Gorman, Soulé and Yang have examined the following introduced anole populations electrophoretically: *extremus* from St. Lucia and Bermuda; *leachi* from Bermuda; *grahami* from Bermuda; *trinitatis* and *aeneus* from Trinidad. These have been compared with the native populations.

In all cases, except Trinidad *aeneus*, there are much lower levels of polymorphism in the introduced populations. This might be expected just from sampling error alone (founder effect).

However, the Bermuda *grahami* introduction was intentional and large scale. 73 lizards were released (45 females) around the turn of the century. Since females can store sperm, we might estimate that around 100 individuals served as founders.

Levels of heterozygosity do not differ too much between Bermuda and Jamaica, but this is because the loci that are polymorphic on Bermuda show more heterozygosity than on Jamaica. 11 of 23 loci were polymorphic on Jamaica, and only 5 of the same 23 are polymorphic on Bermuda.

The data have not yet been analyzed further.

6. *Genetic relationships of the Puerto Rican anole fauna*. Data gathering has been completed and a matrix of relationships (Nei's Genetic Distance) computed for 14 populations of *A. cristatellus*, and one or more populations of the other nine species on the island. In addition, *A. monensis*, *A. cybotes*, *A. scriptus*, and *A. acutus*, plus *A. occulatus* of Dominica were compared.

The highlights of this study are as follows:

a. Variability in *cristatellus* is highest in the east (Virgin Islands, including some of the smaller keys) and lowest in the southwest (around La Parguera). The only exception is that variability drops precipitously on tiny keys.

b. Genetic similarity is *greater* between V.I. *cristatellus* and *scriptus* from Grand Turk than between V.I. *cristatellus* and western Puerto Rico *cristatellus*. The species status of *scriptus* is highly questionable. It is the only lizard karyotypically identical to *cristatellus*. *A. scriptus* is also relatively low in variability; thus it looks like a recent colonizer from the Virgin Islands or eastern Puerto Rico.

c. *A. monensis* is significantly closer to *A. cooki* than it is to *cristatellus*. This confirms the evidence from chromosomes.

d. Perhaps surprisingly, the other species of the *cristatellus* group are about equidistant from one another - i.e. the grass anoles (*krugi*, *pulchellus*, *poncensis*) are not closer to each other than they are to *cooki* or *cristatellus*; *gundlachi* is the outside member of the species group, perhaps implying it is the ancestral form.

e. *A. cybotes* shows no relationship to the *cristatellus* group nor to any of the other species on Puerto Rico. This confirms an earlier chromosomal study, but does not fit with Etheridge's osteological study.

f. The chromosomally primitive *occultus* and *cuvieri* are very distantly related to each other and to all the other species examined in the matrix.

g. The distinction between the *bimaculatus* and *cristatellus* groups is very weak. *Acutus* and *evermanni* (*bimaculatus* group, *acutus* series) are closer to members of the *cristatellus* group than they are to *stratulus* of their own series. *Oculatus* of the Lesser Antillean *bimaculatus* group is surprisingly close to *gundlachi*. On the face of the evidence, we would not now erect separate species groups, and if we did, the *acutus* series would probably go with *cristatellus* and not *bimaculatus sensu stricto*.

7. *Genetic relationships of the Lesser Antillean bimaculatus group*. Data gathering has been completed but a matrix of relationships not yet computed for all Lesser Antillean *bimaculatus* group members (*bimaculatus sensu stricto*, *wattsi* and *A. acutus*). It is clear, however, that some of Lazell's presumed close relationships are not supported by the genetic evidence. *A. ferreus* and *A. marmoratus* differ absolutely at at least three loci; *marmoratus* appears to be closer to *lividus* and *nubilus* than to *ferreus*. Also, *bimaculatus* and *leachi* are very distinct, differing at at least five fixed loci.

8. *Mexican anoles*. A field trip to Guerrero in August-Sept. 1973 yielded about six species of anoles, with some ecological and karyotypic data emerging.

Most impressive to one schooled in West Indian anoles is the absolute scarcity of specimens. At one locality, with dozens of local children aiding in collecting, over a period of two days Gorman's party turned up about nine *A. adleri*. *Sceloporus* (5 or 6 species) were superabundant in this locality, and the children brought them in by the hundreds.

In the lowlands near Acapulco Gorman obtained three specimens (adult males) of a streamlined small grey anole perched on thin branches. It was very reminiscent of *occultus*.

Hobart Smith identified these as *nebulosus* but they were much greyer and less robust than so-called *nebulosus* from Alamos (Sonora) and San Blas (Nayarit). Incidentally, the latter two differ very significantly in karyotype and it is likely that *nebulosus* is a complex of species (the Guerrero specimens unfortunately were not karyotyped).

9. Territory in a grass anole. Gorman's student Harwood finds that males of the Puerto Rican grass anole *Anolis pulchellus* are found day after day in the same areas which they defend with displays. This would contrast with Ross Kiester's description of the mainland grass anole *A. auratus*, which is said to be vagile and without defended territories.

WILLIAM P. HALL (Department of Biology, University of Puerto Rico, Rio Piedras) and his student Alberto Espinoza N have been devoting much attention to karyotypes and karyotype variation in Jamaican anoles.

Their study is still incomplete but some conclusions are already possible, and the questions that should guide further collecting can be formulated.

1. Anolis reconditus has a 2n=30 karyotype not obviously different from the standard pattern shown by lineatopus, valencienni and garmani.

2. Anolis lineatopus, reconditus and valencienni show no indications of intraspecific chromosomal variability.

3. Some complications are evident in A. opalinus. Gorman suspected possible X-Y heteromorphism: Hall and Espinoza are not certain whether this is the condition or a pericentric inversion of pair 7. In addition, one of three individuals from hear Hector's River, St. Thomas Parish had two intermediate-sized chromosomes in addition to pairs 6 and 7, resulting in a 2n of 32. One of two individuals from 2.5 mi E of Yallahs, St. Thomas Parish had an additional microchromosome (2n=31). Obviously, A. opalinus needs to be sampled further.

4. Anolis garmani also shows accessory chromosomes in some populations (e.g. near Golden Spring, St. Andrews Parish and at Southfield, St. Elizabeth Parish).

5. Gorman has long suspected polymorphism in A. grahami. Hall and Espinoza are already able to demonstrate a pattern of considerable complexity. Chromosome numbers range from 2n=30 to at least 2n=36. Two independent phenomena are involved: (1) occasional accessory chromosomes, (2) fissioning of at least three pairs of macrochromosomes. (Although insufficiently documented at the moment, there may also be considerable non-Robertsonian variation in the macrochromosomes.)

The fissioning has a zoogeographic aspect that gives it special interest.

Populations along the south coast appear to carry only one fission (possibly excepting Southfield, where accessory chromosomes may be complicating the picture). At some localities the single fission appears to be fixed (e.g. the UWI campus at Mona), while at others it appears to be present as a morph in addition to the standard Jamaican 2n=30 karyotype (Belvedere, Port Morant). Populations in Portland Parish in the northeast appear to be usually fixed for two fissions (presumably including the south coast fission) and polymorphic for a third. Populations with intermediate frequencies of fissions are found at Hope Bay, along the Wag River (Coakley), on the crest of the pass at Stony Hill separating the Blue Mountains of eastern Jamaica from the main body of the island and in the Hector's River valley draining the eastern end of the John Crow Mountains.

Samples are still inadequate but distribution of chromosome numbers at certain of the "intermediate" localities suggests the possibility that, rather than a wide transition zone between chromosomally different populations, there is limited hybridization in a narrow contact zone between a ca 32-chromosome south coast population and a 34-36-chromosome northeast population. Hall points out that the intermediate populations were taken at or near ecological or physiographic transitions between mesic adapted Blue and John Crow Mountain populations and the somewhat more xeric-adapted populations to the south and east.

Hall, however, calls attention to an apparent lack of correspondence of the karyotypic transition zones and the subspecies boundary between *A. grahami grahami* and *A. grahami aquarum* as described by Underwood and Williams.

There is obviously much here that requires confirmation and further study. Hall and Espinoza plead that anyone doing field work in Jamaica collect *grahami* whenever possible and send them live to the Terrestrial Ecology Division of the Centro Nuclear de Puerto Rico, Escuela de Medecine, Universidad de Puerto Rico, Departo Metropolitana (San Juan), Puerto Rico.

PAUL HERTZ (MCZ), while participating in the summer 1973 OTS course, was able to study the thermal biology of a mainland anole, Anolis polylepis. This forest species appears to be passive to environmental temperature (at least during the rainy season) and neither actively basks nor actively takes refuge from the sun. It nevertheless does maintain body temperatures that on the average are about two degrees above air temperatures. These results parallel Huey's data on cristatellus in forest in Puerto Rico and support the Huey-Slatkin model of lizard thermoregulation.

Hertz also observed that A. polylepis seemed to be more numerous in the small areas of denser vegetation resulting from minor disturbances in the forest. It was not clear what factors might be involved. Possible are higher air temperatures, higher local productivity etc. He hopes to return to Costa Rica in the near future to study polylepis' utilization of habitat patches.

Hertz, in addition, has been investigating the relationships and status of Anolis cochranae. Described as a full species, it has been variously suggested that it is a subspecies of A. semilineatus or a high altitude population of the latter only clinally distinct in scale size from surrounding lowland populations. A search has been made for any characters other than scale size that might distinguish cochranae. No constant external characters have been found, but electrophoretic studies are now under way in collaboration with T. P. Webster. At the moment these suggest that A. cochranae is not a species but only an altitudinal phenotype of A. semilineatus. Topotypic animals from Constanza are, at all events, not as different from white-dewlapped populations called A. semilineatus as is A. olssoni. There is evident considerable inter-population difference within what is called semilineatus (e.g. the major difference may be between south island and north island populations and not between altitudinally separated populations on the north island). Samples, however, have been small and not from localities best fitted to solve the evident problems. It is very clear that large new collections need to be made and that these need to be from places chosen very carefully.

Hertz hopes to find similar clines in other widely distributed Hispaniolan anoles. If patterns comparable to those found in the semilineatus complex are evident in other species, he hopes to develop a general model of the effect of altitude on scale and body sizes. The work must obviously consider the effects of competitive release and possible niche expansion as various species encounter different combinations of congeners along altitudinal transects.

RAYMOND HUEY (MCZ) has introduced some new concepts into the study of lizard thermoregulation, a field dominated by the belief that careful thermoregulation is always beneficial. In particular he has stressed that behavioral thermoregulation has associated costs and that in consequence it is sometimes advantageous in terms of natural selection to be passive to environmental temperatures.

He has demonstrated this point by studies on a population of Anolis cristatellus of Puerto Rico, some members of which live in shaded forest and some in a park-like area with scattered trees. He finds that individuals in the open do indeed behaviorally thermoregulate, basking in the sun in the early and late parts of the day, while shifting to higher shaded perches at midday. These anoles maintain high and constant temperatures because access to radiant energy is very easy, almost cost-free. Their major behavioral reaction is to avoid extreme high temperatures by retreat to shaded situations, again an action with minimal energetic cost.

In contrast, temperatures of animals in the forest were more variable and strongly correlated with air temperatures, reflecting the passive behavior of forest lizards. These animals would have had to move out of their territories to attain the few patches of sun. The energetic cost of such action is clearly great, suggesting that thermoregulation may yield greater net benefits than passivity only when associated costs are low.

The same tolerance of low and variable temperatures was found by Huey and Webster in Anolis marmoratus of Guadeloupe (see details below). Huey and Slatkin are preparing a mathematical model of the cost-benefit relations involved in lizard thermoregulation.

Huey also examined some physiological and behavioral parameters of thermoregulation in anoles of the cristatellus group of Puerto Rico. Previous work (Rand 1964, Heatwole et al. 1969, Huey and Webster in prep.) had shown that the three species form a partially overlapping altitudinal series. Where two forms are sympatric, the one with the higher altitudinal range invariably occurs in the more shaded habitats. Field work did not resolve whether these separations are presently the result of habitat exclusion or of thermal preference. To examine this question, Huey measured the experimental voluntary maximum temperature tolerated, critical thermal maximum, and preferred body temperature of the three species (Table 1). These results show that there are distinct behavioral and physiological differences among the three species, with gundlachi (high altitude) the least thermophilic and the most heat sensitive and cooki (arid lowlands) the most thermophilic and the least heat sensitive. These differences among sympatric pairs may in part account for habitat separations.

Table 1. Thermal parameters of anoles of the *cristatellus* group in Puerto Rico: experimental voluntary maximum temperature tolerated, critical thermal maximum, and preferred body temperature. N = number of individuals.

		Vol. Max.		CTM		PBT	
Species	Locality	$\overline{X}$	N	$\overline{X}$	N	$\overline{X}$	N
gundlachi	El Verde	26.4	10	35.7	10	25.1	6
cristatellus	El Verde	29.7	10	38.1	10	29.0	6
	Pta.Salinas	----		-----		29.6	6
	Guanica	33.2	11	38.9	11	29.6	6
cooki	Guanica	34.0	9	38.9	11	30.6	6

The Huey and Webster study of thermoregulation in Anolis marmoratus, the only anole on Guadeloupe, specifically intended comparison of their results with Ruibal and Philobosian's data on Anolis oculatus, the solitary anole of Dominica. On both islands anoles are active over broad ranges of body and ambient temperatures. MBTS of marmoratus varied from 22.7° C (deep forest subsample) to 30.4° C (road edge subsample) at one locality, and from 22.7° to 32.6° over the total localities sampled. Body temperatures are strongly correlated with ambient temperatures, both within and between habitats, suggesting that marmoratus is passive to most ambient temperatures. Basking was observed only at high elevations.

As Rand found on Dominica (see Rand below), there are social aspects to thermoregulation. At one locality Huey and Webster recorded sex, snout-vent length, body temperature and air temperature for anoles in bananas, palms and mangos (habitats ranked from hottest to coldest). Large adult males and large adult females inhabit palms (intermediate temperatures), small adult males and large to small adult females inhabit the cool mangos and only juveniles inhabit the hot bananas. A few bananas that were shaded by mangos had larger males and females than the unshaded bananas, suggesting that thermal environment, not food, is the key factor for these lizards in what appears to be intraspecific habitat selection enforced by social dominance.

Sex ratios vary with habitat as well: palms (37.6% males), mangos (52.3% males), open bananas (79.4% males), shaded bananas (33.3% males). These data suggest that males living in palms and shaded bananas have both an optimal thermal environment and the optimal sex ratios for maximizing fitness.

THOMAS JENSSEN (Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061) has, as always, his major attention fixed on anole displays. He has done some of the work in Panama at the anole facility and some at VPI.

A study of the Bogota Phenacosaurus brought back by E. E. Williams, Jane Peterson, Kenneth Miyata and Richard Salvato provides him with a display pattern somewhat different from that described by Kästle but nevertheless a typical iguanid display repertoire - very strong stereotypy with a limited assortment of "assertion," "challenge" and courtship displays. The challenge display is an elaboration of the assertion display coupled with throat fan extension and exaggerated amplitude of bobs.

Anolis nebulosus he finds more complex with some modifying movements that exaggerate the assertion and challenge displays. There is also dewlap pulsing which is not found in non-anole species.

Anolis limifrons, which he has worked on along with his student Ed Hover he finds still more complex. He promises that it will be "by far the most thorough behavioral analysis of a lizard to date." Basically there are five agonistic display types and within each a hierarchy of modifiers that indicate grades of motivational intensity. These display types generally appear sequentially. The picture is further complicated by the fact that males usually display in volleys of two to four displays at a time. The first display of a volley is either of a higher motivational state than the following types or has the most modifiers of all the displays if all the displays of a volley are of the same display type.

Anolis townsendi from Cocos Island in the Pacific falls into the limifrons mold. Four agonistic displays were found, but Jenssen suspects a fifth (occurring during very close male-male display exchanges) which was never recorded because the proper social context was not present during observations. A. townsendi, like A. limifrons, is thus a species with an expanded repertoire and with less stereotypy than is seen in A. nebulosus.

