PATTERNS IN THE STRUCTURE
OF MAMMALIAN COMMUNITIES

Edited by
Douglas W. Morris,
Zvika Abramsky,
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and
Michael R. Willig

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SPECIAL PUBLICATIONS, THE MUSEUM
TEXAS TECH UNIVERSITY
NUMBER 28

Series Editor
J. Knox Jones, Jr.

Published 29 December 1989

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INTRODUCTION

During the interval 1979 to 1984, no fewer than six international symposia convened for the purpose of discussing patterns and processes in ecological communities. The breadth of treatment was unequal, with dominant themes dealing with the prevalence of interspecific competition and philosophical discussions on the role of "science" and "scientific methods." The results of some symposia were published in a *pot pourri* of research articles, whereas others concentrated more on review, with readings appropriate for classroom use in senior undergraduate or graduate courses. All resulted in bringing together a diversity of researchers working on an even greater diversity of biological organisms. Participants in every symposium pointed out contentious issues in community ecology, yet none achieved a satisfactory synthesis on the relative roles of different structuring forces in ecological communities. That outcome may say more about the interests of speakers than it does about patterns and processes. Why should ecologists expect guilds of organisms as different as marine algae, insectivorous birds, and stem-boring insects to be structured in exactly the same way?

We have noted one other curious feature of the previous symposia. With a few notable exceptions, studies of mammalian communities have not been covered, and the complexity of interactions among coexisting mammals have not received the attention we feel they deserve. Mammalian ecologists have contributed substantially to the development of ecological theory and to empirical tests of that theory. Mammals, more than any other class of vertebrates, and most invertebrates, represent a diversity of trophic levels, and they have succeeded in colonizing virtually every earthly habitat available to animals of their size. They occur in a diversity of forms and every major habitat is occupied by several closely related species. We reasoned that a comparison among different kinds of mammalian communities would cover a broad spectrum of possible forces in the structuring of ecological systems. At the same time, it controls for major differences in physiology, morphology, and life history that in themselves may be responsible for much of the apparent complexity in the organization of ecological communities. The strength of our approach is to use comparative studies on reasonably closely-related and well-known animals to search for processes that lead to repeated patterns of distribution and abundance. The patterns and processes we discover will be representative of the factors influencing groups of similar coexisting species.

We met in Edmonton during the Fourth International Theriological Congress in August of 1985. We arrived, manuscripts in hand, with the objective of reaching some concensus on factors structuring mammalian communities. Our coverage varied from overviews of repeated patterns in mammalian faunas through millions of years of evolution to ecological

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snapshots of competitive processes in action; from geographical patterns in distribution and abundance to microhabitat use and foraging; from the sands of Mediterranean and North American deserts to tropical forests, heaths, and mangrove swamps in Australia; from the rich grassland savannas of southern Africa to the boreal forests of Canada. Our contributors discussed grazing and browsing ungulates, insectivorous marsupials, fruit and insect-eating bats, omnivorous Carnivora, and seed-eating rodents. They searched for patterns in morphology, trophic relations, competitive interactions, habitat selection, predation, and species assembly. They tested for processes by exclusion, enclosure, and removal experiments, density alteration, habitat modification, and resource manipulation. Together they emphasize the most significant impact of this symposium—its demonstration that understanding and insight come from detailed field studies of ecological relationships. Our contributors have not allowed their perception of mammalian community organization to be clouded by a suspicion that some approaches are somehow nonscientific, or that some are more scientific than others. Instead, they have focused on the fundamental objective of understanding the evolutionary ecology of mammals, and will let history be the judge of their undersanding, and of their science.

We are most grateful to everyone who contributed to our symposium, "Patterns in the Structure of Mammalian Communities," at the Fourth International Theriological Congress. We thank Dr. William A. Fuller, the Secretariat, and the University of Alberta for hosting a first-rate congress, and for performance well beyond anything that reasonably could have been expected. We especially want to thank those contributors whose papers do not appear in this issue; page constraints severely limited what could be published. Their posters at Edmonton contributed greatly to the success of the symposium. We would also like to thank Texas Tech University Press and The Museum, Texas Tech University for their cooperation in publishing these proceedings. In particular, J. Knox Jones, Jr. and Carole Young were most helpful in editorial matters. We also acknowledge W. Broom, D. Carter, C. Jones, E. Jones, E. Sandlin, and M. Ybarra for their cooperation in seeing this work to fruition.

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27 January 1987

THE IMPORTANCE OF HABITAT SELECTION

HABITAT SELECTION, COMMUNITY ORGANIZATION, AND SMALL MAMMAL STUDIES

MICHAEL L. ROSENZWEIG

ABSTRACT.—Community ecology done with or inspired by small mammals continues to play a leadership role. It suggested and led to tests of a new technique for measuring population interactions in the field. It has been a model for long-term studies. It has opened doors for examining the effects of predation on community organization. It has produced fascinating patterns and concepts of species diversity and assembly that remain to be explored. It has shown how morphology and behavior may be integrated to produce a deeper understanding of organization. Finally, field manipulative studies of mammals have been among the most revealing accomplishments of experimental ecologists.

In the past several years, theoretical and field studies on optimal foraging of mammals have joined the list of research programs that mammalian community ecologists are pursuing with success. Those focusing on density-dependent habitat selection have been unusually fruitful. A new analytical technique allows the study of such habitat selection from single-species census data. Two-species studies have produced a novel framework with which to study community organization. The framework is based upon understanding whether species share habitat preferences and whether habitats present foragers with opportunities or stresses. This framework is being validated in the field. It has led to a deeper understanding of niche shifts, and has suggested hypotheses to account for various types of range overlap patterns, taxon cycles, and patterns of abundance and geographical range. Last, it has indicated that a surprising variable is of fundamental importance in community organization: can individuals assess patch-to-patch variability in one habitat type? Overall, the prospects are auspicious for a continued high intellectual yield from mammalian community ecology.

Mammals have been quite useful to community ecologists. When I decided to concentrate on them, it was merely because they greatly interested me. I never dreamed that "Community structure in sympatric Carnivora" (Rosenzweig, 1966) would help to set off intensive investigation and provide the basis for the title of this symposium. I did not foresee that investigations of desert mammals would provide other focal concepts such as niche complementarity (Rosenzweig and Winakur, 1969) and microhabitat selection, and would yield one of ecology's model communities.

I am grateful to have had the chance to participate in these developments. Yet I must confess that about a decade ago, I was suffering from a loss of faith. It seemed to me then that the course had been run, that mammal studies had little promise for testing some of the newer and more sophisticated ideas in community ecology. So much for prophecy! But I never have been so happy to have been so wrong! Here are some examples of front-line work in which mammal studies are involved.

In the past several years, work on small mammals by Crowell inspired Pimm to suggest a new regression technique for measuring population interactions in the field (Crowell and Pimm, 1976). True, it was also suggested independently by Schoener (1974), no doubt inspired by his own

pioneering work with lizard communities. But no one is claiming mammals are the only good subjects for community ecology. Nevertheless, the regression technique has been most used on mammals (for example, Hallett, 1982; Hallett *et al.*, 1983). Ray D. Dueser (personal communication), Zvika Abramsky, and I (Rosenzweig *et al.*, 1985) have tested the regression technique as it stands, with mammals, and found it lacking; however, Morris' (this volume) modification, taking into account the difference between microhabitats may prove to be its salvation.

Both James Brown's (this volume) and Whitford's (this volume) studies have demonstrated the potential benefits of including mammals in long-term studies of ecosystems. Kotler (1984 and this volume) and Thompson (1982) have shown that mammals are more useful than we thought for getting at the effects of predation on community structure. Joel Brown (this volume) has produced an elegant new theory of how species can exploit variance in a resource, and thus achieve coexistence; and he has tested the theory in the field with desert mammals.

Abramsky and I have uncovered a new pattern in mammalian species diversity—a variable we used to think we understood as well as any (Abramsky and Rosenzweig, 1984). The relevant figure in Abramsky's own contribution to this volume shows how diversity first rises then falls as aridity is reduced. Owen (1985) has confirmed the pattern for Texas mammals, and Stenseth (this volume) has produced an ingenious model to explain it.

One could go on and on. Dickman's manipulative experiments on *Antechinus* competition (this volume) constitute a paragon that ought to inspire all ecologists. MacKenzie's (this volume) superb analysis of bat wing morphology, flight path, and bat community structure is perfectly conceived and has had fascinating results. And Owen-Smith's (this volume) detailed modeling of ungulate trophic morphologies and their resource specializations will, I believe, become a classic. And there is more.

Yet this paper is not supposed to be a comprehensive review of all the good that mammals and their students have done for community ecology. Anyone who doubts the benefits merely has to listen to the complaints of the arthropod ecologists, who in the recent past have bemoaned the influence of vertebrate ecologists on ecology as a whole. Is it our fault that we have been more successful at learning how to think like rats and bats than they have at learning how to empathize with gnats and mites? But they will catch up. (See, for example, the recent work of Thornhill, 1987, on scorpionflies.) No doubt the inherent advantages of working with arthropods will even allow them to surpass us in some types of investigations.

I should like to focus on something new; something which Zvika Abramsky and I have been developing over the past several years; something that I believe will be useful and that I hope will further improve the future yield and luster of mammalian community ecologists and augment their reputation for leadership.

I think it is no coincidence that a preponderance of the contributions to the present symposium deal directly or indirectly with habitat selection. No matter anything else, habitat selection is a part of the foundation on which community structure lies. Even Owen-Smith's brilliant treatment of resource partitioning eventually gets to the point that resource partitioning is mainly achieved by habitat selection. And no wonder! The plants on which the ungulates specialize also partition habitats. It is truly hard to imagine a world in which communities are not structured by a pervasive habitat selection. Whether the habitat selection is spatial or temporal; whether it adds to β diversity—in which case it is macrohabitat selection—or to α diversity—in which case it is microhabitat selection, the community ecologist must understand it and use that understanding to design experiments and interpret observations. For example, Fox's assembly rule (this volume) is derived from the assumption that habitat preferences may change more readily than resource preferences. Whereas that principle may not be universal, I share his belief that it is often true. Here is a simple conjecture that may help to explain it.

Habitat preferences are often highly density-dependent, whereas resource preferences are only weakly so. A forager that encounters a specific resource item has only to assess whether pursuit of that item is likely to be its most profitable use of time and energy. This will depend to a great extent on the morphology and physiology of the forager in relation to the structure, size, and chemical composition of the resource, and it will have less to do with what the densities of the other sorts of resources. In deciding to forage in a habitat patch, however, a forager surely needs to take to heart the density of food items in it. This will depend to a large extent upon how many others of its own species and of other species have been in the patch in the recent past.