The variability in A. townsendi or A. limifrons is explainable, however, in contrast to the extreme variability of Jamaican A. opalinus, which is still an unsolved problem. Jenssen is still perplexed by the variability of just its assertion display. He tried analyzing low intensity assertion displays from five Jamaican localities. Five distinct patterns of the basic display were found, along with some regional differences in them. Any individual tended to perform one or two of these patterns but pattern usage by different individuals from the same locality differed considerably. There were a few lizards which had unique patterns as well as one or more of the usual five. To make sense of this, Jenssen will have to look at a lot more films, but his present impression is the displays have a genetic base but are not under strong selection pressure. His final word is: "It is this species that I hesitate to make any conclusions about except to say that I find little evidence for marked stereotypy."

In this regard he contrasts *opalinus* with *brevirostris*, which he is also examining, which have a complex repertoire (at least of display types) which, however, appears (without final analysis) stereotyped.

Jenssen finds this contrast intriguing and thinks that in the smaller fauna in Jamaica evolution of characters for species recognition has taken a different turn and has, for the very closely related forms *A. opalinus*, *A. grahami* and *A. garmani*, meant that they have diverged morphologically (i.e. in size, in some scale characters and in body color) while keeping a common dewlap color and many similarities (and at least remarkable variability) in their display repertoires.

Jenssen also has underway a report on the one - *A. grahami*-*A. lineatopus neckeri* - hybrid that he found during his year long stay on Jamaica. The displays of the suspected hybrid were photographed before it was submitted to electrophoresis by Preston Webster and resulting confirmation of its hybrid status. Its morphological characters have been studied by Jenssen and its displays have now been compared with those of *A. grahami* and will be compared with those of *A. l. neckeri*. The morphological characters in part resemble *grahami*, in part *neckeri*, in part are intermediate. The hybrid display appears to show close affinities to that of *grahami*.

As incidental intelligence and an indication of the variety of behavior possible in the genus *Anolis*, Jenssen reports that large adult females of *A. limifrons* may be solitary and occupy territories that are even exclusive of permanent males.

Both Jenssen and Rand are much interested in the visual phenomenon of critical flicker fusion frequencies (CFF). The speed of resolution of the displays so important in anole behavior is related to the speed of flicker fusion. Similarly, an animal's ability to quickly negotiate a complex habitat, identify and catch swift prey and avoid fast-moving predators is partly dependent upon its CFF.

Jenssen has invented an apparatus for measuring the CFF values for *Anolis* and he and his student, Edward Hover, have now tested quite a variety of anoles, including *auratus*, *onca*, Jamaican *sagrei*, *grahami*, Florida *carolinensis*, *opalinus*, *garmani*, *distichus*, *valencienni*, Panamanian *limifrons*, *lineatopus lineatopus*, *lineatopus neckeri*, *brevirostris*, *oculatus* Correlation is apparently with habitat insolation: *onca* and *auratus* and *cabritensis* have the highest values, *lineatopus neckeri* and limifrons the lowest, the other species intermediate. As Jenssen says, this result seems somewhat anomalous for Jamaican *sagrei*, essentially a terrestrial anole of very open areas. However, ancestral *sagrei*, as he points out, is an edge species, hence intermediate values of CFF may reflect ancestral rather than present conditions, if we assume that there has not been time to evolve to a new adaptive level.

A. ROSS KIESTER (MCZ) has divided his time between theoretical and experimental work.

One paper (with M. W. Slatkin) investigates the consequences of the hypothesis that some species of iguanid lizards (including certain species of *Anolis*) have evolved a strategy of resource utilization in which individuals take into account the distribution of conspecifics in the environment in addition to the distribution of food resources. Kiester and Slatkin propose that the two cues are integrated by their effect on the time budget of an individual lizard. Thus, a model of the time budget of a lizard is used to formulate a model of the tendency to movement of an individual which in turn is used to infer the pattern of movement within a population. Computer analysis of the final difference equation and mathematical analysis of a differential equation approximation to the difference equation yield a picture of the pattern of movements of lizards in a changing environment. The analyses also lead to three qualitative results which differentiate the conspecific cuing model from strategies based on cuing on the resource alone: 1) Gaps may exist in the equilibrium distribution of lizards even if the resource is continuous, 2) the speed of movement of a population is proportional to local population size, and 3) the systems response is most sensitive to changes in the propensity of individuals to move. The quantitative pattern of movement together with these three qualitative results help to understand the biology of certain species of lizards, possibly including such anoles as *A. lineatopus* and *A. aeneus*.

A series of laboratory experiments on the choice behavior related to conspecific association in the Panamanian grass anole (*Anolis auratus*) demonstrated that *auratus* of both sexes would approcah another *auratus* regardless of sex. These experiments have been detailed in the previous grant report. In order to bolster the interpretation of the laboratory experiments, Kiester with G. C. Gorman devised a series of field experiments to be performed on *A. auratus* and on two Puerto Rican species (*A. pulchellus* and *A. cristatellus*). The field experiments made use of a particular behavior shown by these lizards when disoriented, which Kiester and Gorman term post-vantage behavior. Performing it, a lizard crawls slowly up a branch or twig which projects out of the grassland habitat in which it normally lives and moves and then surveys the surrounding area in all directions before climbing back down and heading off. An artificial post was used which had two long ramps running off in opposite directions. A lizard placed on the top of the post would then survey the area and would then crawl down to one or the other of the ramps and on it to the ground. The post and the ramps were set up in such a way so that the ramps each led to a qualitatively different habitat. The lizards could thus choose a habitat in the field. In the experiments with *A. auratus*, the lizards significantly often chose a grassland habitat over a bush habitat, demonstrating that post-vantage behavior and movement directly afterwards was effective in finding the correct habitat. *Anolis pulchellus*, offered a choice between "short grass" and "tall grass," chose the "tall grass" while, offered a choice between "grass" and "trees," chose "grass." In another set of experiments, A. cristatellus were followed visually through the habitat after they had come down off the ramp. The spot where they rested after the movement was then recorded. These results showed that young A. cristatellus chose a grass-like habitat while adults chose a tree-like habitat. This accords with the distribution of the age classes of the species and shows that, contrary to some hypotheses, the young may not be forced by the adults to live in "suboptimal" habitats. Taken together, these experiments indicate that the behavior observed in the laboratory experiments was indeed natural and was similar to that used to select a habitat in nature. Thus the habitat selection interpretation given the laboratory choice experiments gains more credence.

BRADFORD C. LISTER (Department of Biology, Princeton University, Princeton, New Jersey 08540) has been trying to answer two questions concerning the ecology and evolution of *Anolis* lizards: (1) what are the ecological consequences of reduced competition?; (2) how do these species adjust their niche widths, i.e. to what extent are changes in niche width and niche position evolutionary or behavioral events? To answer the first question he has compared the structural, thermal and food niches of *Anolis* populations, primarily insular populations of *A. sagrei*, where they coexist with varying numbers of congeners. The major results of this ecological study are:

(1) Mean perch height and the diversity of perch heights utilized by male and female *sagrei* (measured as $1/\Sigma P_i^2$) decrease monotonically as the number of co-occurring *Anolis* species increases. Adult males in the solitary populations on Swan Island and Cayman Brac have twice the niche width along the perch height dimension, females four times the niche width, of male and female *sagrei* on Jamaica. *A. monensis*, a solitary anole on Mona Island, was also found to occupy a broader range of perch heights than its "mainland" counterpart on Puerto Rico, *A. cooki*. In fact, *monensis* and Swan Island and Cayman Brac *sagrei* have virtually identical perch height distributions.

(2) On islands where more shade-tolerant competitors are absent, *sagrei* populations occupy habitats with high and low insolation. Populations in closed habitats were found to have body temperatures several degrees Centigrade lower than populations in open habitats. Due to habitat expansion, then, *sagrei* populations in the Bahamas and the Cayman Islands have a much broader thermal range than Jamaican *sagrei* which are excluded from forests and shady patches within habitats by *A. lineatopus*. A similar expansion of thermal niche was found to occur in *A. monensis*.

(3) In adult male *sagrei* populations, niche width along the prey size resource axis increases with an increase in mean head length. Unexpectedly, niche width with respect to prey taxa was not found to increase on islands where *sagrei* occurs without more arboreal competitors.

The evolutionary component of these niche shifts was studied by comparing the means and variances of characters adaptively important along the perch height, thermal and food niche dimensions. The results of this morphological analysis are:

(1) Lamellae number in adult male *sagrei* was closely and positively correlated with mean perch height. The coefficient of variation of lamellae number, however, showed no tendency to increase with an increase in the range of perch heights utilized by a population.

(2) Dorsal scale size of *sagrei* populations on Little Cayman and Cayman Brac were convergent and intermediate between Cuban forest anoles (*ahli* and *allogus*) and *sagrei* populations on Jamaica and Cuba. Within the *roquet* group, the solitary species *roquet* and *luciae* were also convergent and inter-

mediate with respect to this character, having scale sizes about twice as large as aeneus and trinitatis and half as large as griseus and richardi. Among sagrei populations there was no correlation between the coefficient of variation of dorsal scale count and measures of thermal niche width.

On Abaco Island, where sagrei occurs in both open and closed habitats, dorsal scale counts were found to be significantly higher in a forest population than in a population occurring in an open habitat within a kilometer of the forest. Coastal forest populations of Cayman Brac sagrei also have a higher number of dorsal scales than populations inhabiting more open areas. Using starch gel electrophoresis, Preston Webster and Lister have found that forest and open populations on Abaco also differ as to gene frequencies at two polymorphic loci. These results suggest that a forest ecotype has evolved on Abaco. Thus Anolis species which have undergone habitat expansion in the absence of competitors should often be more variable, island wide, than on islands where competitors restrict their habitat range.

(3) Among adult male sagrei populations, mean head length was positively correlated with mean prey size and prey size variance. The coefficient of variation of head length was found to increase with increasing niche width along the prey size axis. Populations taking a wider range of prey sizes also had a greater prey size specialization within the head size classes, i.e. a higher between-phenotype component to niche width. These results were consistent with Roughgarden's predictions for the evolution of niche width. However, a model of lizard growth developed by R. McMurtrie and Lister showed that the CV of head length should increase proportionately with an increase in mean head size. This relationship was found empirically both within and between species. Among 10 different populations of A. sagrei, mean head length alone accounted for 75% of the variation in the CVs of head length, and among 19 different Anolis species 77% of the variation in the CVs was explained by mean head length. Our model suggests that patterns of size variation in Anolis may not be the adaptive result of density dependent selection but a direct consequence of the way these lizards grow and mature. Thus the correlation between niche width and the CV of head length in sagrei populations probably results from the fact that both the CV of head length and niche width are positively correlated with mean head size.

To date, the results of this study suggest that the evolution of ecologically specialized phenotypes and adaptive increase in variation are not involved in niche expansion in anoline lizards. Rather, populations that have undergone ecological release have evolved a generalist phenotype capable of exploiting thermally diverse conditions, a variety of perch heights and an optimal range of food items. Indirect evidence indicates that the behavioral component of niche expansion is probably large, at least among good colonizers such as sagrei and carolinensis, and field experiments designed to determine the capacity for behavioral shift in several species are planned.

KENNETH MIYATA (MCZ), traveling with the Williams party in the summer of 1973, has obtained body temperatures and other data on two very special anoles, (1) A. (Tropidodactylus) onca and (2) Phenacosaurus heterodermus. Both of these are in effect "solitary" anoles, since they are not known to share their habitats with any other anoles, though lizards of other genera and families do occur.

(1) A. onca - an anole which has lost the typical anoline pilose pad - is still partially a climber, utilizing especially patches of thorny vegetation with grass at the base, sometimes climbing onto fence posts and even tree trunks and pipelines where these artificial constructions exist. It is sometimes seen on the bare ground (but much less frequently in August 1973 than in November 1972 [observations by Williams, Rand and Kiester], apparently a strong seasonal difference).

Miyata watched one population for a full day on a two acre habitat ca 6 km north of Coro on the Istmo de Medanos - an area of elevated sandy soil with scattered small patches of thorny vegetation separated from other similar habitat islands by corridors of ca 100 m. He was able to keep in sight ca 12 animals; he was the better able to do so because the animals characteristically moved rarely. Most of the animals used perches of small diameter near the ground. Individuals perched on top of thick grass and dense mats of fine twigs and were generally basking in partial sunlight, except early and late in the day when they would be in full sunlight. Others were perched head down on their branches.

Most movement during the day was within the thorn bushes, but later in the afternoon there was more movement into open ground, especially by males.

Mean body temperature (37 individuals) was $33.6^{\circ} \pm 0.6$ (range 28.7°-37.4°). Body and air temperatures varied throughout the day; the warmest part of the day, and the highest body temperatures, occurred near noon. There was a constant high wind at this as at the other localities in which onca was seen, and this must have helped to keep temperatures down.

Feeding was observed on only two occasions, once in the morning and once in the afternoon. In both cases individuals within a foot of the ground jumped down to take some small prey and then returned to their perch. It was not possible to see what was taken. However, in another area one large male was found with a recently taken Cnemidophorus lemniscatus dangling from his mouth.

(2) Phenacosaurus heterodermus is a montane anole believed to have branched off the anole lineage before Anolis proper. Most observations - made during only two days - were in roadside vegetation at a single locality ca 6 km SW of the village of Tenjo, north of Bogota, Colombia.

Phenacosaurs were found primarily in two types of perches - tree trunks and bushes. A single individual was seen on the ground and another on a fence post. There was an apparent preference for small diameter perches near the ground.

Body temperatures were taken for 30 individuals and ranged from 19.0° to 27.8° ($\bar{X} = 22.1^\circ \pm .67^\circ$) in a time period between noon and 2 p.m. The individual of 27.8° was almost three full degrees warmer than the next warmest and was on a fully exposed perch. Other individuals were perched in or near vegetation that tended to obscure the sun.

The behavior of the animals was characteristic - sluggish, slow moving, rarely making any movement to escape capture and then only by moving off slowly or falling to the ground.

Miyata is currently collecting locality data for South and Central American anolines, with several immediate goals in mind:

1. to map the overall distribution of the different species and to point out gaps in extant collections;

2. to store the locality data in readily accessible form (as on punch cards); and

3. to use the locality data to restrict the scope of certain types of studies he would like to carry out.

A trial analysis, utilizing multivariate techniques, was performed on the Anolis faunas of the Greater Antilles, Although there were some ambiguities in the results, they were minor and due to problems in execution rather than in basic design. What Miyata hopes to do is to utilize these techniques to examine community structure on the mainland, in certain selected localities, as both a preliminary and adjunct to field work.

TIMOTHY MOERMOND (Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706) has set as his problem the mode of habitat exploitation by animals and the ways in which the modes of habitat use are influenced by the structure of the habitat. In particular, animals must move through the habitat to find food items and the patterns of their movements will be subject to constraint by the configuration of the habitat.

Moermond's method of study is timed description of movements and postures. In the result, he has been able to show that the frequency of types of movement in anoles is consistent within a given species and is an adaptation to the specific vegetational matrix in which they live. The vegetational matrix is defined by three properties: the diameters of the perches, the lengths of the perches, and the distances between perches. These properties act in concert to determine the proportion of movements between perches (jumps) and the types of movements on perches (crawls or runs) of the anoles. By comparing the relative frequencies of movement types, three general types of anoles are recognized -- jumpers, crawlers and runners - each of which can be identified by characteristic proportions of the limbs (see the following table).

Moermond emphasizes the existence of a gradient of vegetational matrices from open formations with tight matrices (grasses and bushes) to closed formations with loose matrices (forest). No anole can be maximally efficient in every part of the vegetational gradient. It is suggested that discontinuities in the gradient would promote behavioral and morphological specialization to segments of the gradient. The patterns of movements, limb proportions and foraging strategy of a given specialist are all found to be correlated and highly predictable from the structure (tightness and looseness) of the vegetational structure.