The fact that habitat selection depends greatly on the density of conspecifics was first recognized independently by Morisita (1950), Svardson (1949), and Fretwell and Lucas (1970). Alas, the first of these worked on insects and the other two on birds. Nevertheless, strongly under the influence of kangaroo rats and other such reasonable creatures, I and my colleagues have developed over the past decade a set of theories that take density-dependent habitat selection beyond the limits of single-species interactions and into pairwise and multispecies associations (Rosenzweig, 1979a, 1981, 1985; Pimm and Rosenzweig, 1981; Pimm et al., 1985; Brown and Rosenzweig, 1986; Rosenzweig and Abramsky, 1986). Judging from what I have been hearing and reading, the answers we have been getting will surprise you. If they do not also delight you, they will at least give you a target at which to aim brickbats.

I begin with an examination of single-species habitat selection. Then I shall describe briefly a new technique to detect habitat selection in mammals from census data. I shall review how it was applied to some data from gerbils. Finally, I shall consider two-species systems.

Single-Species, Density-Dependent Habitat Selection

The basic idea behind single-species theory is quite simple. Assume that a species can forage profitably in a variety of habitat types. Assume, however, that these types differ in their profitability and that the forager is aware (perhaps unconsciously) of the differences. Assume also that foraging depresses the yield of a patch. Thus the relative profitability of a habitat type depends upon the density of foragers in it; the highest-yielding habitat when only a few foragers are present could become the poorest-yielding haitat if there are a thousand times more foragers and they all elect to restrict their foraging to it.

Now let us assume that our foragers have plastic foraging behavior, and that they try to get as much profit as possible from their foraging efforts. In other words, let us assume the foragers are capable of approaching optimal behavior. There are many models of how the forager may assess its position, what it needs to optimize, and what its searching costs may be. These are all relevant to making specific predictions of forager behavior. But there is a general prediction that transcends the specifics.

When the forager species is rare, it may be able to restrict its activities to a subset of habitats. These will be so much more profitable than the unused habitats that searching for them pays more than it costs. But as the forager population grows, it renders these preferred habitats less and less rewarding. This forces the forager to begin using secondary habits too. The net result is that as population density grows, so should the habitat component of niche breadth.

Demonstrating the density-dependence of the behavior of a nocturnal species in the field can be a problem. Often the only data that are practical to get are the population densities themselves. One way to estimate habitat preferences is to see how the densities compare in different habitat types. Then if we know the proportion of the census that occurs in each habitat type, we can combine the proportions to achieve an index of habitat breadth.

A popular means of achieving the combination is, both in ecology and population genetics, Simpson's Index (Levins, 1968):

$$SI = \Sigma P_i^2$$

where P_i is the proportion of the census found in the ith habitat. But there is a problem. Simpson's Index is, itself, density dependent.

Suppose, for example, that we have defined four habitat types. If 100 percent of the census occurs in one type, then the value of SI is 1.00. As the census is more and more equally divided among the four types, the value falls toward its minimum, 1/4. Often, ecologists use the reciprocal of SI; then the value (1/SI) rises from 1.00 to 4.00 as habitat breadth goes from minimum to maximum. Now, however, imagine that the species has a constant niche breadth, but the investigator has a variable sample size, as one might expect when population size varies. When the sample size is unity, the value of SI is also 1.00. But as the sample grows, the value of SI
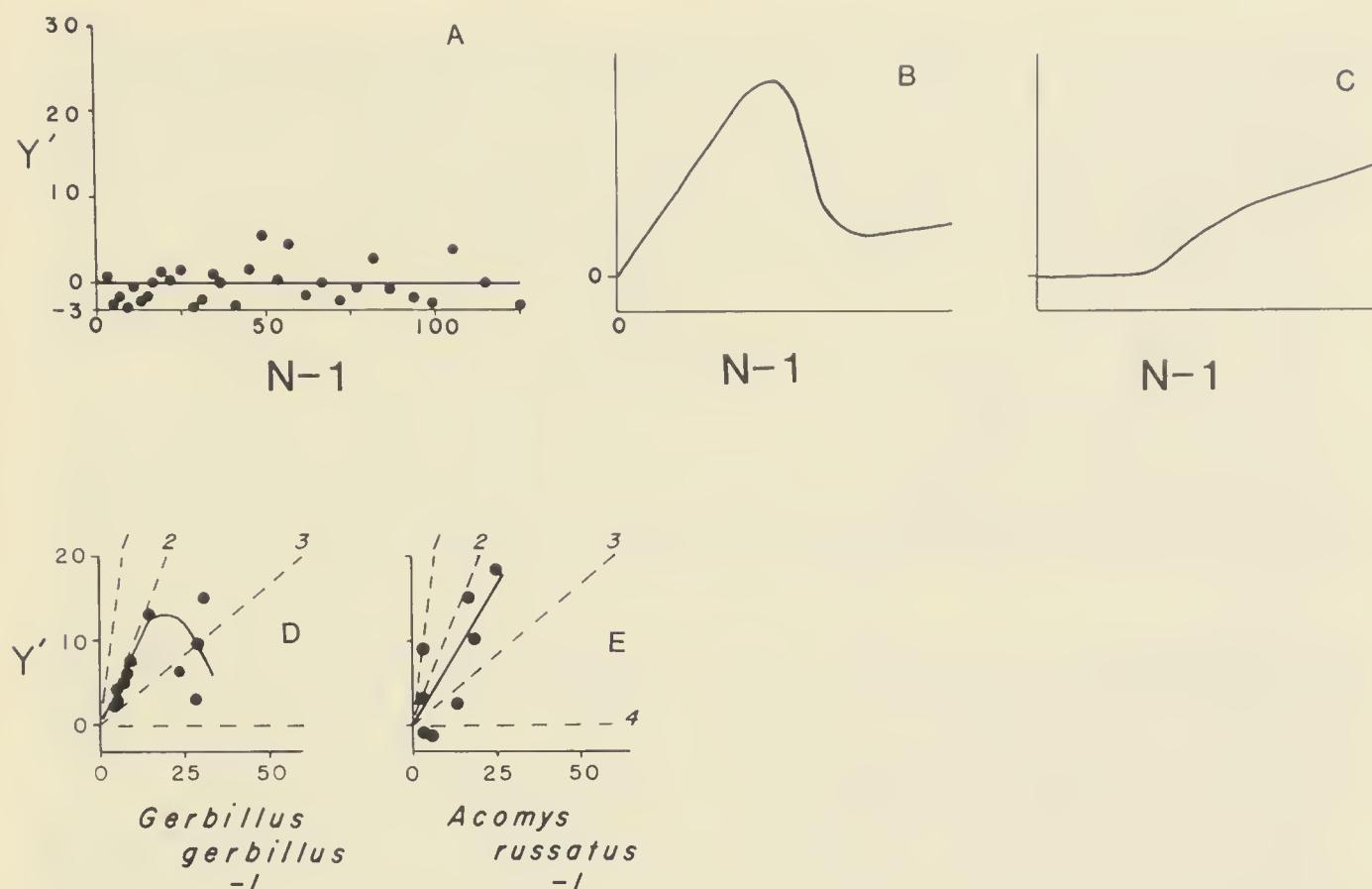
FIG. 1.—Single-species habitat selectivity graphed in a specially transformed space. The abscissa is population density minus unity; the ordinate is the transformed Simpson Index. The estimate of selectivity at any point is the value of the slope connecting that point to the origin. Thus, data that follow a straight line and a slope of zero indicate random use of habitats (from Rosenzweig and Abramsky, 1985). (A) Simulation of a randomly-distributed species. (B) The expected curve of a density-dependent habitat selector. (C) The expected curve of a nonhabitat selector in environments that differ in their ability to support the species. (D) Habitat selection pattern of the lesser gerbil, a density-dependent habitat selector. (E) Habitat selection pattern of the golden spiny mouse, a density-independent habitat selector.

will decline, eventually reaching its true value. Thus, varying sample sizes mimic, to a great degree, varying niche breadths.

Abramsky and I have corrected this problem with a transformation of Simpson's Index (Rosenzweig *et al.*, 1985). The transformation is designed so that any habitat selection strategy that is independent of density will produce a straight-line scatter diagram with positive slope when the transformed variable is plotted against sample size. The steeper the slope, the more selective the species. The transformation is also designed so that all strategies emanate from the origin if the x-axis is sample-size minus unity (instead of just sample size).

Figure 1A shows the simulated case of a species distributed at random. Its transformed SI should be scattered around the x-axis (slope zero), no matter how many individuals are in the sample. Notice that in the simulated points graphed here, the highest value obtained was less than 6.00. Even single values much higher are rather strong indications that the distribution of the census is not random.

If selectivity of a species is density dependent, the scatter diagram will follow a line of variable slope. Suppose a species follows the one-species
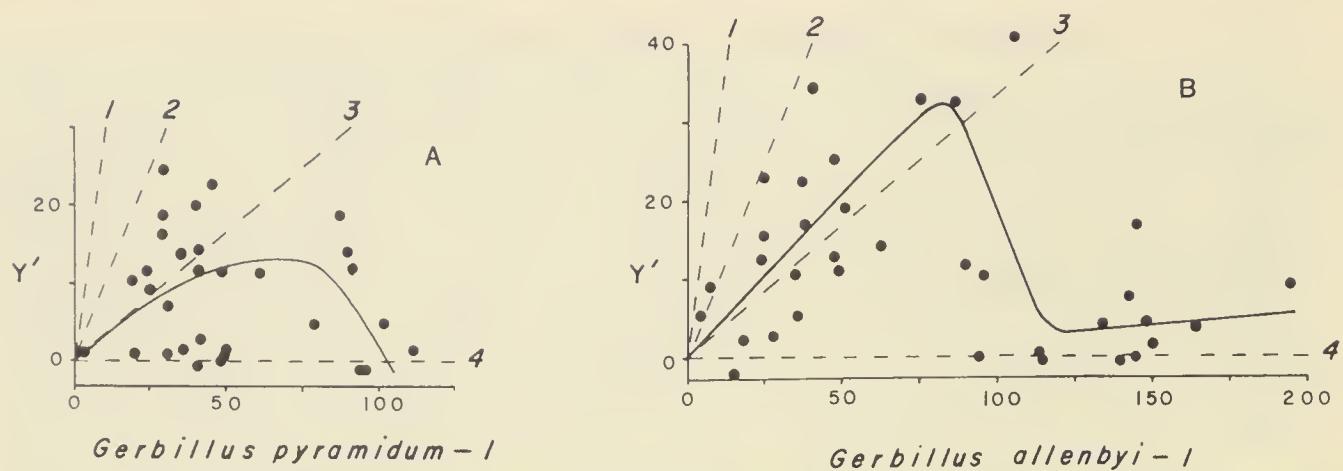
FIG. 2.—(A) Habitat selection pattern of *Gerbillus pyramidum*. Axes as in Figure 1. (B) Habitat selection pattern of *Gerbillus allenbyi* (from Rosenzweig and Abramsky, 1985).

density-dependent theory. Then its points will follow some steep slope from the origin until a threshold density is reached. The line will descend as selectivity is decreasing and perhaps reach a new and lower slope reflecting the disparate ability of the habitats to support the species (Fig. 1B).