The tables and figures which follow describe the correlation of anole ecomorphs' foraging zones and characteristic movement types.

The work described above was done at two localities in western Haiti, one montane with 7 _Anolis_ species, one lowland with 3 species. Moermond has now extended his operations to the two-anole island of Grenada in the southern Lesser Antilles.

The two Grenadian species, _A. aeneus_ and _A. richardi_, were studied in an _Acacia_ wood-lot at Grande Anse.

The two species differ in sun-shade preference, _aeneus_, the smaller of the two, preferring more open situations, and _richardi_, the larger species, preferring more shaded spots with the juveniles of the two species showing the sharpest segregation. Within each species adult males, adult females and juveniles occurred in somewhat separate (although overlapping) microhabitats.

In A. aeneus the adult males utilized the whole trunk and lower crown of trees usually in more open situations, moving frequently with long walks and runs. Adult females were generally lower and in smaller trees and bushes. Juveniles were in the tight matrix of low bushes and grasses and, in particular, brush piles. The proportions of the limbs and body were remarkably like those of A. coelestinus. Likewise the movement patterns were quite similar to those of coelestinus, especially among the juveniles. Relative to other anoles, aeneus are active searchers rather than sit-and-wait predators. (The males of aeneus are particularly active when compared with males of coelestinus, a probable ecological equivalent.)

The juveniles of A. richardi live in the loose matrix of the leaves and sticks of the forest floor beneath the underbrush. They have proportionately longer legs than juvenile aeneus, move much less frequently than aeneus, with a high proportion of the movements being jumps, and often run on the ground (unusual for any species except trunk-ground types like cybotes). Female A. richardi tend to sit head-down at the base of trees quite like A. cybotes in Haiti. Adult male A. richardi are frequently higher in the trees and make fewer jumps and more movements on surfaces. The legs of adult richardi are proportionately not as long as those of juveniles but are still somewhat longer than those of aeneus, toward which they converge. All members of A. richardi are sit-and-wait predators, moving significantly less often than aeneus.

Moermond has 16 species at Wisconsin sent him from grant-supported expeditions. On these he is taking several kinds of data.

1. Observations on methods of prey capture. Several of the smaller species were observed feeding on Drosophila. Etheridgei, olssoni, cochranae and hendersoni use a rapid jump capture in which the lizard aims at the prey item, opens its mouth slightly, and then jumps at the item, capturing it on contact. This technique has been recorded by Moermond for hendersoni in the field and is probably characteristic of 'jumpers'. Insolitus, which represents a specialized crawler, uses a quite different method, stalking the prey item until about 10 mm away, then opening its mouth and protruding the tongue as a fat, wet bulb in the front of the mouth. Insolitus then reaches forward deliberately and presses the tongue on the fly, which is then grasped by the mouth. Longer reaches require a more rapid strike but the remainder of the pattern is the same and insolitus typically remains on the perch from which the strike was made. Both of these capture techniques contrast sharply with the typical pattern used by anoles where the lizard runs (or jumps) up to a prey item, pauses by it, then strikes the item from about 10 mm away. The rapid jump capture has been observed used over a distance of about 20 cm (8 in.).

2. Observations on handling and swallowing time. An attempt will be made to record the cost in time of handling and swallowing for a range of prey sizes and predator sizes. Preliminary observations suggest that a lizard of a given size masticates small prey immediately but first knocks prey above a certain size against the perch.

3. Observations on movement patterns and height distributions on artificially constructed perch matrices. Movement patterns of different species will be recorded on various perch matrices differing in precise ways.

4. Determination of the rates of metabolism for a range of species representing different ecomorphs. This work is only in initial stages and will be largely done by Deborah Crouse in conjunction with Moermond and Warren Porter.

Moermond is also involved in determining an annual energy budget for *Anolis* (with Warren Porter), in constructing computer simulation of predator searching strategies (with Curtis Wilcott) and in measuring spectral properties of *Anolis* dewlaps (with Jack Hailman).

(Extracted from an MS by T. Moermond)

Locomotion Type	leg/body	tibia/femur	humerus/femur	tail/body	species
jumper	.58*	.92	.61	2.4	semilineatus
jumper	.57	.91	.59	2.1	koopmani
jumper	.56	.94	.61	2.6	hendersoni
jumper	.63	.88	.56	2.3	monticola
crawler	.46	.87	.79	2.0	coelestinus
crawler	.44	.82	-	-	aliniger**
crawler	.40	.83	.72	1.2	insolitus**
runner	.60	.93	.72	1.8	cybotes
runner	.59	.90	.80	1.3	distichus
crawler ?	.49	.86	.74	1.9	aeneus
runner ?	.60	.92	.73	2.2	richardi

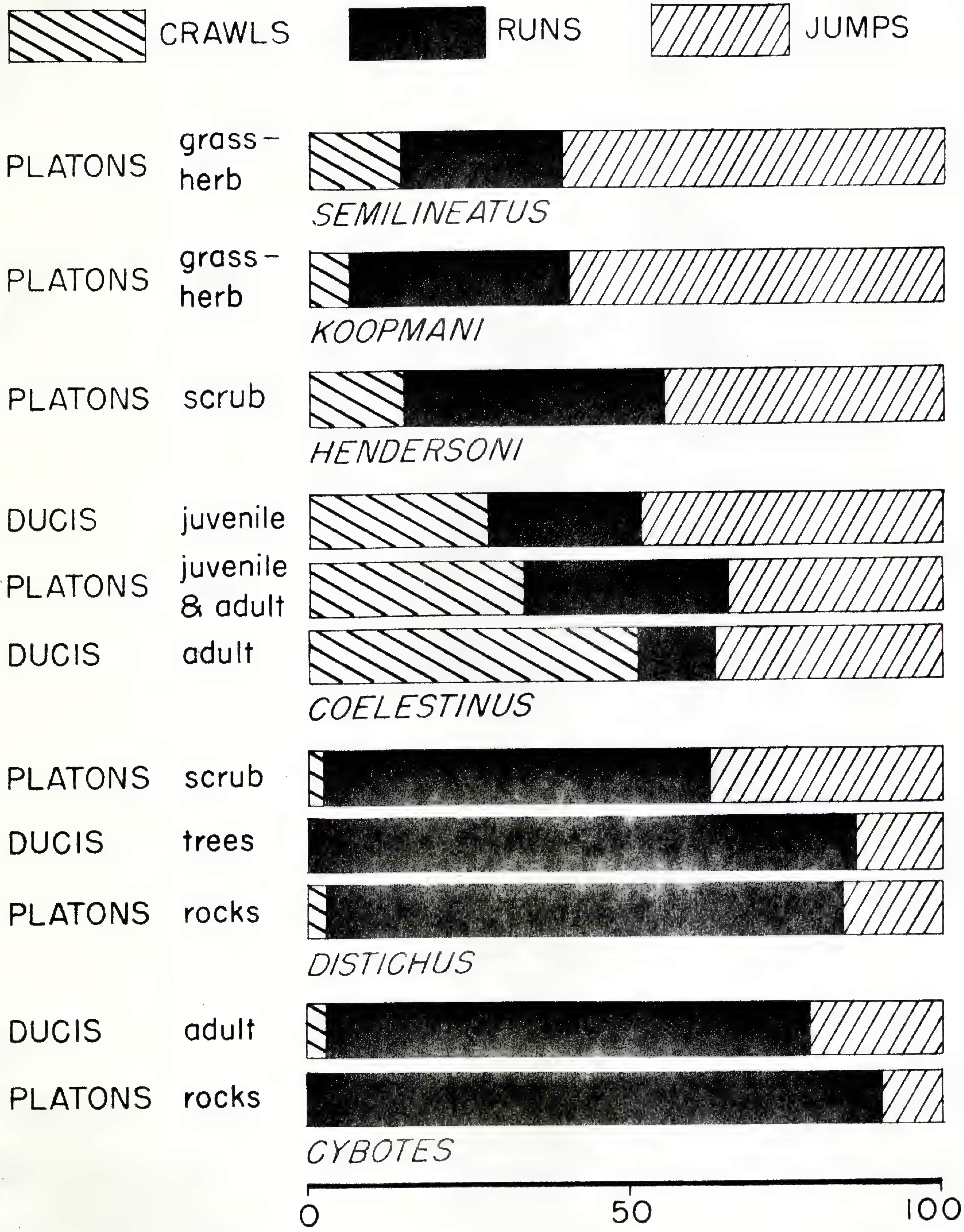
	jumpers	crawlers	runners
LEG / BODY	.56--.63	.40--.46	.59--.60
HUMERUS/FEMUR	.56--.61	.72--.79	.72--.80

* the means are given for all ratios.

** aliniger and insolitus were both observed only in captivity.

Ducis - a lowland locality in SW Haiti.

Les Platons - a nearby montane locality.



(Extracted from an MS by T. Moermond)

(Extracted from an MS by T. Moermond)

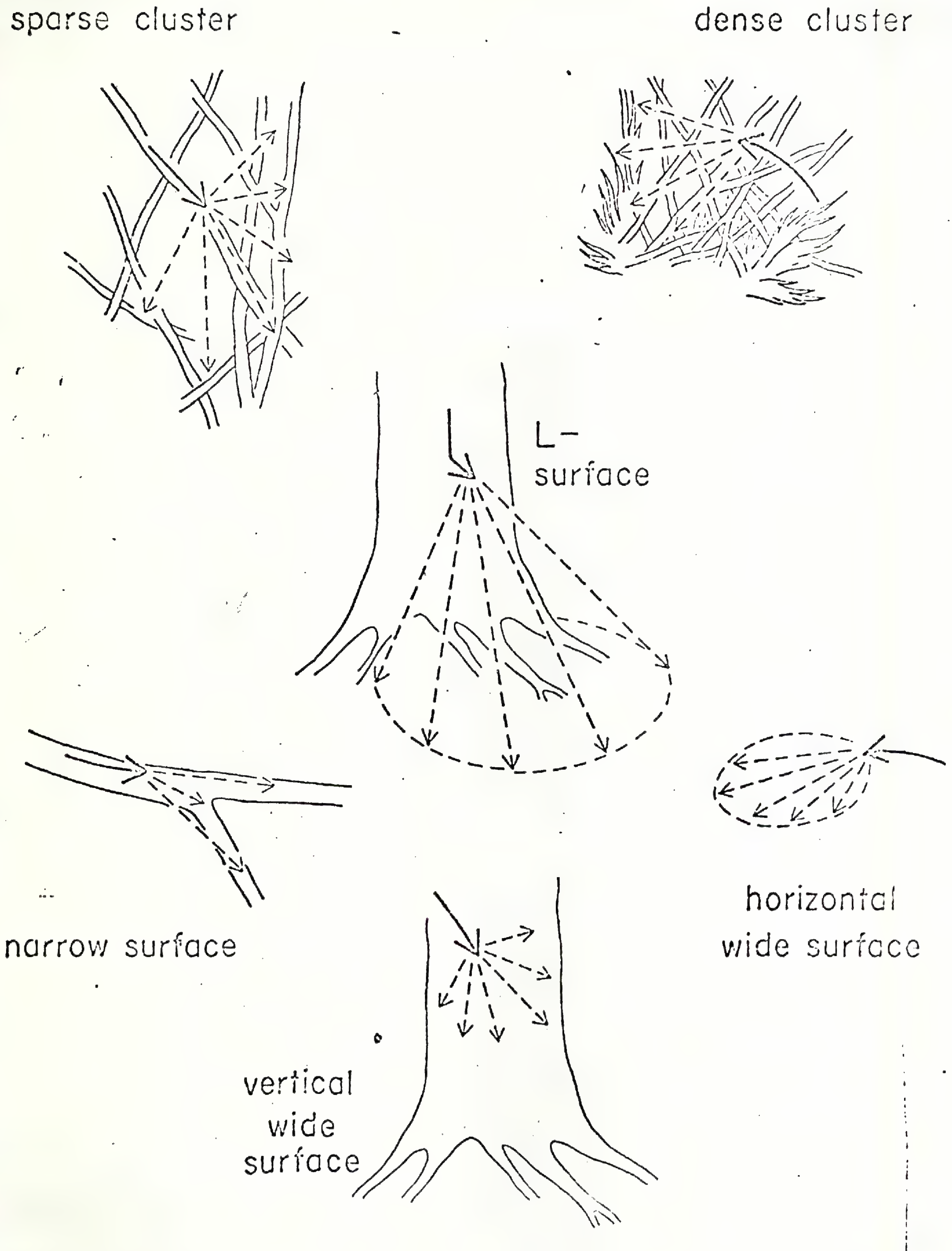
Table 2

(Table V)

ECOMORPHS	HABITAT	FORAGING ZONE	MOVEMENT TYPE
TRUNK-CROWN:	upper trunks of trees or in the crown (vine tangles, edge).	narrow surfaces and wide vertical surfaces	crawler; short intervals between moves.
TRUNK:	confined to tree trunks and rarely climbing to the crown or descending to the ground (wide vertical rock surfaces)	wide vertical surfaces	runner; very short intervals between moves.
TRUNK-GROUND:	lower trunks of trees, foraging from there onto the ground (wide vertical rock surfaces).	L-surfaces	runner; long intervals between moves.
BUSH:	bushes away from trees (edge, understory tangles)	sparse cluster	jumper; long intervals between moves.
GRASS:	(grass-herb fields)	dense cluster	jumper; short intervals between moves.
- - - - - -	- - - - - -	- - - - - -	- - - - - -
TWIG:	thin branches and twigs, often near or in the crown	narrow surfaces	crawler; short intervals between moves.
CROWN(GIANT):	frequently very high within the crown	narrow surfaces (sparse cluster?)	crawler; long (?) intervals between moves.
ROCK:	rocks at edge or in understory.	L-surfaces	jumper; long intervals between moves.