Another possibility is that there is no habitat selection, but that habitats have a disparate ability to support the species. Then we will see a line along the x-axis until the lack of resources begins to affect net reproductive rates. From there on we can expect a sigmoid approach to the set of proportions supported by the habitat types (Fig. 1C).

There are a few other possibilities, but the main point is that the hypotheses produce distinct shapes on the graph. Thus one can discriminate among them by regression techniques.

Here are examples of the application of the technique to some rodent censuses from Israel's Negev Desert. Figure 1E shows *Acomys russatus*, the golden spiny mouse. This mouse has a significant and constant habitat selectivity. Figure 1D shows *Gerbillus gerbillus*, a gerbil that prefers unstable sand dunes. This one is a density-dependent habitat selector. Past 20 individuals or so, its selectivity decays towards zero.

A case similar to *G. gerbillus* is the large sand gerbil, *G. pyramidum* (Fig. 2A). But notice the considerable scatter in the mid-densities. That, as we shall see below, turns out to be an interspecific effect caused by the next species, *G. allenbyi* (Fig. 2B). *G. allenbyi* yielded enough data to reveal the full form of Fig. 1B. Its decay in selectivity is followed by a new distribution that is only a bit more clumped than a random one would be.

Single-species, density-dependent habitat selection has been demonstrated for many more than these few desert rodents. But the fact that we can now analyze them too, means that no longer do we have to wring our hands and wish that our nocturnal subjects were birds or bumblebees or some other diurnal animal easy to observe. We can work with nocturnal mammals too.

Meanwhile, we should underscore the fundamental lesson of the one-species case. *Habitat preferences must be measured when a species is rare.* Preferences are likely to decay at high densities and data obtained at such times are consequently unreliable.

Turning my attention to two-species systems, I begin by considering three sorts of animal community structure and then show a habitat selection theory for each. Two are not yet supported by any mammalian work, but the third is actually the product of a mammal study. Finally, I shall discuss each theory in general, and extract some implications from them that are relevant to some of the other studies in this volume.

The Roots of Habitat Selection

I propose that there are four basic situations that lead to habitat selection. One of these, in which species use habitats to identify mates in courtship will not concern us because, although it has ecological consequences, it has no ecological cause. Moreover, all the examples come from arthropods (Zwolfer, 1974; Rosenzweig, 1979b; Colwell, 1985).

The second is the MacArthurian view of niches and specialization. It starts with a spectrum of habitat types that vary qualitatively. That is, the habitats differ in structure somehow. My favorite example is the corolla shapes and sizes of flowers that form the foraging habitats of nectarivores. An individual that is proficient at foraging in one habitat type is not so proficient in the others. MacArthur's favorite postulate reigns: "Jack-of-all-trades is master of none." This leads to what Stuart Pimm and I have termed the distinct-preference model of habitat selection: each species prefers a distinct part of the spectrum of habitats (Rosenzweig and Abramsky, 1986).

The third situation, not surprisingly, we term the shared-preference model. Here the different habitat types have exactly the same components in the same proportions. But some are richer than others. Examples abound. There are oxygen gradients in fresh water, and gradients of percent time that the ocean covers a point in the intertidal zone. But the most commonly found gradient in the literature is the productivity gradient. Some habitats just have more of the same than do others. A splendid example of this comes from work on bees (Schaffer et al., 1979). Because nighttime is too cold for foraging, bees start each new day with a large, fresh supply of available nectar. The habitat then changes temporally as they reduce their nectar supplies. Of course, all species would prefer to forage in the richest habitats, and they do. But some mechanism of competition often prevents all species from using the poorer times of day. In the Schaffer work, honeybees quit foraging first, then the bumblebees, leaving the carpenter bees to forage alone. Brown (1986) has detailed a similar relationship for desert rodents faced with spatial variation in seed density. The shared-preference model is the best known and the most often seen in field studies (see Connell, 1983, and Schoener, 1983).

The fourth model is new. It is termed the centrifugal preference model (Rosenzweig and Abramsky, 1986). There is a core habitat that all species prefer. But the secondary preference of each species is distinct. Hence, their real specialty is not their preference, but what they do best as a backup. Abramsky and I think that centrifugal preferences could result if ideal

habitats are composed of certain mixtures of components. Altering their proportions could bring stress, and each species could be adapted to deal with the loss or dearth of one of the components. In other words, instead of species' niches being the things they are well fit to do, their niches could be the stresses they are adapted to withstand.

To sum up, habitat selection theories are required for each of three models of community organization: the traditional jack-of-all-trades or distinct preference case; the quantitative variation or shared preference case; and the stress resistance or centrifugal preference case.

Isoleg Theories of Habitat Selection

My colleagues and I have tried to build robust theories to cover each of the three models. Instead of concocting a new set of equations for each special situation, we worked from the general models that I have just presented. Instead of producing specific numerical predictions, we generated graphs called isoleg diagrams which explore the behaviors as functions of species densities.

Figure 3A is the isoleg diagram for a distinct preference case. There are two species, I and II. Their densities are N_I and N_{II}. The densities are the axes of the graph. There are two habitat types available to both species, but one is preferred by I, the other by II. From what we have said about single species, you can expect each to exhibit its preference when rare. But as we move along a density axis, a threshold will be reached after which the species will need to use both habitat types. This threshold is termed an isoleg point after the Greek for "equal choice." At it, a species should not use its secondary patch, but at any infinitesimally higher density, it should.

There is another kind of isoleg point. This is one in which a species should use a certain set of proportions of each habitat type. But I shall not concern myself with it here. Instead let us consider only isoleg points that reflect thresholds of habitat choice; on one side, a particular behavior is optimal, on the other it is replaced by a different optimal habitat selection behavior.

As we add members of the second species, we need to trace the threshold into the interior of the graph. Because of the distinct preferences of each species, the isolegs have positive slopes. This is because the second species tends to select and depress the first's poorer patch type, making it even less attractive to the first species. Recently, Joel Brown and I (1986) have shown that if all examples of a patch type are the same, the isolegs never cross. So, the simplest distinct-preference case results in a tripartite division of the state-space. In the middle is a strip of exclusive behaviors. Both species are selective, and so they do not exhibit any niche overlap. Off to each side, one of the species abandons habitat selection and so there is considerable overlap in habitat use.

The simplest isoleg diagram for shared-preferences is slightly more complicated. To illustrate this type of community structure, I shall describe
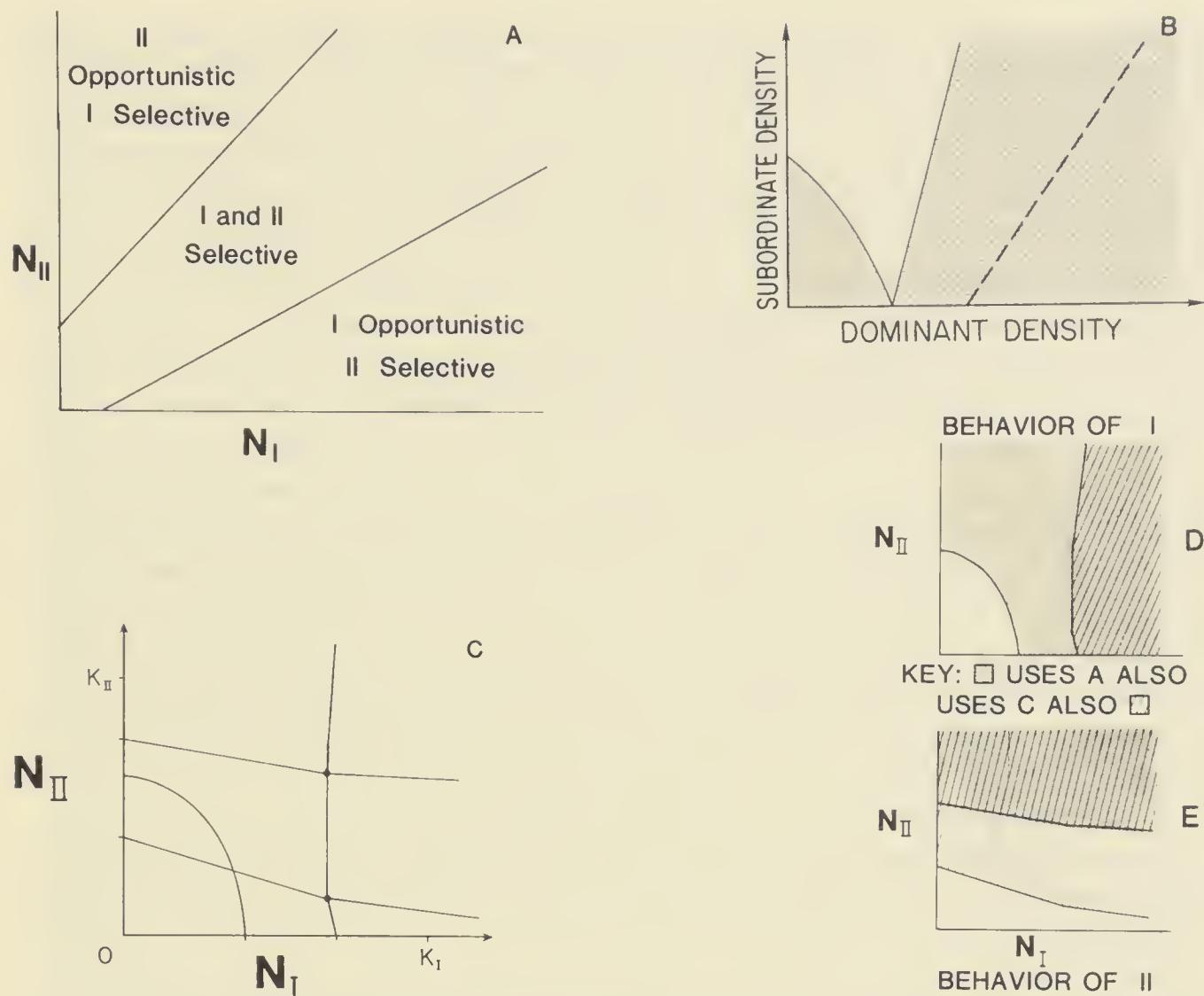
FIG. 3.—Isoleg diagrams. Axes are the densities of two species. (A) A distinct preference case. (B) A shared preference case. The dashed line is the isoleg of the dominant; to its left, the dominant uses only the better patch; to its right, it uses both. The other two lines are the subordinate isolegs. In the dotted area, the subordinate uses only the better patch; in the shaded area, it uses only the poorer patch; in the open area, it uses both (from Rosenzweig, 1985). (C) Isoleg diagram for a centrifugal preference case. There are three habitats, A, B, and C. Habitat B (unshaded) is the core habitat for both species; secondary preference for species I is A, that for species II is C (from Rosenzweig and Abramsky, 1986). (D) Illustrates behavior of species I separately. (E) Illustrates behavior of species II separately.