(Extracted from an MS by T. Moermond)

FORAGING ZONES



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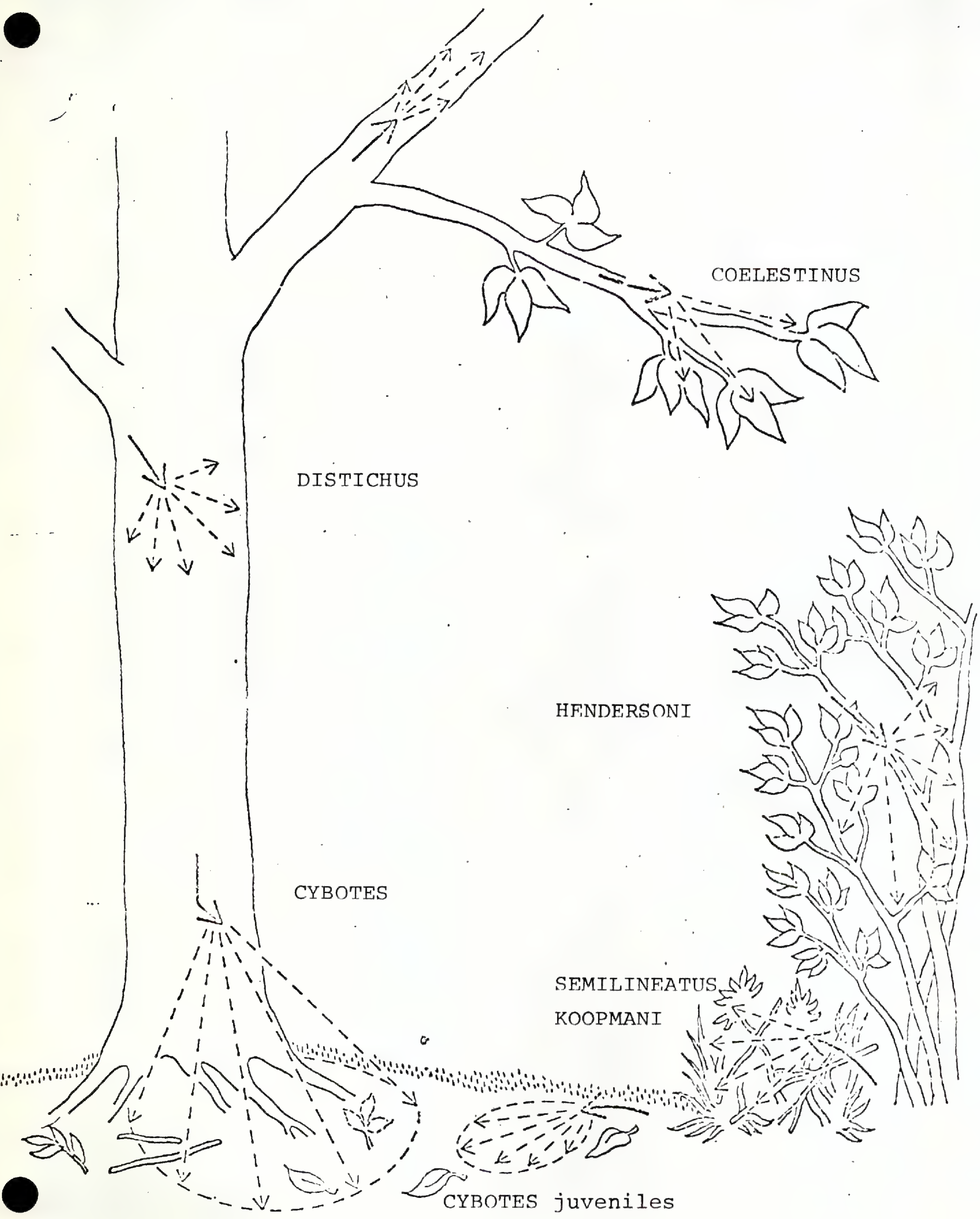

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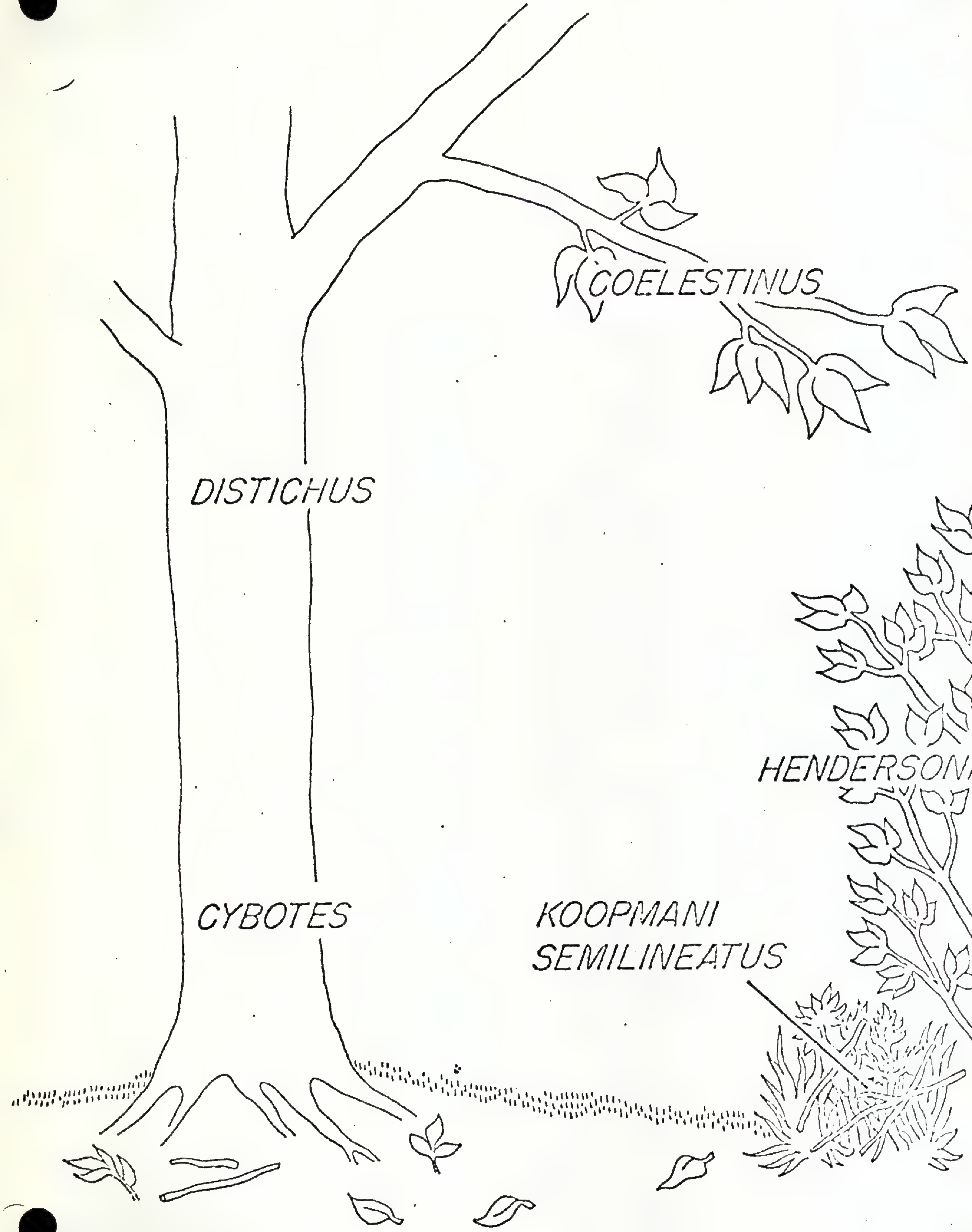
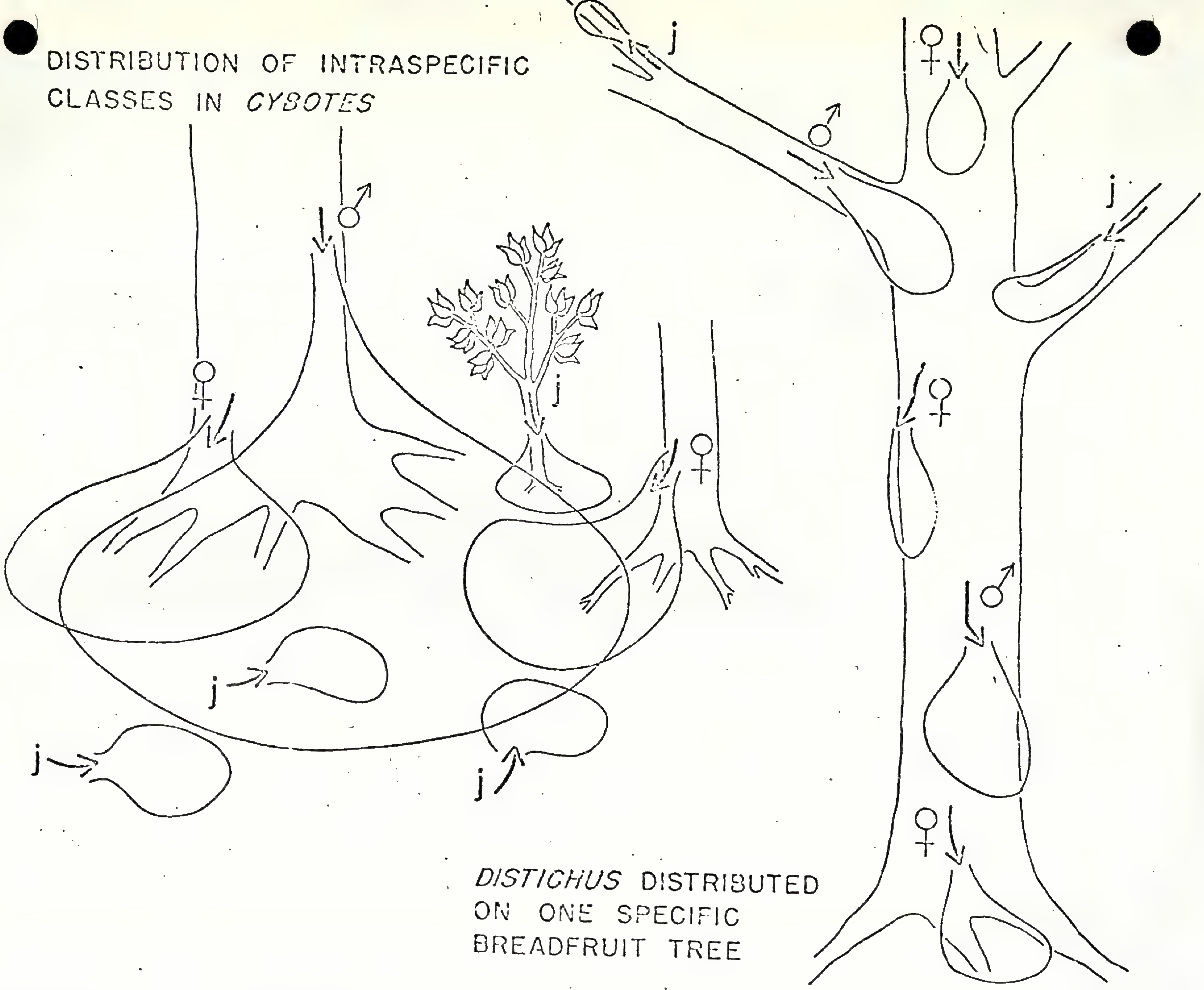


DISTRIBUTION OF INTRASPECIFIC CLASSES IN *CYBOTES*



DISTICHUS DISTRIBUTED ON ONE SPECIFIC BREADFRUIT TREE

(extracted from an MS by T. Moermond)

JANE PETERSON (MCZ), starting from a base of detailed knowledge of locomotor anatomy and function in *Chamaeleo*, *Agama*, *Dipsosaurus* and five anole species, has begun analyzing locomotor behavior and structure in selected anole ecomorphs from Jamaica, Hispaniola and Puerto Rico. Many of these she has seen and filmed in the field; a large number of species are being studied in a facility at Harvard's Concord Field Station.

Five anole species representing five ecomorphs demonstrate very significant differences in functional morphology of the shoulder region and locomotor behavior. The broader comparative project now underway is designed to explore the relationship of locomotor behavior and morphology with the physical and ecological aspects of locomotor habitat. Data on functional morphology is based on dissections of six to ten specimens, osteometry and manipulation of ligament preparations. For the larger species functional inference will be tested by cine-radiography and electromyography. Locomotor behavior is being surveyed by filming each species on a variety of perches simulating different locomotor habitats.

The morphological and behavioral trends exhibited by a number of arboreal lizards (compared to their terrestrial relatives) suggest that arboreality selects for increased range of movement (mobility) and for a greater variety of positions in which the limb can grasp the perch and propel the animal. A relatively stereotyped locomotor cycle is inappropriate where the substrate is varied in orientation and diameter and is discontinuous so that the animal must change perches frequently.

The limb is composed of a series of elements the most distal of which transfers force between the limb and substrate and must meet requirements for stable contact with a given substrate. Arboreal adaptation in distal segments, whether by adhesive, suction or prehensile devices, is reasonably well documented even if the mechanisms are poorly understood. Adaptation of the most proximal segments (girdle and humerus or femur) has the greatest bearing on the total arc of limb movement; selection for a greater range of movement should be evidenced in these regions.

Lizards seemingly demonstrate a variety of biomechanical solutions to the problem of increasing the range of movement. A greater arc of movement at a given joint is generally bought by decreased stability in the articulation. Tissues with relatively poor stress bearing characteristics, e.g. groups of muscles, are substituted for elements which are adapted to resist stress and confine joint excursion, e.g. ligaments, cartilaginous menisci and bony cups or prominences. This substitution reduces overall joint stability and by implication limits the amount or kinds of forces that can be transmitted through the joint efficiently or without mechanical failure. Given 1) selective pressure to increase mobility with minimum cost in stability, 2) three linkage areas available for modification, and 3) a variety of behavioral and morphological "starting points" in different phyletic lines, biomechanical adaptations are likely to vary. Increased glenohumeral mobility may be a common factor but some lizards depend upon a long, highly flexible body axis to increase the reach of the limb, e.g. Gerrhonotus multicarinatus, while others modify the shoulder region to permit movement of the shoulder girdle on the body wall, e.g. Chamaeleo, Polychrus, Phenacosaurus and Anolis. In the majority of lizards the shoulder girdle is fixed to the body wall. (There is actual data for only a few, but literature reports on the existence of a critical ligamentous arrangement is reasonable evidence for the generality of a fixed girdle). Adaptation for rotation of the girdle in the sagittal plane as seen in these four lizard genera requires reorganization of three or four articulations between the girdle and dermal-axial elements. The girdle-axial muscles not only have different architecture and attachments, but must have different periods of activity in the locomotor cycle (EMG data). Parallel adaptations occur in the reptile-mammal transition and are the basis of the more widely discussed postural and weight transfer shifts in mammals. Not surprisingly, these arboreal lizards can approach mammalian postures and converge on mammalian locomotor mechanics in many respects. In Chamaeleo, Polychrus and Phenacosaurus slow movement permits the animal to avoid the large forces associated with impact and acceleration, thus decreasing (perhaps by half) the applied force. Adaptation for mobility is extreme; stress bearing arrangements are dramatically reduced (ligaments absent; clavicle absent or weakly articulated); muscles are arranged to provide maximum excursion of elements at the expense of more favorable leverage. Adaptation in the recovery musculature is more marked than that in the propulsive muscles. This correlates with the long reach and slow acrobatic maneuvers these animals use to change perches. The recovery stroke involves not only swinging the limb forward, but reaching, obtaining purchase and reorientation to a spatially different substrate. The range of movement in quadrants anterior to the shoulder is much greater in these arboreal forms than in their terrestrial relatives. Among other adaptations they have a more laterally facing shoulder articulation.

Anoles parallel many of these adaptations, including most of those associated with modification of the recovery muscles (although different muscle groups are involved), more lateral orientation of the shoulder joint and girdle mobility. But they are less specialized for mobility than the related Polychrus or Phenacosaurus. This is not an indication of less arboreal specialization, but rather a different behavioral strategy relying on acceleration (leaping) to change perches and higher speeds for movement on a given substrate. An anole presents a mosaic of adaptations for compromising increased mobility with the stability required by higher speeds and leaping behavior. The compromise has been achieved by structural innovation. For example, many anoles have a clavicular mechanism which allows rotation of the girdle during protraction and the early stage of retraction (phases when the limb is in quadrants anterior to the shoulder joint), but fixes the girdle relative to the body wall when the forearm is being extended (forearm extension occurs at the onset of a leap and in landing and is the most important component of the propulsive stroke). If the girdle were free to displace during these periods, there is presumably the danger that it would displace forward relative to the body wall with loss of efficiency in transfer of propulsive force. The presence of such a "locking mechanism" reduces the total amount of girdle mobility which is available, but it provides the critical option for coupling the advantages of a mobile girdle with those of a linkage between the body and girdle which is efficient for higher speeds and leaping.

The trends which are evidenced in the generic comparisons are also operating within the genus. There are significant differences in preferred speed of movement, arcs of limb movement, the mobility of the girdle and adaptations of the glenohumeral articulation.

The behavioral survey of anoles examines the following variables: 1) the range of perch diameters a species can negotiate, 2) differences in behavior related to perch orientation, 3) behaviors used to move to a new perch, 4) preferred gait and speed on a given perch, 5) amount of undulatory movement, 6) variation in the way cycles are combined into movement patterns, and 7) planes of limb action used in walking and the repertoire of limb positions available. There is sufficient film and observational data to indicate that ecomorphs converge rather markedly. With few exceptions they share more behavioral characteristics with each other than with any of their relatives which were examined or with any other member of their respective faunas. Comparison of the three faunas suggests that there is more behavioral differentiation within the Hispaniolan fauna than within the Jamaican fauna. Although the morphological comparisons are yet fragmentary, the available data suggest strong morphological convergence within ecomorphs and marked differentiation among them. The following behavioral-morphological profiles of the six ecomorphs being studied are preliminary and necessarily too brief, but they suggest preliminary correlations with the ecological observations and a pattern within the radiation which is unexpected and interesting. Profiles for each ecomorph include morphological and behavioral data. Species referred to in the two sections are enclosed by parentheses.

1. _Canopy giant behavior_ (_A. cuvieri_, _A. equestris_, _A. garmani_): The preferred gait on 1.5" diameter perches is a walk. Two feet are always in contact with the substrate. Giants sometimes have difficulty on perches of this diameter and can't progress normally along perches of 1/2" diameter. They shift to suspensory or crosswise postures and leap away. Suspensory or crosswise postures permit the long hind limbs and short front limbs to grasp the same perch. Giants are reasonable though not spectacular leapers. Adaptation for leaping in the form of a disparity in fore and hind limb length coupled with large body size makes it difficult for them to negotiate single very narrow perches. They do, however, hop between mats of small diameter perches using two or more small perches simultaneously (one foot may even spread over more than one perch).

Morphology (_A. equestris_, _A. richardi_): The girdle is set on the body at an angle of 28-32° to the sagittal plane (compared to 27° in _Chamaeleo_ and about 58° in Gecko). This low angle makes sagittal (anterior-posterior) movement of the girdle highly effective in increasing the length of the stride and versatility of the limb. The glenoid faces more laterally than in most anoles (except chlorocyanus and pulchellus); both the recovery and girdle muscles are more highly modified for mobility than for any other anole (except perhaps twig species). The movement of the girdle observed in films of equestris is greater than that in cybotes (comparable film observation) or distichus (anatomical inference).

2. Twig anole behavior (A. occultus, A. valencienni): The preferred gait is a walk or slow walk in which two feet always contact the ground. Twig anoles are generally slower than the canopy forms. A. valencienni can negotiate much finer diameter perches than garmani juveniles of a comparable size. The short and evenly proportioned limbs permit the animal to go through a full locomotor cycle with all four feet using the same perch. Twig animals frequently walk with the body pressed to the perch (crawl); they can, however, shift to a straight legged or erect slightly faster walking gait. Perches are changed by a short hop (leaps are apparently only feasible where the animal can actually drop) or by slow acrobatic maneuvers reminescent of Chamaeleo or Phenacosaurus. As in the latter genus the short limbs and thus short reach is partially compensated for by axial movement. Range of limb movement is at least comparable to the canopy giants.

Morphology (A. valencienni - incomplete): The girdle is set at 28-30° from the sagittal plane, and available data suggest that girdle mobility is probably at least as great as in equestris. Glenohumeral morphology includes some adaptation related to the short humeral segment and greater emphasis on long axis rotation of the humerus. These features parallel chlorocyanus, but modification of the protractor musculature for a wider arc of movement is much more prevasive and clear cut than in the latter species.

Twig anoles appear to converge on the anoline genera, Phenacosaurus and Polychrus, in morphology and behavior.

3. Trunk-crown behavior (A. evermanni, A. chlorocyanus, A. grahami): These animals generally move faster than the twig forms, but unlike the trunk or trunk ground forms do not appear to have a trotting or very fast walking gait. They negotiate small perches with greater difficulty than valencienni but more readily than equestris. This is perhaps a size effect, however, because they cannot move surely and rapidly on perches half their own diameter.

Morphology (A. chlorocyanus): The girdle is set at 37° to the sagittal plane, but some of the girdle muscles are poorly adapted to rotate the shoulder girdle. The morphology of the clavicular articulations suggests that chlorocyanus represents a different phylogenetic "experiment" in acquiring girdle mobility. It is highly likely that some girdle mobility is present but quite unclear how much the clavicular articulations will permit.

The glenoid is turned far laterally but muscular adaptation is again equivocal.

4. Trunk-small trunk-crown behavior (*A. stratulus*, *A. distichus*, *A. opalinus*): This ecomorph uses a very fast walk or trotting gait consistently. Moermond reports that *distichus* rarely moves slowly and this is certainly true in the film sequences. The combination of cycles is quite distinctive. There are five to six cycles followed by a dead stop and then repeat. They appear to skitter. Moermond reports that *distichus* at least leaps for about a third of its moves, but they appear remarkably unacrobatic compared to *cybotes* or the grass anoles. The behavioral repertoire in terms of gaits, variation in limb position, etc. is the narrowest among the anoles observed.

Morphology (*A. distichus*): The morphology of *distichus* strongly suggests secondary adaptation to reduce both girdle and glenohumeral mobility in favor of joint stability and muscle leverage. There is probably very little girdle movement because 1) a ligament connection is shifted close to the main articulation between the body wall and girdle, 2) the ventral clavicular articulation lies just anterior and in the plane the girdle would have to occupy if it shifted anteriorly, and 3) the girdle muscles poorly discriminate the clavicular articulations; they may act on both sides of the joint with consequent ineffective action. The glenohumeral articulation faces entirely laterally but is more closed and cuplike with very robust ligaments. The humeral head is reflected at an angle to the shaft (like the human femur). The major protracting muscle originates so that it can effect little more than 90° of protraction (abduction). Th mode of origin is also seen in *Agama* but apparently in no other lizards.

5. Trunk-ground behavior (*A. cristatellus*, *A. cybotes*, *A. lineatopus*): Like the trunk ecomorph these species have a fast or running walk gait. But, unlike the trunk forms they are quite spectacular leapers and more frequently use acrobatic postures and maneuvers. The latter permits them to use relatively small diameter perches (1/2-1/4 inch). The plane of forelimb action is usually erect or semi-erect. This is partially due to the proportional disparity between the fore and hind limbs.

Morphology (*A. cybotes*): The girdle is set at a relatively high angle to the sagittal plane (44°). In spite of this, films indicate that at least 35° of girdle rotation is used during fast walking. This rotation occurs entirely during the cycle phases when the limb is anterior to the transverse plane of the shoulder. The clavicular locking mechanism is most well developed in *cybotes* and stops girdle displacement as the limb is extended. The girdle and glenohumeral musculature is very highly specialized. The bellies are generally placed to provide for maximum limb and girdle excursion frequently at the expense of leverage, but there are architectural adaptations of the bellies which permit many more muscle fibers to be packed into the belly. Conflicting selection for mobility and stability is nowhere more evident than in *cybotes*.

6. Grass behavior (A. pulchellus, A. olssoni): The grass anoles are specialists in fast acrobatic maneuvers on small diameter perches. Their gait patterns and limb movements resemble the trunk-ground forms, but they may also crawl like the twig anoles. They have a very long arc of limb movement, but it is more restricted in the anterodorsal quadrant than that of twig anoles.

Morphology (A. pulchellus): A less restricted version of the locking mechanism of cybotes is apparently present in pulchellus, but there is generally very marked convergence on the canopy forms. This is indicated by the 32° orientation of the girdle on the body. The protracting musculature reorients as in the canopy forms but does so by different morphological pathways indicating functional convergence. The shoulder joint faces more laterally but is less open than in the canopy forms. This permits more anterior excursion of the humerus but less dorsoventral excursion of the limb in these anterior positions.

A variety of ecological interpretations for the interspecific patterns are available.

1) Naively one might look for a continuous ground to canopy series reflecting more specialization for arboreality. But the anole ecomorphs represent quite distinct types rather than a continuous series. A. distichus and A. pulchellus would be very poor fits in such an interpretation.

2) Schoener and Williams have suggested that body size differences partition food resources and are an important factor in species diversification. Body size also affects the range of perches which can be used and the kinds of behaviors which are appropriate to shift from one perch to another. The size difference of canopy giants and twig anoles clearly suggests their different structural habitat and behavior. But in other cases it is difficult to interpret the behavioral and morphological data in this manner. Size differentiation appears to induce complex rather than simple allometric effects. Behavioral and functional strategies are adapted not strictly to size but to the relationship among perch size, body size and the distance between perches.

3) The variation in anole structural habitats as viewed by Rand, Williams and lately by Moermond is characterized by perch height, perch diameter, density of perches and variation in perch orientation. Perch diameter correlates with more of the comparative data than any other single factor. For example, it predicts the marked convergence of grass and canopy forms in features related to girdle and limb mobility. Small perches with varying orientations probably provide the major selective force for increased mobility. Variation in speed of movement, which is apparently correlated with perch elevation, is not as dramatic as that in perch diameter preference. But it separates the canopy animals from the trunk or grass forms. Adaptations for stability in the proximal forelimb articulations and for power in leaping

and climbing are more important in the latter group. Canopy animals maintain at least two feet in contact with the substrate while trunk and grass forms can use much faster gaits. This seems to suggest that balance is quite important at higher elevations. But the higher speeds of grass anoles compared to twig anoles are unlikely a matter of equilibrium alone. Different escape and foraging strategies related to cover and the feasibility of getting to the ground may be more significant than simply maintaining balance.

4) Perch diameter and elevation are inadequate to explain the major differences between *cybotes* and *distichus*. Moermond's data clearly indicate that *cybotes* uses a three-dimensional foraging zone while *distichus* uses a two-dimensional, wide vertical surface. The more stereotyped substrate and very "two-dimensional" behavior of *distichus* may be responsible for species adaptations which converge markedly on terrestrial lizards. The trunk-ground zone of *cybotes* is, indeed, less varied than the grass or twig habitats, but *cybotes* uses the area in such a dimensional manner as to make limb mobility an important factor in its morphological specialization.

The six anole ecomorphs that are briefly compared here illustrate major adaptive differences in behavior and functional morphology. Behavioral variables within the genus include the speed of movement, the amount and type of acrobatic movement used to change perches and the range of limb movement which is available to the animal. Much of the variance in behavior can be attributed to differences in the relationship among body size, perch size and distance between perches; however, foraging and escape strategies are necessary to account for additional differences among ecomorphs.

The comparative morphology of anoles is directed toward the resolution of two conflicting selective forces: 1) that for a very mobile limb which allows the animal to use a highly dimensional and varied locomotor substrate, and 2) that for a proximal limb region which is stable enough to permit the transmission and generation of the larger forces associated with higher speeds and leaping behavior. A greater range of limb and girdle movement is found in ecomorphs which use acrobatic movements, particularly at low speeds, and small diameter perches. Greater stability is found in forms which are fast moving, less acrobatic and use large diameter perches. Trunk-ground and grass anoles which are fast acrobats on large and small diameter perches respectively are particularly interesting studies in functional compromise.

Locomotor diversification in *Anolis* has occurred with a high degree of habitat specificity in behavior and innovation in functional morphology. The analysis to date suggests that functional morphology is adapted to 1) physical characteristics of the substrate, primarily perch diameter, 2) ecological-physical factors which influence speed of movement, and 3) behavioral utilization of the perch, particularly the foraging zone.

A. S. RAND (Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone) has continued his study of the evolution of display in anoles of the Northern Lesser Antilles, utilizing frame-by-frame analysis of male-male interaction. He has been able to show that on any one island there may be considerable microgeographic variation in male coloration and pattern but little in display. In sharp contrast between islands separated on different banks, males in addition to differing in color and pattern differ also in display. This is true even of populations inhabiting very similar microhabitats.

He has now investigated an intermediate condition, that seen on the three islands of St. Barts, St. Martin and Anguilla, now separated by water but all on the same bank. Here the males show very little variation from sample to sample in either appearance or dewlap display. He suggests two possible explanations: (1) *a time hypothesis*: the islands on the same bank were continuous dry land during the last glacial maximum. Hence, since display evolution is a slow process, the presently isolated populations have not had time to diverge; (2) *a founder hypothesis*: display evolution occurs primarily during the gene pool reorganization which follows the colonization of a new island by the very small founder population. Since islands on the same bank were not independently colonized over water, populations on such islands show no founder effect.

Rand has now visited and filmed displays on all the northern Lesser Antillean banks except Redonda. Dominica, however, which was visited very early, should be revisited.

Rand continues to maintain the anole facility in Panama. This permits study of displays and of much else for anoles captured elsewhere. Among the exotic species filmed this year at the facility were *Phenacosaurus heterodermus* (Bogota), *Anolis insolitus* (La Palma, Hispaniola) and *Anolis townsendi* (Cocos Island). (See Jenssen for comments and discussion.)

The anole colony maintains breeding populations of various anoles, ordinarily selected because of their divergent behavior. Colonies are continuing of *Anolis cuvieri*, *A. agassizi*, *A. oculatus cabritensis*, *A. o. winstoni*, *A. leachii* and *A.* (*Tropidodactylus*) *onca*. Two species have been added during the year: *A. gingivinus* (Anguilla) and *A. townsendi* (as mentioned, from Cocos Island in the Pacific). There is still difficulty in maintaining montane species such as *Phenacosaurus* but there are hopes that some problems of this sort will soon be solved.

Information on growth rates and reproduction is provided by the anole colony as well as on social behavior. Rand has, for example, collaborated with Robin Andrews on her studies on reproductive effort in anoles and in her experiments with growth rates and egg laying rates in *A. limifrons* in captivity. The latter observations provide comparisons with Robin Andrews' long term study of population fluctuations in *Anolis limifrons* on Barro Colorado Island (again in collaboration with Rand).

Thomas Jenssen has used the anole facility in his film loop experiments, investigating display repertoire and other behavior in A. limifrons. Rand hopes to continue and extend Jenssen's efforts in the development of techniques for the production of animated anole display films and an apparatus for showing these to anoles.

Some additional minor discoveries have been permitted by the anole facility:

1. The displays of Anolis (Tropidodactylus) onca are strikingly like those of Anolis chrysolepis and may be good evidence of relationship.

2. Juvenile A. cuvieri are tan boldly crossbanded with darker on neck, pelvic area and limbs. This pattern changes to the essentially unicolor green or brown of the adults. The banded pattern of the young may (as in some skinks) be a device to prevent cannibalism by the adults.

3. The adults of cuvieri have two morphs, brown and green. The change to the mottled grey brown of the brown morph is largely a fading of the juvenile crossbanding. The change to the green morph involves in addition a gradual enhancement of a greenish cast.

4. Check of the stomachs of A. cuvieri shows little evidence of the extensive use of fruit that has been suggested for other giant anoles. A. cuvieri seems to be a specialist in large animal prey. They take very large insects as well as (as mentioned above) anoles.

5. Anolis oculatus winstoni populations have been allowed to flourish at the Panama anole colony. They have now reached a very high level; adults are very numerous, eggs are being laid, but surviving young are few. Cannibalism may be one of the reasons for the dearth of young.

With Williams, Rand has been studying the relationship of dewlap function to species recognition and faunal size. In simple faunas (one or two species islands) dewlaps serve to increase the displaying animal's apparent size, to identify its sex, to distinguish an adult from a juvenile, to discriminate the territory-holder from wandering animals, to signal the mood (aggressive, sexual etc.) of an animal and to call attention to an animal by making it conspicuous. Very clearly the dewlap is a major social signal but it is not a cue to species identity. This is demonstrated in the two species islands of the Lesser Antilles where the two species have very similar or identical dewlap colors. On these islands species identity is encoded primarily by body pattern. (In single species Lesser Antillean islands deme identity is similarly encoded by body pattern [A. marmoratus of Guadeloupe, A. oculatus of Dominica, A. roquet of Martinique].)

Body pattern is a permanent advertisement of species identity. Its drawback is that the animal is always conspicuous. Where predators are few, this drawback is minimized. One or two species islands are small; the fauna including predators is depauperate; hence the permanent conspicuousness of body pattern does not in these animals override its benefit.

In larger faunas the situation is quite otherwise. The islands are large, the predators relatively numerous. Body pattern is now less important, and dewlap color and pattern usually highly important, especially so in animals similar in size and shape and ecology (i.e. representatives of the same ecomorph).

Here the mobility of the dewlap increases its utility as a cue to species identity: when social situations require, the animal may flaunt its identity; on other occasions, and particularly if predators appear, the dewlap is retracted and the animal may become relatively cryptic.