it for a case where there is interference competition. In such a case, we must distinguish between the dominant species and the subordinate. When densities are substantial, it is the dominant species that gets to use the best places; the subordinate must give way. Also, the subordinate should have two isolegs. One is the threshold past which it must use both preferred and secondary habitats. The other is the threshold past which the better patch type is so polluted with dominant individuals that the subordinate is better off using only the secondary patch type.

Such a shared preference isoleg diagram should look like Figure 3B. The area near the origin has both species selecting the same habitat and it is the best. Then we cross a subordinate isoleg, which has a negative slope. Now the subordinate becomes opportunistic. The second subordinate isoleg,

which is vertical, or nearly so, brings us to the region of total habitat separation; in it the dominant uses the preferred patches and the subordinate restricts itself to the poorer patches. For the subordinate, what was better has become useless, and what was useless and poor has become selected. This reemphasizes the need to measure true preferences at low population densities. Finally, we cross the isoleg of the dominant, which, by the way, does not have to exist at all. If it does, however, it should have a positive slope. To its right, the dominant uses both habitats.

The third isoleg diagram is for centrifugal community organization (Fig. 3C and its two satellite figures 3D and 3E). There are a minimum of three habitat types. One, which both prefer, is the core (Habitat B); in the graph, points near the origin are characterized by both species using only the core habitat (unshaded regions of 3D and 3E). The second habitat (Habitat A) is the backup preference of species I. The third habitat (C) is the backup preference of species II. Selection of Habitat A is indicated by stippling, whereas selection of Habitat B is indicated by cross-hatching (Figs. 3D, 3E).

The isolegs in a centrifugal system are characterized by negative slopes (Fig. 3C). Additionally, unlike the previous two cases (Figs. 3A, 3B), there is no region of the diagram in which the species have nonoverlapping habitat use; they always share at least the core habitat.

Later we shall examine some of the consequences of the various models. But first let us ask whether any are known to be present in natural communities, in particular those of mammals.

Evidence for Different Models of Habitat Selection

Despite its domination of the literature of theoretical ecology, distinct preference organization is quite rare in the empirical literature of habitat selection. It is known in two mussel species of California (Harger, 1972) and in bumblebee communities (Inouye, 1978; Ranta et al., 1981; Pyke, 1982). But there is no completed example of an isoleg diagram for it. (I am working on one for bumblebees at the present time.) So far it has been hard to spot in mammals. That does not mean it never exists in mammals. The browsing ungulates studied by Owen-Smith may well be a case. And the first two published cases of body-size/food-size niche organization—which is the classic distinct preference example—were for mammalian carnivores (Rosenzweig, 1966) and avian raptors (Storer, 1966). But these are cases of resource partitioning, not habitat selection. Montgomery's (this volume) analyses of *Apodemus* distributions are the most convincing case for distinct-preference in small mammals. Later I shall explain why I think this model is so difficult to identify in mammals that exhibit habitat selection. Despite this, I think it is common among them.

Quite unlike distinct preferences, shared preferences seem to pop up again and again. Pimm, Mitchell, and I (1985) recently have published the experimental analysis of two pair of hummingbird species. They fit the isoleg predictions well (see also Rosenzweig, 1986). Perhaps within the

decade, someone will undertake an isoleg analysis of an appropriate mammal interaction and succeed in producing results as convincing as we now have for hummingbirds. But shared preference-interference competition is already well known in mammals.

Frye's (1983) work on large and small kangaroo rats—confirmed and extended by James Brown and his students (this volume)—has shown that the larger dominates the smaller and restricts its use of habitats. Dickman's perturbation experiments with large and small species of *Antechinus* produced the same sort of asymmetry. The larger species exerts great effects upon the smaller, but not vice versa. In addition, the larger has the superior food habitat, because the food in the habitat of the smaller *Antechinus* disappears in the winter.

Centrifugal organization, undoubtedly because it is so newly hypothesized, is the least well known. And yet, because it is actually the product of work with mammals, we do have an isoleg diagram and some associated habitat data suggesting that it exists in mammals. Abramsky and I produced this isoleg diagram for *G. pyramidum* and *G. allenbyi*. Because both its isolegs have negative slope, it resembles a centrifugal diagram (Fig. 4A). Also, we think we know what the habitats are.

Both these species are psammophiles, but one tends to dominate censuses in the barest dunes and the other in well-vegetated sand fields. Inbetween is a habitat where either may be found in abundance (Fig. 4B). Good gerbil habitat seems likely to be a mixture of the cover and architectural support provided by perennials, along with the opportunities for food-gathering from seed-producing annual plants growing in open spots. Intermediate grids have both. The larger species, *G. pyramidum*, seems better able to get along without much cover, but needs more food. *G. allenbyi* should require less food, but appears to need the cover more. The results have all the earmarks of centrifugal organization.

Stenseth (personal communication) has suggested another mammalian case that involves a pair of microtines in Scandinavia. But much more needs to be done to nail down cases of this form of organization.

GENERAL IMPLICATIONS

Niche shifts.—Now we can ask what general principles these theories teach. The first I will address is the question of niche shifts. Distinguished ecologists have concluded—or better still, taken for granted—that if two species are competing and the density of one is lowered or even diminished, the niche of the other will expand. This conclusion has pervaded community ecology (for example, Cody, 1974; Colwell and Fuentes, 1975; Diamond, 1978; Werner and Hall, 1979; Blondell, 1985).

If we examine the distinct preference case (Fig. 3A), we shall see that the conclusion always holds. If we reduce one species, we may cross the isoleg of the other. If we do, it will always be from a region of narrower selectivity to one of greater opportunism. If we actually eliminate a competitor, this always happens.
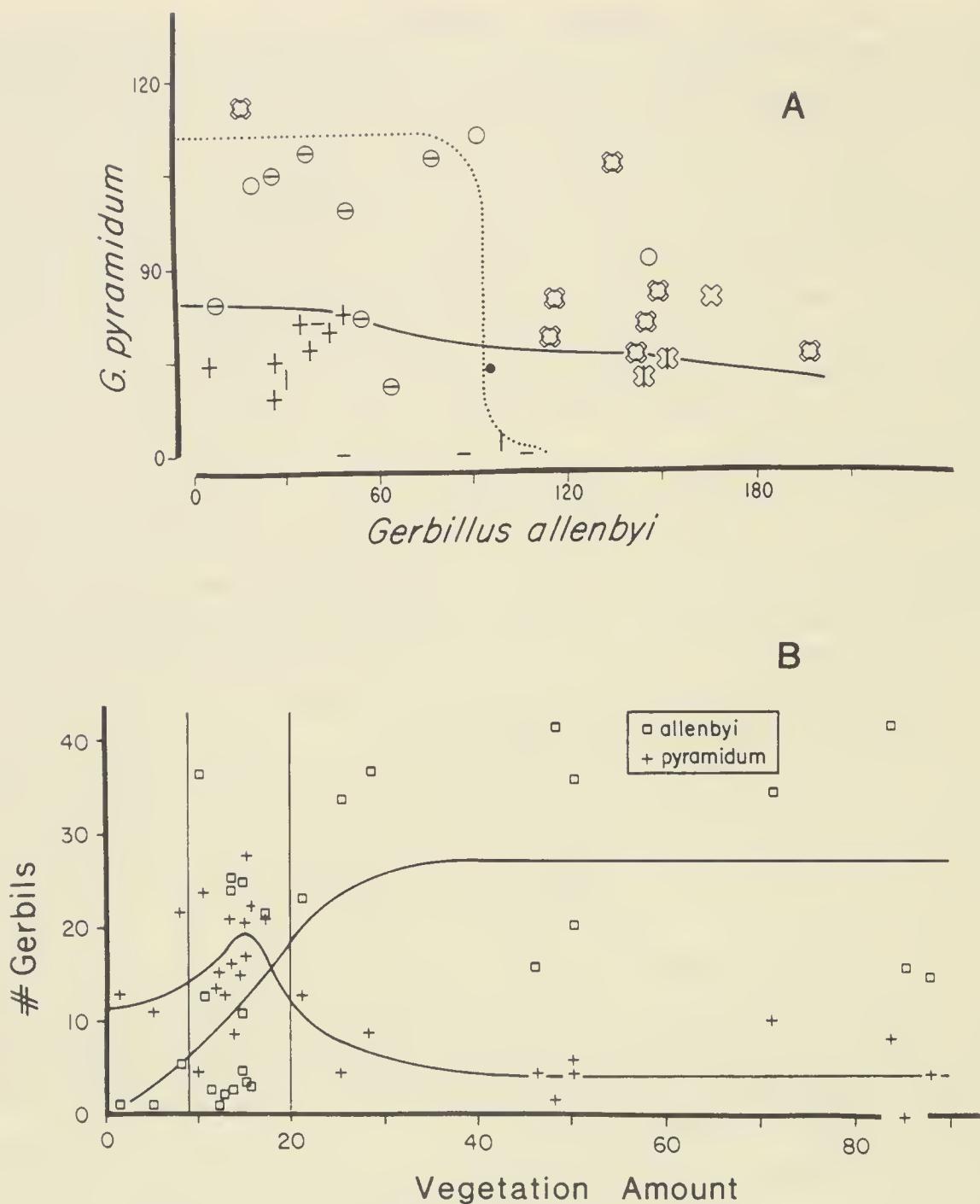
Fig. 4.—(A) Isoleg diagram for G. *pyramidum* and G. *allenbyi*. Symbols for G. *pyramidum*—selective (vertical line), opportunistic (open circle); symbols for G. *allenbyi*—selective (horizontal line), opportunistic (open cross). Two superimposed symbols indicate that both species exhibit determinate behavior, whereas a single symbol represents circumstances in which only one species exhibits determinate behavior. The solid dot near the isolegs' intersection was a case of both species having indeterminate behavior (from Rosenzweig, 1985). (B) Gerbil census as a function of vegetation density. Squares are the density of G. *allenbyi*; crosses are that of G. *pyramidum*. Vertical lines subdivide vegetation density into three regions as described in text. Peaked and rising curves are approximate and merely meant to allow quick inspection of the overall tendencies of the two censuses (from Rosenzweig and Abramsky, 1986).