Body pattern, size and shape may all be aids to species recognition. The new function of the dewlap in complex faunas adds a new signal for the same purpose. It adds redundancy, and as Rand and Williams have said previously, redundancy is itself selected because it is important in allowing species recognition in a variety of circumstances.

Rand has some observations on the social aspects of thermal niche in *Anolis oculatus*. His conclusions are drawn from data collected first with Ross Kiester and later with Patricia Rand at the locality on the west coast of Dominica already discussed by Ruibal and Philobosian (1971) as showing the wide thermal niche width of a "solitary" anole.

Kiester and Rand in November found a difference between the populations in open sunny coconut groves (mostly small adults and more males than females) and in adjacent denser stands of trees with heavier shade (large males, more females and many juveniles).

In May at the beginning of the rainy season, Rand and Rand saw no juveniles but a shaded hedge now had a higher proportion of males to females and a larger average size of adult males than adjacent rows of coconuts. The differences were statistically significant.

Rand suggests that in areas of high population density the preferable microhabitats - the shaded areas - are inhabited by the largest males. The smaller males are forced into adjacent tolerable but less preferable areas. He further suggests that in the Greater Antilles, with many species present, adjacent habitats not optimal for a given species would be occupied by other species, forcing younger males to wider dispersal in the search for suitable habitats.

Rand therefore predicts (1) that in single species islands like Dominica the spread of a species through adjacent differing microhabitats will be greatest where the population densities of that species are greatest and least where they are least; (2) in the Greater Antilles such spread of a species through differing microhabitats will occur only in local habitats where one species is very abundant and others rare or absent, i.e. situations that locally approximate the conditions of one species islands. Rand, however, further predicts that where, as on single species islands, an appreciable portion of the population is forced to live in sub-optimal habitats selection will favor adaptations which fit the population for the wider niche.

Rand has studied the ecological relationships of the two anoles on St. Kitts in the Lesser Antilles - *A. bimaculatus* and *A. wattsi*.

They differ in classical fashion in size, structural niche and climatic niche.

Size: *Bimaculatus* is the giant: males (mean of largest third) 85.5 mm snout-vent length; females 60.5 mm. *Wattsi* is much smaller: males 47.5 mm; females 41.2 mm.

Wattsi shows little variability in size; *bimaculatus*, on the other hand, varies greatly. The reason is not clear. It may be (1) that *wattsi* is short-lived and *bimaculatus* long-lived, or (2) there may be a difference in the variability of the size at which growth slows or stops.

Structural niche: *Bimaculatus* is much more arboreal than *wattsi*. In the coconut groves at Conaree this is very striking. *Bimaculatus* lives in the crowns of the coconut trees and on the trunks, *wattsi* in the dead fronds and other heaps of trash at the tree bases. The crowns are refuges for *bimaculatus*, the interior of the trash heaps for *wattsi*.

Climatic niche: Moisture seems to be the climatic variable separating the species. *Wattsi* is more moisture-dependent and finds in the trash heaps of coconut groves moisture reservoirs in dry periods. A series of censuses of the two species consequently leads to quite different results: the number of *bimaculatus* seen remains essentially constant but the number of *wattsi* fluctuates widely. A plot of census results as per cent *wattsi* shows correlation with the number of days since the last rain (and also with the time of day).

Feeding differences were studied using artificial flies. *Bimaculatus* moved long distances to catch large flies, but the males ignored small flies unless they were very close. *Wattsi*, on the other hand, ignored large flies or moved away if they were close. Small flies were taken by *wattsi*, but they did not move as far as did *bimaculatus* females.

JONATHAN ROUGHGARDEN (Department of Biology, Stanford University, Stanford, California 94305) has utilized Anolis species to test theoretical measures of niche width. He distinguishes within phenotype (WPC) and between phenotype (BPC) components of niche width, the measure of the second being the variance of the frequency distributions of the different resource utilization phenotypes and of the first, the average variance of individual phenotypes' utilization functions. Total niche width is the variance of the population's resource utilization functions and is the sum of WPC and BPC.

Roughgarden, operating with samples collected under GB 37731X, finds the within phenotype component of niche width to be strongest in Anolis. Anolis ferreus, as a solitary anole unique in its large size and hence perhaps in its size variation, was chosen for special study as possibly showing the upper bound for the between phenotype component in niche width. Calculation was based on total sample of 44 adult male lizards. The resource axis was prey size and data taken were jaw size and length and weight of insects from the stomachs of the measured lizards. The per cent composition of total niche width so determined was 32.5% BPC and 67.5% WPC. If A. ferreus represents, indeed, the upper bound for BPC in Anolis (polymorphism), then this component is never the primary one in Anolis niche width and Anolis is characteristically monomorphic and generalist in strategy.

Roughgarden makes also a number of predictions which he tests for various Anolis communities: (1) A population has a smaller niche width and is less polymorphic (has less BPC) as environmental productivity decreases or the number of competing species decreases. (2) If both productivity and the number of competing species decrease, there is little change in total niche width but BPC decreases. (3) Change in variance (e.g. in jaw length) is slower than displacement of the average phenotype (e.g. mean jaw length). Hence jaw size variance patterns should have a strong lineage component, whereas patterns in average jaw size will not. Ecological events in the relatively remote past should be more important in explaining jaw size variance than average jaw size.

Roughgarden uses an indirect approach in testing these predictions. The coefficient of variation (CV) in lizard jaw size is taken as an index of BPC. Then CV should be explained by a function whose value strongly increases with productivity, weakly decreases with species diversity and involves a lineage component.

His data for 24 Anolis populations do show (1) a strong productivity effect, (2) a weak species diversity effect, (3) lineage components are necessary to explain the pattern of jaw size CV but (4) not necessary to explain the pattern of jaw sizes.

In regard to the last point, he points out that *A. cristatellus*, the mesic lowland trunk-ground lizard of Puerto Rico, has a jaw length differing from its analogue in Hispaniola, *A. cybotes*, by less than 1 mm. This pattern is largely explainable in terms of present day environment. In contrast, the CV pattern cannot be explained on such a basis. Present day factors cannot explain why *A. cristatellus* of Puerto Rico should have a very low CV value relative to *A. cybotes*, even though it has almost the same jaw size. The data are consistent with prediction (3) that compression and release of BPC occurs more slowly than niche displacement.

THOMAS SCHOENER (Biological Laboratories, Harvard) has continued his studies of species ecology on the several Bahaman banks. In winter to spring 1973 he visited Bimini, Abaco, and Andros, censusing plots of varying vegetational diversity in order to discover what the species abundance and population composition (age, sex) are in the main areas of these islands. He will use his results as a baseline for his fringing micro-island study planned for 1974. Tentative results are:

1. There is an increase in species diversity (by any measure) from low to high vegetational complexity.

2. Equitability is perhaps highest in the areas of highest vegetational density, but the number of individuals is highest in areas of intermediate to high complexity.

3. Mangrove areas apparently show the lowest species diversity for a given level of vegetational complexity.

4. Population structure varies with both overall number of individuals and with vegetational complexity.

In particular, for *Anolis sagrei*:

(a) In very low vegetation the ratio of males to females is very high. In the most complex vegetation (forest) the male-female ratio is lower.

(b) In deep forest (with little understory) the male-female ratio is high, but there are few juveniles and subadults of either sex. In broken forest, male-female ratio is also high but there are lots of small immature lizards. Hence, age structure and male-female ratio are not always correlated.

5. (a) Some individual anoles on Bimini (ca 2-3% of individuals in all species combined) have lived at least three years. All but one of these are the largest of *all* the lizards in the study areas. Thus age and size are very closely correlated.

(b) On Abaco survival is higher in the area of low population density (mature beach forest) than in that of high density (successional legumes). Population density in any year may reflect differences in food abundance. However, there may also be a long-term trade-off between growth and survival, making the two areas equally favorable.

(c) On Abaco survival is overall less than on Bimini. There are more birds on Abaco and the climate is somewhat more rigorous.

(d) On the large island of Andros the number of species of *Anolis* is the same as on Bimini but *all* species are smaller. There are many more species of birds on Andros, and it is possible that 1) greater bird predation favors anoles that mature at smaller sizes, or 2) reduction in food availability due to greater competition with birds makes the anole size optimal for feeding smaller.

Schoener has for some years been studying the circumstances under which widespread *Anolis* species shift or fail to shift their habitats. At each of 20 Caribbean localities, he measured the structural habitats utilized by all the diurnal arboreal lizard species (the only non-anoles were *Leiocephalus*) and the availability of these habitats. Schoener selected localities so as to include for the chosen four widespread *Anolis* species - *A. carolinensis*, *A. sagrei*, *A. distichus* and *A. grahami* - nearly all of the species combinations in which they occur. The data were fitted to equations that adjust for locality-specific differences in vegetation and that estimate the direction and intensity of apparent interaction between classes of the widespread species and the forms sympatric with them.

Among the results are: 1. *Carolinensis* and *sagrei* show more instances of habitat shift, apparently because of competitors, than *grahami*. 2. Female-sized lizards show more such shift than adult males. 3. Pattern 2 is not independent of species but is most evident in *sagrei*, somewhat less so in *grahami* and entirely absent in *carolinensis*. 4. Locality-specific tendencies to shift or not shift exist within species, e.g. *sagrei* adult males. 5. The widespread species *carolinensis*, *distichus* and *sagrei* frequently negatively interact. On the other hand, *angusticeps* is rarely a competitor with *carolinensis* and *opalinus* (Jamaica only) rarely a competitor with *sagrei*. 6. Males tend to respond more strongly to other males than to female-sized individuals. However, except in *sagrei*, female-sized individuals are more likely to respond to adult males than to their own class. 7. Climatic similarity is a major factor determining effect of a sympatric species upon one of the widespread species. 8. There are more cases where apparent competitors are similar in size than the reverse. Examined with regard to sex, the greatest effects appear to be against female-sized individuals of the widespread species. 9. Classes of larger size, on the other hand, seem to operate especially against adult males. 10. The most abundant classes are the apparent strongest competitors for *distichus* but not for the other widespread species.

Indirect evidence implicates both behavioral and evolutionary adaptations in habitat shift.

Thus *carolinensis*, where it co-occurs with three other species and its perch is most often on leaves, is often a vivid green, though it may facultatively turn to brown. On Crooked where two arboreal species are absent, perch shifts upward and is less often on leaves. Coloration is now brown with only the option of occasional olive tinges. On Acklins where over most of the island *carolinensis* is the only anole, perch height decreases and it is more terrestrial than elsewhere. (See figure for this remarkable habitat shift.) Here the coloration is a stony brown. Clearly genetic changes have taken place which suit the coloration to the shift.

Similar habitat and coloration shifts occur in *distichus*, but here less striking instances of habitat shift are accompanied by less striking color changes.

In sagrei habitat shifts can occur without much color change. There are, however, morphological changes, as in number of toe lamellae.

Grahami is morphologically similar throughout its range but very different in its structural habitat within Bermuda. Here, however, grahami is non-native, having been introduced rather recently (in 1905). It co-occurs in a small area of Bermuda with the still more recently introduced A. leachi, a much larger species. Grahami occupies lower perches in the presence of the highly arboreal leachi. Here there is no phenotypic suggestion of genetic change; possibly this is a behavioral response to individuals of a larger and aggressive species.

4 SPECIES

1	4	3	3	1	12
2	6	4	29	14	54
1	1	1	8	17	28
–	–	1	2	4	6
3	11	8	41	36	

3	14	6	3	3	28
8	26	10	9	9	62
1	2	3	2	2	9
–	0	0	–	–	1
11	42	19	14	13	

0	3	5	3	1	12
4	5	10	32	14	65
1	2	4	9	5	22
–	–	–	1	–	1
6	10	19	45	20	

2 SPECIES

1	3	2	1	1	8
3	11	12	13	6	45
3	5	10	12	4	34
1	3	2	2	3	10
9	21	25	28	14	

1 SPECIES

↑ PERCH HEIGHT

← PERCH DIAMETER

(extracted from a MS by T. Schoener)

Legend for figure

Habitat oscillation in female-sized *Anolis carolinensis*. Numbers are percents; separated column at right are observations on leaves. On a 4-species island (Bimini), individuals are mostly on leaves, thin twigs and at moderate heights. On a 2-species island (Crooked, 2 localities), individuals shift upward and away from leaves. The species absent are trunk or twig-inhabiting arboreal species, *distichus* and *angusticeps*. On a 1-species island (Acklins), individuals shift downward again and toward thicker diameters. The additional species absent is *sagrei*, a trunk-ground form.

ROBERT TRIVERS (MCZ) demonstrated that in both sexes of the giant anole of Jamaica, *A. garmani*, reproductive success (as measured by the number of copulations) correlates positively with increasing adult size, but much more strongly in males than in females. Female territoriality and male-male competition for territories containing females could also be demonstrated and together provide an explanation for the differences within and between the sexes in the relation of size to reproductive success. Associated with this social structure is strong sexual dimorphism in adult size and in growth rates.

Trivers generalized from these observations to the hypothesis that female distribution controls male-male competition which, in turn, controls adult sexual dimorphism in size. This generalization could then be tested on species markedly less sex-dimorphic in size.

On Jamaica *Anolis valencienni* is the species that shows least sex dimorphism in size. Trivers had already studied this species sufficiently to know that its social structure was strikingly unlike that of *A. garmani*. In the summer of 1973 he and Robert Hicks endeavored to get quantitative data for *A. valencienni* which would be as comparable as possible with that available for *A. garmani*. Three kinds of data were gathered.

1. *Copulation data*. Because *valencienni* does not mate preferentially on open conspicuous perches as does *garmani*, collection of data on *valencienni* copulations was more difficult than had been true for *garmani* and the problem of sighting biases seems more severe. However, the following conclusions seem permitted: size is less important for reproductive success for male *valencienni* than it is for male *garmani* and in fact in *valencienni* size is no more important for reproductive success in males than in females. Unlike *garmani*, adult female *valencienni* copulate with more than one male on the same day and (in the absence of interruption) with the same individual on successive days. Females were seen rejecting males, and one apparent case of "rape" was observed. Both these phenomena were unobserved in *garmani*.

2. *Male and female home ranges*. Females overlap extensively in their wanderings and have never been seen to display aggressiveness toward one another. Male home ranges overlap less than those of females but considerably more than those of adult male *garmani*.

3. *Male aggressiveness*. It is established for the first time that male home range overlap in *valencienni* is accompanied by aggressiveness. Males display before and after fighting and fight by jaw-locking. The outcome of such fights is less dramatic than in *garmani* (or *lineatopus*, *grahami* or *sagrei*): the apparent loser turns dark and retreats slowly. He is rarely routed from the territory and may copulate within the defended home range (territory) of the adversary on the day of the fight.

T. P. WEBSTER (MCZ) has employed the technique of gel electrophoresis to attempt to evaluate intraspecies genic variation and interspecies genic similarity for a number of anoles. The following are the cases currently under investigation.

(1) A "solitary" anole: *Anolis agassizi* of Malpelo Island. This morphologically very distinctive species was available from collections made by A. S. Rand, A. R. Kiester, G. C. Gorman and others, with the assistance of the U. S. Navy.

(a) From data on proteins representing 30 genes, *A. agassizi* was estimated to show an average heterozygosity at 2.1% of its loci. This low value is similar to that found in other solitary anoles and in some anole populations of very recent origin (i.e. interpreted as showing the "founder effect" restriction of genic variability).

(b) Very little genetic similarity was found in the comparison of *A. agassizi* with five congeners, including two members belonging to the South American *latifrons* group from which the Malpelo species is believed to be derived.

(2) The *Anolis distichus* species group. Webster and Burns combined the evidence of dewlap color variation and electrophoretic difference to demonstrate that a north-south series of populations of the *brevirostris* complex in Haiti in fact includes three species (A, B. C). The pattern of dewlap color variation strongly suggests that this character has an important role in reproductive isolation. Webster is now extending his analysis to other populations of *A. brevirostris*, specifically those on Gonave and at many localities in the Dominican Republic.

On the basis of four animals from Picme, Gonave is inhabited by Species B. It is identical to populations on the coast north of Port-au-Prince, except that further work is required to establish differences or similarities in the esterases. Earlier it was found that *A. brevirostris* from Jacmel and Marigot, Haiti, are identical to populations north of Port-au-Prince, except for esterases. Thus, at present, Species B is known from two geographically isolated areas of Hispaniola and one of its peripheral islands.

Populations from the western Valle de Neiba in the Dominican Republic have monochromatic dewlaps and on this basis are probably a continuation of Species C in the Haitian Plaine de Cul de Sac. In the eastern Valle de Neiba and along the coast of the Barahona Peninsula, from Barahona to Enriquillo, the dewlap is often bicolor with the basal spot offset toward the rear margin. Populations from the arid tip of the Barahona Peninsula have pale or bicolored dewlaps with the basal spot centered.

However, although there is substantial geographic variation in protein phenotypes, there is no evidence for genetic discontinuities like those observed in Haiti. All populations should probably be considered Species C. In the western Valle de Neiba *A. brevirostris* is nearly identical to Cul de Sac Species C, but between that area and Barahona two proteins (αGPD and IDH-2) change to variants formerly thought to be characteristic of Species B. Populations of the Barahona type occur down the eastern side of the Barahona Peninsula, but on the arid plain stretching from Oviedo to Pedernales there is a partial (IDH-2, but not αGPD) return to Cul de Sac conditions. A sample from Belle-Anse, Haiti, is also Species C. It seems that *A. brevirostris* from the San Juan Valley is also Species C of the type around Barahona.

With the finding that some populations of Species C in the Dominican Republic are more similar to Species B than are Haitian populations, the number of proteins diagnostic for Species C has slipped to 3 (transferrin, PtE, and esterase, with the last in need of confirmation). Species A remains very distinct.

Hybrids between *A. distichus ravitergum* and *A. brevirostris* were found at three localities in the Dominican Republic. The two species differ in average male size and in body color (brown versus grey, plus a shoulder spot in *brevirostris*) and in the usual presence of a preoccipital in *distichus*, but tend to have similar dewlaps. Hybrids are intermediate in color, larger than *brevirostris*, similar to *d. ravitergum* in dewlap (the species differ in detail) but tend toward *brevirostris* in the usual *absence* of a preoccipital. The number of hybrids indicates that hybridization is frequent at the zones of contact, but whether females of one or both species err in choice of mates is unknown. Of 19 hybrid males examined, all had active testes. However, the prophase of the first meiotic division shows there is considerably asynapsis with chiasma formation between unhomologues. The first division is not reductional. Male hybrids are certainly sterile.

Hybridization has been confirmed by an electrophoretic study. The species do not share alleles at six of the loci so far examined. Hybrid individuals are heterozygous for all six.

Animals electrophoretically recognized as hybrids were collected at Balneario la Zurzas (Banos de la Surza) (5 km WNW Duverge) and 0.5 km E of Cachon. The linear distance between these localities is 45 km. Some of the females from Balneario la Zurzas, although quite similar to *A. d. ravitergum*, were suspected hybrids. Unexpectedly, however, two males classed as *A. d. ravitergum* were also hybrids.

Morphologically, hybrids 0.5 km E of Cachon are intermediate to the two parental species. The characteristic markings of *A. brevirostris* are present but subdued, with light browns predominating in the body coloration.

Hybrids are sufficiently different from both parental species that, of those specimens identified as hybrids when collected, about 90% were correctly classed. Two A. brevirostris and one A. d. ravitergum were confused with hybrids.

Differences in hybrid coloration at the two localities may be determined by genetic differentiation in A. brevirostris. A. d. ravitergum at the two localities are quite similar.

There is as yet no evidence for backcrossing. As hybrids are locally common, their successful reproduction must be rare. As mentioned above, the karyology of male hybrids from 0.5 km E of Cachon indicates complete sterility for that sex.

Hybridization of A. d. ravitergum and A. brevirostris is additional evidence that the dewlap is a major cue, perhaps the major cue in species (or deme - see Williams below) recognition within the distichus group. At localities where A. distichus and A. brevirostris differ strikingly in dewlap color, hybridization is less frequent. Of 82 A. brevirostris A and 22 A. distichus dominicensis from Montrouis, Haiti, only one "A. distichus" was an F_1 hybrid. At Manneville, Haiti (A. brevirostris C and A. d. dominicensis), hybridization is unknown, but no A. distichus from this locality have been examined electrophoretically.

Of the many subspecies of A. distichus, Webster is giving d. ravitergum most attention. In its tolerance of, indeed restriction to, arid conditions, it is more similar to A. brevirostris than any other distichus.

3. Anolis cybotes species group. Webster is studying geographic differentiation in A. cybotes electrophoretically with emphasis on genic variation but with attention to allelic frequencies. Relationships within the species group are also being studied, but in both cases some additional populations should be sampled.

4. Anolis karyology. The two most recently discovered species of West Indian Anolis have been karyotyped by Webster. Anolis sheplani, a close relative of A. occultus of Puerto Rico, has the saurian ancestral diploid pattern of 12 macrochromosomes and 24 microchromosomes. In contrast, the single male A. fowleri provided by Albert Schwartz gave peculiar results. Diploid number was 44, but the 20 macrochromosomes do not sort into 10 pairs of morphologically identical homologues. There is considerable asynapsis in the first meiotic division and the first division is not reductional.

5. Anolis fowleri and the monticola group. Schwartz considers the recently described species A. fowleri a member of the monticola group. Electrophoresis was therefore used in an attempt to illuminate two problems with A. fowleri: its peculiar karyology (as known from one male) and its relationships with other Hispaniolan anoles. Tissues from the single

available male were compared with those from a few individuals of *A. insolitus*, *A. hendersoni* and two species of the monticola group: *A. rimarum* and *A. christophei*.

There is no evidence that *A. fowleri* is an F_1 hybrid (with both parental species remaining undiscovered), nor that it is a species of hybrid origin that has retained a high level of heterozygosity because of the unusual cytogenetics.

Anolis christophei and *A. hendersoni* are both strongly differentiated from one another and from the other three species. There are greater similarities in the comparisons of *A. fowleri*, *A. insolitus* and *A. rimarum*, with the last two being the closest of the ten possible pairings.

	fowleri	*insolitus*	*rimarum*	*hendersoni*
christophei	14	17	14	16
fowleri		11	11	19
insolitus			8	17
rimarum				15

All comparisons are based on the same set of proteins. Numbers are the proteins showing complete differentiation, with the reservation that few individuals and only a single population per species have been examined. Average numbers of differentiated proteins are:

hendersoni	16.75
christophei	15.25
fowleri	13.75
insolitus	13.25
rimarum	12.00

Collections for other individuals. Material of the three *brevirostris* siblings in Haiti (species A, B, C) were shipped to Thomas Jenssen who will test directly the importance of dewlap color (and any behavioral aspects of the display) in species recognition. Samples of plasma and whole animal homogenates were sent to Dan Schochat who is using albumin to ascertain relationships between anoles. Live animals were also sent to A. S. Rand, T. C. Moermond and A. R. Kiester.

E. E. WILLIAMS (MCZ) has a miscellany of topics under review.

1. South American anoles

Williams' work on South American anoles has progressed to the point that provisional species groups can be recognized (Table 3). Certain biogeographic patterns are evident. Among alpha anoles, one marked instance of disjunction is evident: the *tigrinus* group occurs only in the Northern Tier (northern Colombia, northern Venezuela) and in the Atlantic Forest of Brasil (in the state of Espirito Santo only). These are dwarf anoles apparently paralleling the twig-anole ecomorphs of the West Indies. In contrast to this obviously relict series is the *punctatus* group, species of moderate to small size, diverse and widespread, closest in ecomorph type to the trunk-crown anoles of the West Indies. Some, *punctatus* itself is an extreme example, have very wide distributions while showing very little evidence of intraspecies differentiation. Others are relatively local or known at present from single specimens. The group is Amazonian-Guianan but with a series of representatives west of the Andes.

The *laevis* species group is the proboscis anoles. The *punctatus* group tends to long-headedness but this is achieved either by real attenuation of the head itself or, as in *punctatus*, by a swelling of the rostral scale. In the *laevis* group the head may be somewhat elongate but a fleshy protuberance is added involving scales above the rostral, small in *laevis* itself (the Amazonian periphery in Peru), much longer in *A. phyllorhinus* (central Amazonian) but half as long as the head in *A. proboscis* (west of the Andes in Ecuador). From the toe pad development, it is clear that this group is arboreal, but only seven specimens are known (four *A. proboscis*, the type and a second specimen of *A. phyllorhinus* and the type only of *A. laevis*).

The two remaining alpha groups both tend to giant size but, in contrast to the West Indies anole giants, they are not so highly arboreal, tending to a trunk-ground or even ground structural habitat.

The *latifrons* group and the *aequatorialis* group differ most importantly in the narrow digital pads of the latter. Narrowed pads should imply less arboreality, hence the *aequatorialis* group is suspected of more of a ground habitat than the *latifrons* group. One species - *eulaemus* - is known to sleep in grass and bushes.

The *latifrons* group extends from the trans-Andean area in Colombia and Ecuador into Panama and Costa Rica (two species - *microtus* and *insignis* - are in fact wholly Central American). An outlying Northern Tier species is *A. squamulatus* in the coastal range of Venezuela.

The *aequatorialis* group is primarily trans-Andean in Colombia and Ecuador but extends into Amazonia thru the low mountain passes in Ecuador.

The South American beta anole groups are all invaders from the north. There have been multiple invasions and hence a layered succession includes older groups with strong or even relict endemism and younger groups in which there may even be forms conspecific with those in Central America.

The southernmost of South American beta anoles - *A. meridionalis* - appears, on Etheridge's osteological characters, to be the most primitive of South American betas, a relict of the oldest beta invasion of the continent. It is clearly an isolated species deserving a group of its own.

Etheridge has described as the *petersi* species group the most primitive Central American anoles. Two species of the group occur in South America: one, *A. biporcatus*, extends from Mexico to Ecuador and Venezuela, with a distinctive race in southwestern Colombia and western Ecuador. A close relative of *biporcatus* - *apollinaris* - occurs in the inter-Andean valleys of Colombia, perhaps the result of an earlier invasion than that which has resulted in only racial difference in the trans-Andean region. The other species, *A. sulcifrons* in Colombia, both west of the Andes and in inter-Andean valleys, is the geographic representative of *pentaprion*, a species ranging from Mexico to Panama. *A. biporcatus*, *A. apollinaris* and *A. sulcifrons* are probably best compared to West Indian crown anoles.

A. lemurinus is the Central American-Mexican member of another series of three. *A. vittigerus* replaces it in southeastern Panama and trans-Andean Colombia. Trans-Andean Ecuador has a third undescribed member of the series. This is another independent invasion of South America.

The *humilis* group is distinguished by its peculiar axillary pockets. Its South American representative is *A. notopholis* in trans-Andean Colombia. *A. notopholis* appears to be a grass-bush anole.

The four groups - *petersi*, *lionotus*, *humilis*, *lemurinus* - may be the most recent invaders of South America. They appear not to have got very far and, though endemic South American species when present are amply distinct, their northern relationships are very clear.

A northern relationship is equally clear for the *fuscoauratus* group (in Williams' usage a more restricted and surely more natural group than envisioned by Etheridge). *A. fuscoauratus* of Amazonia, the Guianas and the Atlantic Forest is not easy to separate from the *limifrons* complex in Central America. The trans-Andean populations - probably to be called *maculiventris* - in northwestern Colombia are in contact with undescribed species of the limifrons complex and in central Ecuador abut on or intergrade with *A. fuscoauratus* and are more different from the members of the *limifrons* complex than these are from Amazonian *A. fuscoauratus*. A boldly patterned undescribed fuscoauratoid occurs on Gorgona Island. Another quite distinct and also patterned undescribed species occurs locally in northern Colombia. *A. antonii* represents *fuscoauratus* in the inter-Andean valleys of Colombia.

Sympatric with A. fuscoauratus in its cis-Andean range is another species referred to the group, A. ortoni, a stockier species which, in contrast to most fuscoauratoids, occurs outside the forest.

In western Amazonia A. trachyderma is sympatric and sometimes syntopic with A. fuscoauratus in shaded forests.

The fuscoauratus group is differentiated enough to imply there has surely been more than one invasion. All appear to be trunk or trunk-ground anoles.

The remaining South American anoles are without obvious Central American relatives, though they may extend from a larger South American base into Panama. All except onca (and recently described annectens - see below) are here associated in a single group, less because of confidence that they belong together than for lack of clear grounds for separating them. Three are restricted to trans-Andean South America (gracilipes, granuliceps and bitectus). Two extend from Panama into northern South America, tropidogaster (an edge species) to Ecuador west of the Andes and in the Northern Tier to western Venezuela, auratus (a grassland species) likewise to Ecuador west of the Andes, also in inter-Andean valleys but in the Northern Tier reaching to the Guianas and in Amazonia reaching the south bank of the Amazon in Brasil. The last species of the group, A. chrysolepis (cf Vanzolini and Williams, 1970), has a wide distribution in forests throughout Amazonia and the Guianas, but not to the coastal forest of Brasil or the trans-Andean area. It lives on the ground or the lower trunks of trees.

The remaining species group centering on Anolis (Tropidodactylus) onca is believed to be closest to A. chrysolepis (similarities in posture and display) but exhibits a morphological difference (partial or total loss of the anole infradigital pad) sharp enough to be appraised as worthy of group distinction. A. onca - an anole without infradigital pads - has a restricted distribution in arid areas near or along the coasts of Colombia and Venezuela. The newly discovered second species of the group, A. annectens, is at present known from a single specimen with the imprecise locality "Lago de Maracaibo." Nothing is known of the ecology of annectens but onca occurs on thorn bushes, matted vegetation or on the ground in very arid, mostly coastal localities.

In addition to Anolis annectens, three further new species of South American anoles are described in a paper in press. At least eight more require description and it is clear that this is not the end of the story. The South American anoles remain poorly known. They are nowhere abundant (especially by West Indian standards) and it will clearly be a long time before the local species are all made known. Even in the West Indies they are still being discovered.

Williams has begin a series of papers (two presently in press) which will figure and briefly characterize all known South American species. It is his hope that with this first necessity taken care of there can be an approach for South American anoles to the degree of sophistication of study now possible for the West Indies.

Table 3

Distribution of *Anolis* species groups

		CIS-ANDEAN			
	TRANS ANDEAN	Northern Tier	Amazonia	Mato Grosso and south	Brasilian Coastal Forest
α *anoles*					
groups					
tigrinus	-	+	-	-	+
punctatus	+	+	+	+	+
laevis	+	-	+	-	-
latifrons	+	+	-	-	-
aequatorialis	+	-	+	-	-
β *anoles*					
groups					
meridionalis	-	-	-	+	-
petersi	+	+	-	-	-
lemurinus	+	-	-	-	-
lionotus	+	-	-	-	-
humilis	+	-	-	-	-
fuscoauratus	+	+	+	-	+
auratus	+	+	+	+	-
onca	-	+	-	-	-

Special comment is possible on two of the South American groups:

(1) The one interesting point about the *laevis* group is, of course, the proboscis itself. The natural question is: What do they do with it? Williams' current answer it: They do nothing with it. The proboscis is comparable to the crests on the head and body of males of *Basiliscus* - an extraordinary, quite bizarre species and sex recognition character, but only that.

(2) Since the discovery of a species (thus far represented by a single specimen) morphologically intermediate between the genera *Anolis* and *Tropidodactylus*, special attention has been given (1) to a search for additional specimens of the new intermediate species and (2) to observations on the ecology of the species *onca*, the single species that has been referred to the genus *Tropidodactylus*.