If we now examine the centrifugal isolegs (Fig. 3C), we observe that the opposite prediction may hold. Because of the negative slopes of the isolegs, forcing a species across one by reducing its competitor's density will force it to be more selective; that is, to restrict its foraging to the core habitat. This is a reverse niche shift. It can even take place if we remove the competitor

entirely. In the latter case, however, the numerical response of the remaining species will eventually carry it back across its isoleg to resume its original niche breadth. Population growth even may carry it across a second isoleg, where it has greater niche breath than originally. If we wait long enough then, the direction of the niche shift may agree with the prediction everyone thinks is automatic. But, on the other hand, even then it may not agree. And, at least in the short term, reverse niche shifts are what to expect.

Reverse niche shifts are less likely but also possible with shared preference organization. Here the response should be mixed. It will depend on where in the graph you begin the perturbation, how extensive it is, and if you perturb the dominant or the subordinate species. For example, a perturbation from right to left across the negatively-sloped isoleg of the subordinate (Fig. 3B) causes the subordinate to restrict its use of habitats, a reverse shift, but one across its positively-sloped isoleg causes it to expand it.

I would guess that shared preference systems rarely find themselves in the part of the graph where secondary habitats are empty. Therefore, if we find reverse niche shifts in nature and we have not performed a large experimental perturbation, it is quite probable that their cause is centrifugal organization.

Predation, parapatry, and the elusiveness of distinct preferences.—There are two reasons why I think distinct-preference organization has been a rare discovery. First, most of us, baffled, have avoided investigating the effects of predation on competition. But if predators are important, they may well foster distinct-preference habitat selection. The bipedal desert rodent with large auditory bullae is well suited to escape in the open, but may have problems negotiating a tangle of litter under a shrub with the grace and agility of the more ordinarily-structured small mammal. Kotler's work (1984) illustrates this. The bipedal kangaroo rats and kangaroo mice have inflated bullae and spend more time in the open. Kotler showed that rodents of different body plans may well depend upon predators for their coexistence. In short, if we start looking up the food chain rather than down it for our explanations of habitat selection, we should find many cases of distinct-preference organization.

The second reason we have rarely found distinct-preferences is that we may expect them to be haunted by the Ghost of Competition Past. Let us return to Figure 3A. If the steady-state point of the interaction lies in the middle strip, then there is no overlap in habitat use. But that is exactly where the steady-state must lie (Pimm and Rosenzweig, 1981; Brown and Rosenzweig, 1986). Thus, the competitive interaction will not be detectable under ordinary circumstances. It is this situation, which I have termed the Ghost of Competition Past. Connells' (1980) application of that phrase to all forms of competition is not yet supported by theory or field work, and both the theory and field work reviewed here suggest it cannot be so general. The "ghost" first suggested itself to me as I pondered the

predictions of distinct-preference habitat selection. In truth, the "ghost" is rooted in that form of community organization. True, it may also occur in shared-preference cases, but there, it is not so likely. In centrifugal organization, the "ghost" cannot occur because in this type of habitat selection all species always use the ideal core habitat regardless of their densities.

If distinct preferences can lead to zero habitat overlap, then they are also likely to produce parapatric distributions. But what do good investigators of competition look for as an appropriate study site? A place where there are sympatric species! They thus have biased the search away from distinct preference cases. More attention to the contact zones of parapatric species might well bring some astounding results (Diamond, 1986). More to the point, I want to speculate and suggest that parapatry itself may be caused by distinct-preference habitat selection and the Ghost of Competition Past.

Abundance, shared preference, and geographical range.—Recently, it has been noted that there is a positive correlation between geographical range and abundance in mammals (Bock and Ricklefs, 1983; Brown, 1984). Rare species tend to have small ranges. I suspect this may be the result of shared-preference habitat selection, and here is why.

Shared-preference systems are founded on a spectrum of habitat types that differ quantitatively. Like every other variable in the natural world, their richnesses may be expected to show a frequency distribution biased in favor of its central tendency. That is, very rich and very poor habitats should be rare compared to moderately rich ones. What then happens to the dominant species specialized on the richest places? Its habitats should be rare and narrowly distributed, and so should it. There is no known tendency for other forms of habitat selection to exhibit such asymmetry, so any trend imposed by shared preferences should dominate the results. And indeed that is what we see.

Taxon cycles.—It seems to me that some taxon cycles may be driven by shared-preference habitat selection. The rare species are in the greatest danger of extinction. They occupy the richest end of the spectrum at the cost of having narrow niches and often of being inefficient. Again and again the pattern emerges from the literature. The aggressive species succeed because they can interfere with others, not because they are particularly good exploiters. They probably waste much of the wealth they expropriate for themselves. And yet, as individuals, they are doing quite well. Odum and Pinkerton (1955) long ago pointed out that efficiency is not important for success in life. It is power that counts. Hence, when hard times come and the dominant species becomes extinct, its niche will not long stay vacant. The meek will inherit the niche. But in so doing, they will be driven by natural selection to become dominants themselves. Thus the taxon cycle. It is a constant asymmetrical parade past a judge whose ultimate sentence is extinction. Judgment is visited upon the aggressors, only to be followed by the corruption of the meek.
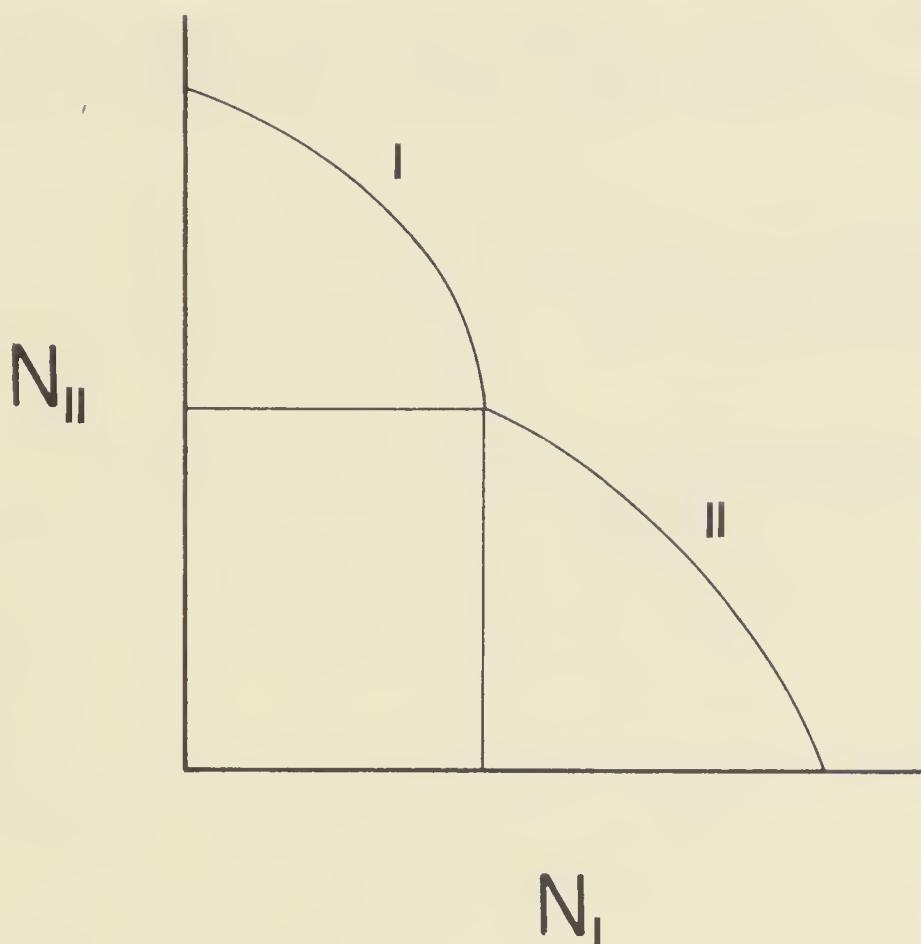
Fig. 5.—Isolegs of two species in a distinct-preference relationship in which individuals can recognize the spatial variability from patch to patch even among patches of the same type. Except for the assumption of recognition, this case is exactly like the distinct preference case of Figure 3A. Notice how the single changed assumption has profoundly affected the shapes of the isolegs, eliminating their positive slopes, and forcing them to cross. The region northeast of their crossing is a combination of behaviors that does not appear in Figure 3A; at points in this region, both species are using each type of habitat (from Brown and Rosenzweig, 1986).

Allowing for spatial variation within a patch type.—Isoleg theory needs far more testing, and it needs to be extended. One extension results from relaxing an assumption that has been implicit in all these theories. The assumption is that at any single instant, all patches of a single-habitat type are the same. There is no spatial variation within a habitat type, only temporal variation.

Joel Brown and I (1986) recently have investigated what happens when this assumption is relaxed for the distinct-preference case. This had many interesting results, one of which is on the shapes of the isolegs (Fig. 5). Here you can see the intratypical spatial variation allows the isolegs to cross. This actually prevents the appearance of the Ghost of Competition Past, and may lead to reverse niche shifts. Thus, extension of the theory helps to specify more precisely the conditions under which we expect various outcomes.

I could do worse than to conclude by quoting Douglas Adams (*The Hitchhiker's Guide to the Galaxy*): "Mice are merely the protrusion into our own dimension of vastly hyperintelligent, pandimensional beings. The

whole business with the squeaking and the cheese is just a front."
Obviously, we have a lot to learn from them and from their relatives.