The search for the annectant species has been unfruitful. It has, however, confirmed that the habitat of the species *onca* is a very special one - arid with sparse vegetation and a high wind. This limits the species to certain coastal areas in or near coastal northern Colombia and Venezuela. Back of these areas in situations which may be quite as arid but are without wind, *Anolis auratus* occurs in small numbers. Clearly *A. auratus* is a much more eurytopic species, since it extends from areas of extreme aridity with scattered cacti and thorn bushes to rather lush grassy areas in fields or forest edge. We nowhere saw *onca* and *auratus* together. *Onca* was in some places abundant, but *auratus*, in our experience of the very arid areas adjacent to the range of *onca*, was never so. *Auratus* was abundant in grass or fields in essentially mesic situations. (For more information on *onca* see the observations by Kenneth Miyata above.)

The difference between *Anolis*, the annectant species, and *onca* is in infradigital morphology. *Anolis* has an adhesive pad under phalanges ii and iii with smooth transverse lamellae with a free edge and microscopic hairs. The annectant species has a narrowed *Anolis*-like pad under phalanx ii but keeled scales under phalanx iii. *Onca* has keeled scales under both phalanges ii and iii.

Collaboration has begun with Paul Maderson on the histology and development of the infradigital epidermis in *onca*. He has also been able to confirm the sharp difference between the areas under phalanges ii and iii in the annectant species. A curious phenomenon in which hatchling *onca* appear to have *smooth*, hence lamellar-like, scales under the toes is being investigated. Maderson has been able to show that the infradigital scales of hatchling *onca* have none of the hairs of anoline adhesive pads but lack also the spikes of larger *onca*. The change-over occurs after only a few millimeters of growth. Maderson finds the change itself extraordinary and its rapidity even more so. He is very interested in following the cellular changes involved.

2. West Indies problems

The discovery by Albert Schwartz of a new primitive montane anole on Hispaniola has forced Williams to make a reassessment of his opinions on the evolution of the Hispaniolan fauna and its relationship to that of Puerto Rico. Williams has previously held that *A. occultus* on Puerto Rico had originated there and represented the ancestral stock for the whole *carolinensis* group (from which the distinctive elements of Hispaniola's montane fauna derives). Williams, in fact, believed that the first event in the radiation of the eastern Greater Antillean anole fauna was the division within Puerto Rico of the ancestral stock into *carolinensis* and *bimaculatus* groups *sensu lato*. With Schwartz's discovery of *A. sheplani* in the Sierra de Baoruco of the Dominican Republic - undoubtedly the most primitive member of the *carolinensis* group - this position is no longer tenable. Discussion between Etheridge and Williams involving consideration of many possible phyletic schemes and colonization sequences has resulted in agreement that the most plausible of these has been one in which the *carolinensis* group originated in Hispaniola.

The modification of Williams' scheme required by this proposes that division of the ancestral stock occurred not within but between islands, the *carolinensis* group differentiating from the ancestral stock in Hispaniola, the *bimaculatus* group in Puerto Rico. We then explain the richness and distinctiveness of the *carolinensis* group in Hispaniola by its earlier start and hence greater opportunity for radiation there, and the absence of such richness and distinctiveness for the *carolinensis* group on Puerto Rico (with only the one representative, *A. occultus*) by the earlier start and greater opportunity for radiation of the *bimaculatus* group (*sensu lato*) on that island.

For Williams, the peculiar division of the anole fauna of Hispaniola into phyletically distinctive montane and lowland faunas has been a central problem. In Puerto Rico wet montane and dry lowland faunas are present, but except that *A. occultus* has no lowland representative, the two faunas are very closely related, each montane species has a lowland closest relative.

Williams has explained the montane *carolinensis* group endemics of Hispaniola as true autochthons, while regarding such elements of the lowland fauna as the *cybotes* and *distichus* species groups as latecomers from Puerto Rico.

This postulated history has been opposed because all of the *cybotes* group on Hispaniola are karyotypically more primitive than their Puerto Rican relatives, the *cristatellus* group (see Gorman above). Similarly, the *distichus* group on Hispaniola is karyotypically less derived than *A. stratulus* which appears to represent them on Puerto Rico.

But there is much that opposes the conception that the primitive member of any lineage will be found at its place of origin. On the contrary, there is much that suggests that lineages that still survive at and near their place of origin will, because of the factor of greater time available for differentiation and because of the severe competition of close relatives, show more derived states than those members of the lineage that have escaped to other areas. It is not in fact an unusual observation that the colonizing derivatives of mainland stocks show primitive states that are no longer represented in their place of origin. Within *Anolis* Williams calls attention to the persistence of fracture planes in the caudal vertebrae of species of the *roquet* group while all their mainland relatives of the *latifrons* group have lost caudal autotomy. Similarly, Etheridge regards the Jamaican betas as the most primitive in some regards of that entire series. Other instances could be provided.

Differentiation of the *carolinensis* group on Hispaniola and the *bimaculatus* group on Puerto Rico puts each of these in a geographic position suitable for the colonizations each has achieved: the *carolinensis* group has colonized Cuba and Puerto Rico from Hispaniola, the *bimaculatus* group Hispaniola and the northern Lesser Antilles.

Williams had imagined that Puerto Rico, as the first landfall for anoles in the eastern Greater Antilles, was a "generator island," i.e. an area that, by the accident of time of colonization was a first center of *radiation*, supplying stocks as they arose to later colonized islands. He is now compelled to admit for Puerto Rico, with the invasion from Hispaniola of the ancestor of *occultus*, the classic pattern of double invasion and accumulation.

With the demonstration that Puerto Rico has been colonized by anoles more than once, it appears that all Greater Antillean anole faunas present a pattern of both *radiation* and *accumulation*. Jamaica is now the island that appears to be most nearly a "generator island," since according to current belief all but one of its species originated within the island. According to this Jamaica has, despite its relatively small size, furnished the *sagrei* group to Cuba (and the *grahami*-related *conspersus* to Grand Cayman) and has received in its turn only the back invasion of *sagrei* itself - a late and perhaps even human-aided invasion. Now, in view of the *sheplani-occultus* case, Williams wonders whether the *sagrei* group did not differentiate on Cuba (from, of course, a stock invading from Jamaica) and whether there have not been two back invasions - an old one, *valencienni*, and a much later one, *sagrei*.

Discussion of these examples of radiation-colonization sequences logically leads on to the review planned by Williams of these phenomena for the West Indies as a whole. Antecedent to this, however, is a more precise assessment of the relationships - affinity *and* phyletic distance - of all West Indian anoles. Williams has prepared a new arrangement of West Indian anoles into species, basing his judgments on the accumulated evidence of morphology, karyology and electrophoresis and, where relevant, behavior and ecology. He will, almost of necessity in so wide a review, be in disagreement at some point or other with the private opinions of almost every *Anolis* worker. He promises only to discuss the points of controversy.

3. Anoles out of place

In several instances anoles which have been intentionally or unintentionally introduced to areas strange to them have been the subject of very useful ecological or even genetic study. A. trinitatis and A. aeneus on Trinidad have been carefully examined by Gorman and others. The introductions of A. grahami, A. leachi and A. extremus into Bermuda have been documented by Wingate and the animals studied by Schoener (see some remarks under his name above) and more recently by Gorman. The colonies of A. extremus and A. wattsi on St. Lucia have been examined by Rand and by Gorman. There are a considerable number of other introductions, some of which may be as interesting. Williams has in preparation a survey and summary of the known cases.

Among the more interesting cases that have received little or no previous mention are: (1) Anolis cristatellus of Puerto Rico within the city of La Romana in the Dominican Republic (this population has received mention without comment in a paper in press by Roughgarden); (2) Anolis marmoratus in the city of Cayenne, French Guiana; (3) A. extremus in the back part of a restaurant in Caracas, Venezuela (bare mention by Peters and Donoso-Barros in the Checklist of Squamata).

4. Bicolor dewlaps

Williams has been investigating the significance of bicolor dewlaps in certain anoles. In A. distichus of Hispaniola and A. lineatopus of Jamaica there appear to be an association of dewlap color (amount of orange versus yellow or white) and climatic adaptation. In A. distichus the evidence currently suggests that the association extends to deme level and that the variable dewlaps may be signals that ensure a greater probability that individuals of like physiological type will mate with one another (semi-assortative mating).

Williams points out that a bicolor dewlap with a dark center and light margin has the possibility of extreme variation from solid dark to complete light with every intermediate stage with very little ambiguity at any stage. This is then a flash signal that is both highly visible and readily interpretable, and one that will be so under many conditions (light or shade, obstructed or unobstructed vision). If the precise mix of light and dark were strongly correlated with genotypes finely tuned to certain environmental conditions, such a signal could be important in the choice of a mate, could in fact permit considerable subtlety in a mate. It could maximize the probability of choosing a mate of optimum genetic makeup - most likely a near relative - while permitting some variability in choice if the optimum genotype as signaled by a particular dewlap pattern were not available.

This hypothesis has arisen out of (1) the general observation that the amount of orange in the bicolor dewlap of Anolis distichus in Hispaniola correlates roughly with major climatic areas within the island - more orange in wetter areas, less in drier regions, and (2) the subjective judgment that minor variation seems to correlate rather subtly with very local variation in vegetation and climate - more orange in the dewlaps of distichus in woodland, less in those of open and arid areas.

Williams and Roughgarden plan joint field surveys of distichus in the Dominican Republic, testing this preliminary judgment. They plan to compare an index of extent of orange in the dewlap against some vegetational index of mesic/arid conditions.

The bicolor dewlap of A. lineatopus is strikingly like that of A. distichus. Again, over major areas a greater extent of the central orange and a diminution of the lighter margin correlates with wet versus arid climates. There is also certainly considerable local variation in the extent of orange, but in Jamaica there has not been yet even an attempt at subjective and crude correlation of this local variation with local climate.

There are other bicolor dewlaps in the West Indies but none but these two species emphasize a dark center and a light edge. The most nearly similar other species is A. cristatellus of Puerto Rico in which, however, the populations with a sharply bicolor dewlap have the center green and the edge brownish.

Cristatellus dewlaps were regularly checked during a circuit of the Puerto Rico lowlands in 1973. It was at once evident that whatever the function of the bicolor pattern in A. cristatellus there was no possibility of fitting the distribution and variability of that pattern into the scheme that seems satisfactory for A. distichus and A. lineatopus. The bicolor pattern - green center and wide brown edge - is sharpest on the Virgin Islands, including arid Culebra (where it was first described); it extends to northern and northwest mainland Puerto Rico but is there in variable frequency (but without evident correlation with climate), partly replaced by a smudged or unicolor brownish dewlap. South of Mayaguez on the west coast at approximately the point of vegetational change to acacias and other arid adapted plant cover, the cristatellus dewlap becomes nearly consistently unicolor brownish. A shift in the reverse direction occurs on the east coast somewhat south of Hunacao. There are thus broad trends in geographic variation but there appears to be little of the obvious relationship to climatic zones characteristic of A. distichus and A. lineatopus. Both of the two major dewlap types occur in arid areas and in more or less mesic situations as well.

5. New species

Two new Hispaniolan Anolis are being described by Williams and Webster. In each case there are some special aspects:

(1) A red-dewlapped sibling of white-dewlapped Anolis cybotes, sympatric with the latter in the vicinity of San Jose de Ocoa in the south central Dominican Republic, differs minimally in scale characters: the two mid-dorsal scale rows on the trunk are usually less enlarged than in cybotes. However, it is strongly different at 10 of 22 loci examined electrophoretically.

Ecologically the two species do not differ impressively. At San Jose de Ocoa (ca 1,000 feet elevation) both occur commonly and the habitats for each differ enough from year to year and from site to site to make any summary statement difficult. Above San Jose de Ocoa, on the southern slopes of the Cordillera Central, the red-dewlapped form occurs on bare, open hillsides and cybotes only in the small villages (to which it may have received artificial transport). Cybotes appears to occur in enclaves surrounded by the red-dewlapped species. Below San Jose de Ocoa the red-dewlapped species is known from fence rows and a coconut grove, but it now is in enclaves and cybotes appears to surround it.

(2) A larger sibling of Anolis monticola is now known to occur syntopically with the nominate subspecies. It is readily distinguished by colors in life as well as size. (It lacks the nape ocelli of monticola and has a light line on the side and a red rather than yellow belly.) In scales it is sufficiently like monticola that it has become obvious that some of the literature records for the latter based on old and discolored specimens now are in error, including the specimen on which maximum size for monticola has been reported.

More interestingly, the new species is the third in a very close knit group of species distinguished by karyotype in which some of the chromosomes have undergone fission.

A monticola species group has previously been described: it is now clear that this divides into two sections. The first is rather diverse and dispersed with unfissioned chromosomes and occurs on the northern "island" above the Cul de Sac Plain; the second is restricted to the western tip of the Tiburon Peninsula of Haiti, two of them wholly syntopic so far as known and differing primarily in size and color (monticola and the new species) and the third a grass anole, this differing somewhat in shape and climatic niche but similar to monticola in size and adjacent in locality. This second subgroup, clearly closest relatives on the basis of both karyotype and scales, now prove to be one of the more interesting of the sets of local species in the West Indies. It is obvious that in the West Indies it is in these local isolates that there are surprises still to come.

Editorial Notes and Comments

The Editor does not suppress some exultation at the breadth of the coverage of one vertebrate group that is here achieved. But he is happier still that broad advance has been and continues to be one in which the separate assaults on particular problems turn out in fact to be mutually reinforcing.

It is to aid this mutuality of effort that this Newsletter has been invented. Already in 1972 George Gorman thought that the operation had become large enough that it was threatening to come apart, and it was for this reason that he invented the First *Anolis* Symposium. That went well enough to encourage further efforts at cross communication. Hence the demi-journal that is before you.

It is to be informational. It will sometimes record work that, for one reason or another, will not for a long time, or perhaps never, be printed in the regular journals. It will sometimes be a vehicle for ideas that may be shot down or abandoned. But above all, the Newsletter, in this issue and any subsequent ones, has the function of informing *Anolis* workers of what their colleagues are doing and of doing so in one format and one place.

Two in-house communications preceded the present Newsletter. The first was a "Progress Report," a very informal personal statement of those *Anolis* operations plus my own comments and expressed prejudices. The second was a much more formal, much longer report to NSF on two years of grant operation. There was too much information in it not to circulate it among the local group. This NSF report, because of its length and formality, came to be called the *First Anolis Newsletter*, and I thereafter began promising a *Second Anolis Newsletter* and promising it rather widely after the Gorman-organized First *Anolis* Symposium in 1972. Much delayed the promised SAN, but above all the preparation of a new grant proposal which, in its time, had to serve, for lack of energy - and time (I immediately after preparation of the proposal went off to Brasil) - as a kind of Newsletter.

The stimulus to the present semi-publication came from the required report to NSF of research under the first year of the new grant. The report - always, as a matter of my psychology, more elaborate than is quite necessary - dealt only with our grant-supported research but it is the base of the expanded summary of *Anolis* research that is before you.

SAN is still a report by the local group and those who work at least part of the time with us. We are partially aware of other work but we are not in close enough touch to report it. It is not our intention at this time to cite or abstract already published work.

Whether the Newsletter in the future remains as parochial as it is now depends upon response. If other workers wish to join us in the dissemination of mutually interesting information, they are welcomed. The Editor does, however, reserve the right to reject contributions. Required will be a certain information level, some degree of concreteness, some amount of specifics. The Editor prefers to report results, even if tentative, rather than intentions, even if promising. Generalities and theory are not discouraged, but their empirical base should be specified or, at the least, it should be indicated where and how that base is to be sought.

The Editor has in mind as the content of the Newsletter neither a travelogue nor a gossip sheet nor a list of theses topics, but a vehicle for exchange of information that in more expanded and documented form would be publishable somewhere in its own right.

Controversy and contradiction are not avoidable; there are already hints of this in the present issue. The Editor does not plan a forum: only in exceptional cases and only *within* the section "Editorial Notes and Comments" will disputes be accorded space and then only in terms of temperate comment and measured replies - *both brief*.

E. E. Williams