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THE EFFECT OF SPATIAL SCALE ON PATTERNS OF HABITAT USE: RED-BACKED VOLES AS AN EMPIRICAL MODEL OF LOCAL ABUNDANCE FOR NORTHERN MAMMALS

Douglas W. Morris

ABSTRACT—The scaling of habitat use by *Clethrionomys gapperi* was evaluated in southern Alberta and central Labrador. In both geographic locations, *Clethrionomys* density was significantly related to macrohabitat and not to microhabitat variation. These results are similar to those reported for temperate-zone small mammals in Ontario. Density responses to macrohabitat suggest that these rodents are coarse-grained foragers, the abundance of which responds to overall resource productivity. Microhabitat selection may not evolve in such a system, and detecting differences in microhabitat use between species may do little to reveal the factors responsible for patterns of distribution and abundance. This is opposite to conventional models that recognize differences among species, but suggest that interference competition for space should lead to habitat selection.

Our interpretations of structural processes in ecological communities are directly related to the scale of investigation (Wiens, 1986), and our progress at making correct inferences regarding process depends on asking questions appropriate to the scale of our analysis (Wiens *et al.*, 1986). Analyses of distributional patterns at a local level are appropriate for addressing questions about the influence of ecological interactions on population dynamics. Regional and larger scale biogeographical studies outline the ecological constraints to adaptation and the environmental contexts within which local interactions operate. Local populations do not exist within an ecological vacuum, conveniently defined by study site boundaries, and any complete analysis of general processes structuring ecological communities has to incorporate regional and biogeographical patterns. In the same way, patterns do not exist in a vacuum either, and there is a logical dependency between patterns we observe, regardless of scale, and underlying ecological processes. Observations of the relationship between relative abundance and geographical distribution led Brown (1984) to propose a causal link between those patterns, and their dependence upon the local use of multidimensional and covarying resources by similar species with similar ecological requirements.

The scaling patterns we observe tell us at least as much about how biological species respond to their perceived scaling of the environment as they tell us about the limits of our own perception. To interpret the structure of local communities, we must understand how species respond to, or at least perceive, the scaling of their resources. A profitable first beginning would be to choose an environmental dimension known to be important in the structuring of a particular community, or group of

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communities, and evaluate how species respond to changes in the scale of that dimension. Such studies will play a pivotal role in ecology because they are at the crucial interface between life history, population and genetic processes, the behavioral and evolutionary mechanisms of foraging, and community structure.

Distributional patterns of north-temperate small mammals depend in large part on differential habitat use (Hirth, 1959; Pearson, 1959; Wirtz and Pearson, 1960; Shure, 1970; M'Closkey, 1975; M'Closkey and Fieldwick, 1975; M'Closkey and Lajoie, 1975; Krebs and Wingate, 1976; Sly, 1976; Brown, 1978; Dueser and Shugart, 1978; Hansen and Warnock, 1978; Morris, 1979, 1983, 1984a, 1984b; Vickery, 1981; Hansson, 1982). Species interactions also may be important (Koplin and Hoffmann, 1968; Murie 1971; Grant, 1972; Crowell and Pimm, 1976, Rowley and Christina, 1976; Henttonen et al., 1977; Master, 1977; Redfield et al., 1977; Dueser and Hallett, 1980; Hallett et al., 1983), but the overall influence of competition is probably subsidiary to habitat preference (Morris, 1983; Galindo and Krebs, 1985; Wolff and Dueser, 1986). Habitat can exert its influence over patterns of distribution and abundance at different scales (Morris, 1985), and habitat selection in northern small mammals provides a convenient system to evaluate how animals respond to environmental scaling.

There are no general rules on how to measure habitat, nor is there any concensus on what spatial scales habitat use should be monitored. In practice, ecologists have identified two alternatives—between- and within-habitat components (for example, Cody, 1974), more recently termed macro- and microhabitat. There are no standard operational rules on how to differentiate between them. Morris (1987) has suggested the following working definitions: define habitat type as the spatial scale within which similar physical or chemical variables, or both can by used to describe its variation. Different habitat types are described by different suites of physical or chemical variables. Within habitat types, define macrohabitat as distinguishable units whose minimum area corresponds to that within which an average individual performs all of its biological functions (home range) during a typical activity cycle. Microhabitat can be quantified by physical or chemical variables that influence the allocation of time and energy by an individual within its home range. When viewed in this way, habitat variation becomes a continuous process that can be partitioned into separate components, and analyzed statistically by analysis of variance and its analogues.

For comparisons among co-occurring species, habitat scaling can be evaluated by multidimensional contingency tables among habitats and their replicates, followed by discriminant functions analyses of microhabitat differences within plots (Morris, 1984a). This approach answers questions about differential habitat use among species, but cannot be used to evaluate possible density responses within species. Morris (1987) suggested multiple regression analysis, using dummy variables to represent habitat treatments

and their spatio-temporal replicates, as one method to reveal patterns of habitat scaling within species. The scaling of habitat use can be represented by a linear model of the form

$$N = a_0 + b_1F_1 + b_1F_2 \ldots + b_nF_n + b_{n+1}D_1 + b_{n+2}D_2 + \ldots + b_{n+m}D_m + e,$$

where N is the predicted density, the Fs represent microhabitat factors, the Ds are dummy variables scored 0 and 1 representing m + 1 macrohabitats, and e is the normally distributed error variation. I used the regression method to look for scaling patterns of density-dependent habitat selection in two subspecies of the red-backed vole—(*Clethrionomys gapperi athabascae*) in the Rocky Mountains of southern Alberta and (*Clethrionomys gapperi proteus*) in the boreal forest of central Labrador. My objectives were to (1) reveal the scaling of habitat use by this important northern herbivore, and (2) interpret this scaling in terms of its importance to the structure of boreal small mammal assemblies.

Study Areas

Red-backed voles were live-trapped, individually marked and released in each of two 0.81-hectare replicates of six habitats in the Kananaskis Valley of Alberta, and in four 0.03-hectare hexagonal plots spaced 150 meters apart in three forest habitats replicated in each of the Churchill and Goose River valleys of Labrador. Single Longworth live-traps baited with oatmeal and peanut butter, apple or potato slices (for moisture), and mattress stuffing (for insulation) were placed at permanently marked trap stations located at 15-meter intervals. In Alberta, traps were set on alternate trap lines in the evening, checked at first light and mid-evening the next day, and collected at first light on the second day. Each station was monitored three times from 16 May to 31 August 1977. In Labrador, traps were set in the morning, checked that evening, and first light and mid-evening the second and third days, and collected at first light on the fourth day. Each Labrador station was monitored twice from 16 July to 2 August 1984.

In Labrador, each hexagon represented a sampling subplot. In Alberta, subplots were created as three by three trap grids at each of the four corners of the seven by seven habitat replicates. Forested habitats only are used in the regression analyses. In Labrador, these were: mixed forest—black and white spruce (*Picea mariana, P. glauca*), balsam fir (*Abies balsamea*), poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*) with an understory of alder (*Alnus crispa*), mountain maple (*Acer spicatum*), Labrador tea (*Ledum groenlandicum*), and pin cherry (*Prunus pennsylvanicus*); mature spruce-fir—black spruce and balsam fir, with an alder, Labrador tea and blueberry (*Vaccinium* spp.) understory on a deep carpet of mosses; and spruce-lichen woodland—interpersed black spruce, with clumps of blueberries, Labrador tea, sheep laurel (*Kalmia angustifolia*), and dwarf birch

TABLE 1.—*Variables used to quantify microhabitat across five forest habitats in the Kananaskis Valley of Alberta. Other forest variables measured included tree and shrub diversity and biomass, but they and their transformations failed to meet the statistical criteria for inclusion in the analysis.*

Variable	Description
Q1	Amount of vegetation from 0 to 0.25 meters
SUMQ	Total vegetation below 1.75 meters
AP1	Arcsin proportion of vegetation from 0 to 0.25 meters
VERT	Vertical vegetation density from 1.75 meters
DVERT	Vertical density diversity
LMAT	Log_{10} mat depth
CMAT	Coefficient of variation of LMAT
CDIV	Diversity of cover types
DEBRIS	Square root of logs, fallen trees, and other debris within 3 meters

(*Betula* sp.) on a rich lichen tapestry (*Cladonia rangiferina*). Complete descriptions of the Kananaskis habitats can be found in Morris (1984*a*).

Red-backed voles occurred with variable densities in all habitats, and their abundances were estimated as the number of different individuals captured per subplot. In Alberta, microhabitat was quantified at every station. Arithmetic means of each variable were calculated over all nine stations per subplot (Table 1). In Labrador, microhabitat variables were recorded only at the central stations of each hexagon (Table 2). Microhabitat data complexity was reduced by principal axis factoring (PAF method, SPSS[x]) with varimax rotation. The generated microhabitat factors and appropriate dummy variables representing alternate habitats and replicates were entered as independent variables into a stepwise regression (STEPWISE method, SPSS[x]) predicting *Clethrionomys* density. In both locations, the dummy variables for macrohabitat were contrasted against the standard of mature coniferous forest.

RESULTS

Three microhabitat factors explained 77.8 percent of the estimated microhabitat variation in the Kananaskis Valley (Table 3). All of these factors described various components of understory and forest floor physiognomy and composition. Forest and shrub structure also could be viewed as suitable components of microhabitat, but variables representing tree and shrub biomass, density and diversity did not meet data screening requirements of the factor analysis. Nevertheless, for forest-floor rodents like *Clethrionomys*, the three factors are likely good estimates of microhabitat variation experienced by these animals.

In Labrador, four factors explained 78.7 percent of the estimated microhabitat variation (Table 4). Two of these were related to understory and forest floor characteristics, one to "shrub density" and the other to "tree-shrub structure". Again, the microhabitat factors should provide good estimates of microhabitat variation experienced by *Clethrionomys*.

TABLE 2.—*Variables used to quantify microhabitat in three forest habitats along the Goose and Churchill River valleys of Labrador.*

Variable	Description
MAT	Mean of four estimates of mat depth
VERT	Mean of four estimates of vertical density
DVERT	Vertical density diversity
HEIGHT	Understory height
CDIV	Cover diversity
SQTREES	Square root number of tree species within 3 meters
SQDISTT	Square root of distance to nearest tree
LPBASAL	Log_{10} basal area of nearest trees in four quadrats
SQSHRUBS	Square root number of shrub species within 3 meters
LOGSHRUB	Log_{10} total shrub surface area within 3 meters
SQDISTS	Square root of distance to nearest shrub
ACOVER	Arcsin proportion of moss and lichen cover

In both geographic locations, stepwise multiple regression analysis revealed the dependence of *Clethrionomys* density on macrohabitat (Table 5). In Alberta, *Clethrionomys* density per subplot was significantly related to the rarity of red-backed voles in the two aspen replicates. No other single variable significantly contributed to the pattern of density variation. *Clethrionomys* density in replicate plots was marginally significant for inclusion in the overall regression equation (P = 0.09). A two-variable model containing the effects of replicate plots was significant (F = 5.21; P = 0.01), but accounted for only an additional six percent of the residual variation in population density (r = 0.469). No other variable was close to statistical significance for inclusion in the equation ($P \geq$ 0.21). Similarly, in Labrador, *Clethrionomys* density was significantly related to vole density in the mixed macrohabitats. Again, only one dummy variable and no microhabitat factors were significant ($P \geq$ 0.22 for all remaining variables).

TABLE 3.—*Varimax rotated factor loadings of microhabitat variables in the Kananskis study sites. The magnitude of the loading coefficients are used to interpret their respective microhabitat factors.*

	Factor		
Variable	Understory density	Understory and forest floor structure	Mat heterogeneity
SUMQ	.94	.14	.12
VERT	.85	.00	−.24
Q1	.81	.48	.04
DVERT	.64	.31	−.04
AP1	−.07	.96	−.08
LMAT	−.20	−.70	−.15
DEBRIS	−.01	−.55	−.48
CDIV	.34	.47	.15
CMAT	−.08	.07	.91

TABLE 4.—*Varimax rotated factor loadings of microhabitat variables in the Labrador study sites. The magnitude of the loading coefficients are used to interpret their respective microhabitat factors.*

	Factor			
Variable	Tree-shrub structure	Shrub density	Understory structure	Forest-floor structure
SQTREES	−.84	−.10	−.25	−.02
SQDISTT	.82	−.07	.07	.06
LOGSHRUB	.75	−.02	.41	.11
ACOVER	−.34	.88	−.09	−.03
SQSHRUBS	.12	.84	.06	−.13
SQDISTS	−.39	−.77	−.34	.17
VERT	.19	.07	.84	.06
DVERT	.23	.09	.80	−.07
LPBASAL	−.22	.04	−.34	.73
CDIV	.14	−.22	.19	.58
HEIGHT	.50	−.05	.41	.56
MAT	−.20	.29	.04	−.34

Discussion

The effect of habitat on local abundance of red-backed voles in two disparate geographical locations depended upon habitat scaling. In both locations, the local abundance of voles depended upon macrohabitat identity and not microhabitat preference. Morris (1987) reported similar results for the abundance of *Microtus pennsylvanicus* and *Peromyscus leucopus* in southern Ontario. Microhabitat selection consistently disappears when macrohabitat effects are included in analyses of density-dependent habitat selection (see also Morris, 1984*b*, 1985).

For temperate-zone rodents, it now appears that macrohabitat and not microhabitat is differentially selected by coexisting species. At the local scale, it is difficult to speculate on the possible importance of microhabitat structure to patterns of species coexistence. I wonder what our perception of small mammal interactions would be if early studies of "microhabitat selection" had clearly distinguished between micro- and macrohabitat effects?

The density responses to macrohabitat suggest foragers with densities that respond primarily to overall resource abundance within macrohabitats, not to local variation in resources among microhabitats (Morris, 1987). In temperate and boreal forests, macrohabitat is probably a more reliable indicator of resource abundance than is microhabitat structure (Morris, 1987). Fundamentally different patterns of habitat selection may occur in other mammal faunas where variation in resource abundance occurs at smaller scales. As an example, desert rodent habitat use and abundance responds to local and ephemeral patches of high seed production (M'Closkey, 1983). Patterns of local distribution and abundance may be

TABLE 5.—*The relationship of* Clethrionomys *density with macrohabitat. Analysis was by stepwise multiple regression of* Clethrionomys *density with microhabitat factors and macrohabitat dummy variables. Only one variable was statistically significant in each location (P < 0.05).*

ALBERTA

	Regression Summary		
Step	Variable	b	r
1	Density in aspen	−1.59	−.397
	ANOVA Table		
Source	df	Mean Square	P
Regression	1	16.28	0.011
Residual	38	2.28	

LABRADOR

	Regression Summary		
Step	Variable	b	r
1	Density in mixed forest	−2.75	−.585
	ANOVA Table		
Source	df	Mean Square	P
Regression	1	40.33	.003
Residual	22	3.52	

understood only in the context of the environment to which the organisms are exposed. I suggest that a central feature of these environmental comparisons or classifications will depend upon the spatial and temporal scaling of resources. We should be surprised only if the habitat selection and life history strategies of the organisms we study do not respond to the scaling of their environments.

Resource depletion and competition at the macrohabitat level is unlikely to lead to the typical scenario of ecological segregation by microhabitat divergence, but would instead result in reduced population density. This may explain anomalies in competition studies on northern small mammals. Species removal and introduction experiments frequently have shown a depressive effect on population density by putative competitors (Koplin and Hoffmann, 1968; Crowell and Pimm, 1976; Redfield *et al.*, 1977), whereas carefully investigated patterns of spatial overlap do not (Morris, 1983; Wolff and Dueser, 1986). Even slight differences in diet and foraging could allow the coexistence of macrohabitat "selectors" with densities that fluctuate primarily in response to overall resource or microhabitat abundance. Among macrohabitats, they may exhibit complementary densities in response to resource differences among those habitats. Alternatively, their densities could be positively or neutrally correlated with one another depending upon the availability of covarying resources in specified macrohabitats. In this latter case, correlation analysis of their joint densities across suitable macrohabitats would indicate no competition because both are determined by overall habitat quality. But removal of one or the other species could reveal interaction as the density of the remaining species

responded to the overall increase in resources, or to the artificial increase in jointly consumed resources. Coarse-grained foraging with overall resource depletion also may account for my failure to capture *Peromyscus* in the relatively unproductive forests of Labrador, despite the co-occurrence of *Peromyscus* and *Clethrionomys* throughout most of the geographic range of red-backed voles. In resource poor environments, *Clethrionomys* simply may deplete resources below that which can sustain both species.

As ecologists begin to abandon purely deterministic models of species coexistence, the effects of spatial and temporal scales on our perception of ecological events, and the influence of scaling patterns on ecological communities, must be addressed. One way to do that would seem to be to acknowledge the influence of scale on our observations, decide upon which scale we are going to ask questions, work at that scale, and leave it at that. If only nature were so simple. Ecological processes have a profound influence on local and regional biogeography and evolution. These ecological interactions are as much a pawn to past evolutionary and geographical events as is our perception of them. All spatial and temporal scales interact in complex ways to feed back onto each other. The fundamental question is not how our perception of ecological processes is limited by the scale of our inquiry, but is, instead, how do biological organisms perceive and respond to the temporal and spatial scaling of their environment? One of the big challenges facing evolutionary biology is to describe that complex mapping.

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THE LONG-TERM EFFECTS OF HABITAT MODIFICATION ON A DESERT RODENT COMMUNITY

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Abstract.—Data are presented from the results of a 14-year study of changes in composition of a desert rodent community following habitat perturbation. We studied rodent populations in an area where herbicide treatment reduced shrub cover from 16.7 percent to less than one percent and increased grass cover from 1.3 percent to 22.3 percent. In the first two years following the perturbation, *Dipodomys ordii* was the most abundant rodent in the grass habitat, whereas *D. merriami* remained the most abundant species in the shrub habitat. From 1976 through 1984, the rodent community in both areas was dominated by *D. merriami* and *D. ordii* was absent or occurred at low densities in both habitats. Species richness was highest in 1976 and 1985 following successive "wet" seasons. In 1985, following three above average wet seasons, *D. ordii* once again became the most abundant rodent in the grass habitat. *Neotoma micropus* increased in abundance with increased grass cover. These results suggest interspecific competition between *D. ordii* and *D. merriami* during average to dry periods of limited resources. Successive wet seasons allow *D. ordii*, which has higher fecundity, to increase because resources are not limiting during such periods. Successive wet seasons result in increased species richness due to immigration of opportunistic species like *Sigmodon hispidus* and *Reithrodontomys megalotis*.

Numerous studies of rodent communities have emphasized the relationships between characteristics of vegetation such as species composition, percent cover, and foliage height and the diversities, densities, and species compositions of the rodent assemblages (Allred and Beck, 1963; Rosenzweig and Winakur, 1969; Brown, 1973; Hallett, 1982). Several studies have utilized field manipulations of the habitat to examine responses of rodent species composition to marked habitat modification (Rosenzweig, 1973; Price, 1978; Holbrook, 1979; Parmenter and MacMahon, 1983). Such studies of habitat use characteristically are conducted for less than one year to as long as three years. They provide documentation of the changes in rodent communities resulting from the change in vegetation architecture, microclimate, or food but provide no data on the stability of the resultant rodent community nor insights into which parameters are the most important in structuring the assemblage.

As part of the US/IBP Desert biome studies, we studied changes in vegetation and rodent communities resulting from the habitat modification of shrub removal by herbicide treatment. The rapid increase in grass cover and initial changes in the rodent community were reported in Whitford *et al.* (1978). We continued to sample the treated area and an adjacent untreated shrub habitat from the end of that program in 1974 to the present in order to study the stability of the differences in rodent community structure through time. Data were not collected in 1978, 1982, and 1983. If differences in structure of the rodent communities on the herbicide treated

and untreated areas were the result of vegetation architectural differences, then the species rankings should remain relatively constant through time providing the vegetation structure remained relatively constant.

STUDY AREA AND CLIMATE

The study site was an 18-hectare area approximately five kilometers east of the Desert Biome Jornada Site, which is 40 km. NNE Las Cruces, Dona Ana County, New Mexico. The site is part of the drainage of the watershed on which the Jornada Site is located (Whitford, 1976). The study site was located at the lower end of the alluvial fan of the Dona Ana Mountains. Soils were sandy loam alluvia, and supported a Chihuahuan desert shrub community. The soil composition was as follows: stones greater than two millimeters in diameter made up 16 percent of the weight; the remaining soil fraction was 63 percent sand, 16 percent silt, and 21 percent clay by volume. Soils were the same on the treated and untreated areas.

The 75-year average annual rainfall for this area is 211 millimeters (Houghton, 1972) with most of that rainfall occurring in late summer convectional storms. Summer maximum air temperatures regularly reach 38° to 40°C. Temperatures below freezing are recorded between October and April.

Data from the pretreatment census of rodents on the area that was subjected to herbicide treatment and the adjacent area used a control showed no differences between the areas (Whitford *et al.*, 1978). Although we used only one grid per area, we are confident that the data represent responses of the mammal communities to the habitat changes and climatic conditions of the period of studies. Before the area was divided into a control and treatment sprayed with herbicide, it was a shrub desert with a total shrub cover of 16.7 percent. Creosotebush, *Larrea tridentata*, accounted for 57 percent of the shrub cover (Whitford *et al.*, 1978). Nine hectares were treated with the herbicide dicamba applied at the rate of 2.5 kg. $\cdot$ ha^{-1} in September 1971 and September 1972. The herbicide killed most of the woody shrubs (Fig. 1). Within two years of the herbicide application, grass cover had increased from 1.3 percent to 8.6 percent primarily due to the increased diameters of pretreatment clumps of *Mullenbergia porteri* and *Hilaria mutica*. Between 1975 and 1984, grass cover increased to 22.3 percent and shrub cover to 1.8 percent. From 1975 to the present, there has been little recovery of shrubs on the treated area but the grass cover has increased to more than 16 percent (Fig. 1). In 1975, the trapping grid on the shrub habitat had a total vegetative cover of 14.1 percent: 10.4 percent shrub cover and 3.7 percent grass cover. In 1984 and 1985, the shrub habitat grid had 10.4 percent shrub cover and 4.6 percent grass cover. Snakeweed, *Xanthocephalum* sp., accounted for only 0.6 percent of the vegetative cover in the shrub habitat throughout the study period.
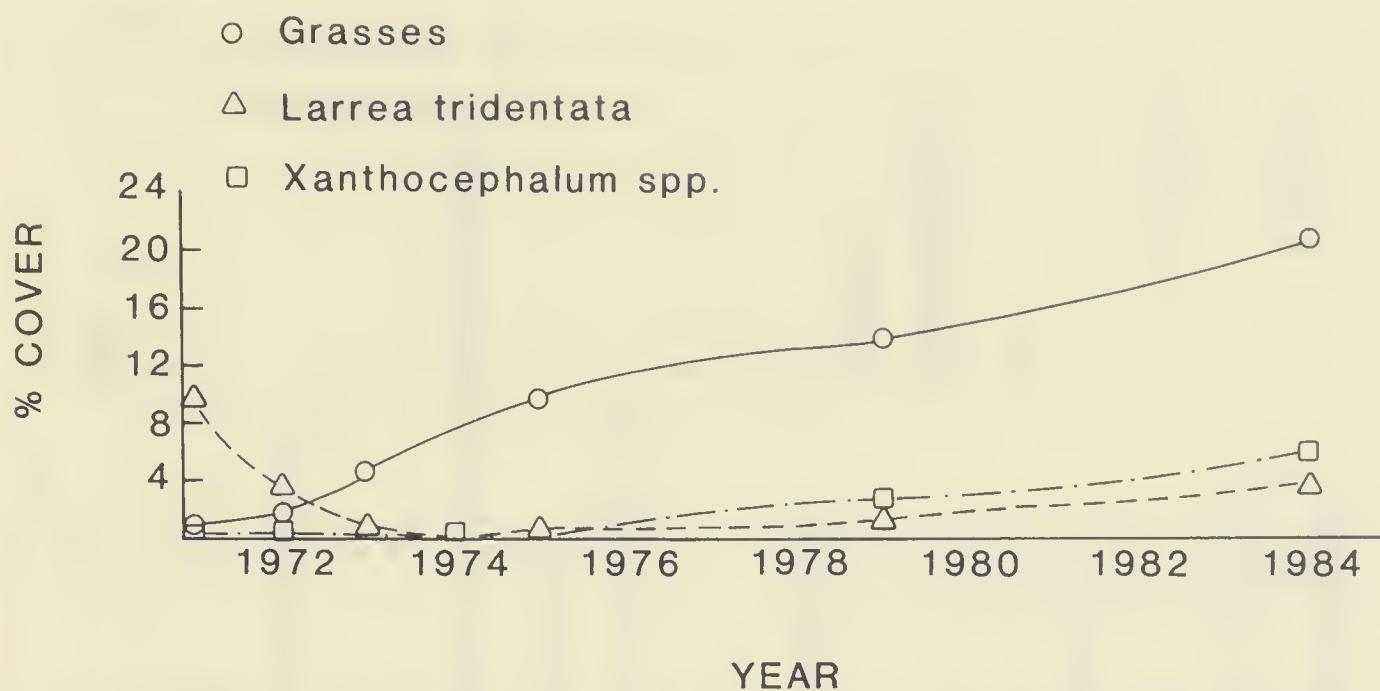
FIG. 1.—Changes in percent cover of grasses and shrubs; recovery of the shrub *Larrea tridentata*, and increases in grass and snakeweed, *Xanthocephalum* sp. on the study area treated with the herbicide dicamba (to kill woody perennials) in 1971 and 1972.

METHODS

Rodents were sampled over four consecutive nights in mid-summer or early autumn. The grass and shrub habitats were trapped simultaneously. Sherman live-traps baited with cracked milo or mixed seeds were set on grids of 100 by 100 meters, 100 stations, 10 meters trap spacing. On several sampling dates in 1975, we used assessment lines to obtain data on the effective grid size for use in density computations. The trapping grid for the herbicide-treated grass habitat was placed in the center of that area. The shrub habitat grid was placed 50 meters east of the herbicide-treated area. Traps were checked at dawn; trapped animals were marked by toe clipping and released. Population densities were estimated by the Lincoln Index. When insufficient numbers of marked animals were captured to provide an accurate Lincoln Index estimate, the total number of different individuals captured over the four-night period was used as the estimate of the population density.

Vegetation cover was estimated by running a series of line intercepts down the trap lines in both the grass habitat and shrub habitat sites.

RESULTS

In the years immediately following the herbicide treatment, the rodent community structure changed with *Dipodomys ordii* replacing *D. merriami* as the most abundant large heteromyid on the area that had increased grass cover and decreased shrub cover (Fig. 2). However, within four years after herbicide treatment, the *merriami* to *ordii* ratio was 2:1 in the grass habitat as compared with a 5:1 *merriami* to *ordii* ratio on the shrub area (untreated
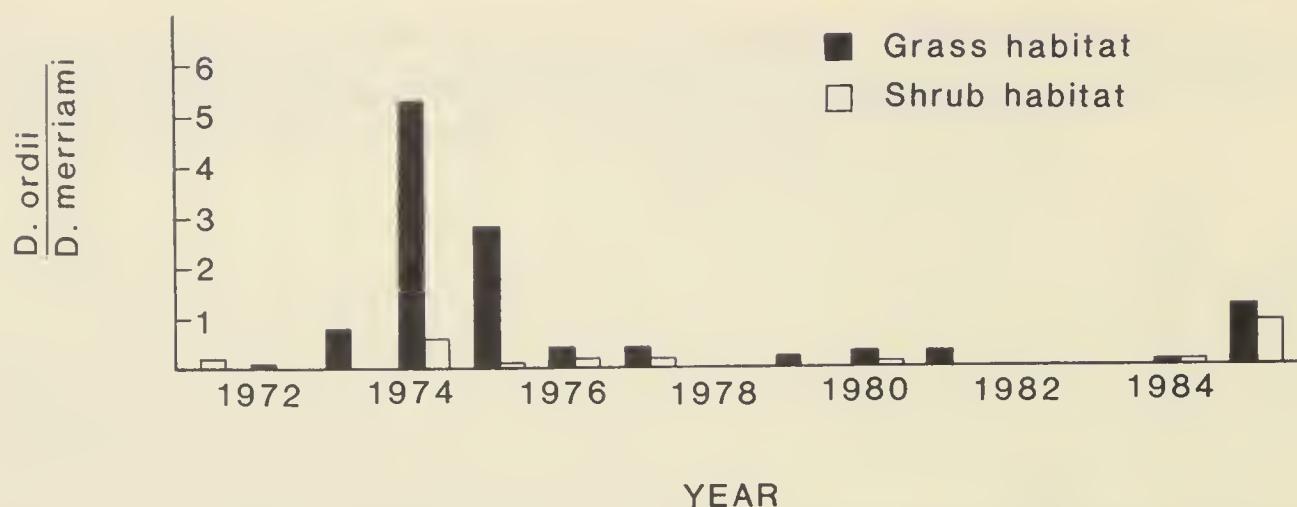
Fig. 2.—Variation in the ratio of *D. ordii*, *D. merriami* densities in a herbicide-induced grass habitat and adjacent shrub habitat.

control) (Fig. 2). By 1979, the *merriami* to *ordii* ratio had changed to 4:1 on the grass area and in 1980 was 4:1 for the grass habitat and 9:1 for the shrub habitat. Thus during the years 1976 to 1984, *D. merriami* was more abundant than *D. ordii* in both the grass and shrub habitats (Fig. 2). Densities of desert rodents were extremely low in 1984, not only on the study area but also on other areas in the vicinity. In July-August 1985, the ratio of *ordii* to *merriami* was greater than 1.0 in the grass habitat and 0.8 in the shrub habitat (Fig. 2).

Rainfall during the study was separated by season, that is, predictable rain season (July-October), season of variable precipitation and below freezing temperatures (November-March), and dry hot season (April-June). The first shift in *ordii* to *merriami* followed three years of above-average summer or winter precipitation, or both, that resulted in exceptionally high herbaceous plant production (Fig. 3). The years between 1975 and 1984-85 generally were characterized by occasional above average wet seasons preceded and followed by dry seasons. In 1984-85, there were three consecutive above average wet seasons (Fig. 3) that were followed by a second shift in *ordii* to *merriami* ratios (Fig. 2) and increased rodent density and species richness (Table 1).

Total rodent densities were exceptionally high in 1976, then dropped to 29 · hectare^{-1} in the grass habitat and 17 · hectare^{-1} in the shrub habitat in 1977; moderate population levels, ranging from 33 · hectare^{-1} to as low as 7.1 · hectare^{-1} in the shrub habitat in 1979 (Table 1) occurred during the remainder of the study. Species richness was highest in 1976 and 1985 with seven and eight species, respectively, in the communities during those years (Table 1). There has been an increase in *Neotoma micropus* in the grass habitat and variable but low numbers of *N. micropus* or *N. albigula* in the shrub habitat. In 1985, there was a newly established mound of *D. spectabilis* at one edge of the trapping grid in the grass habitat (Table 1).
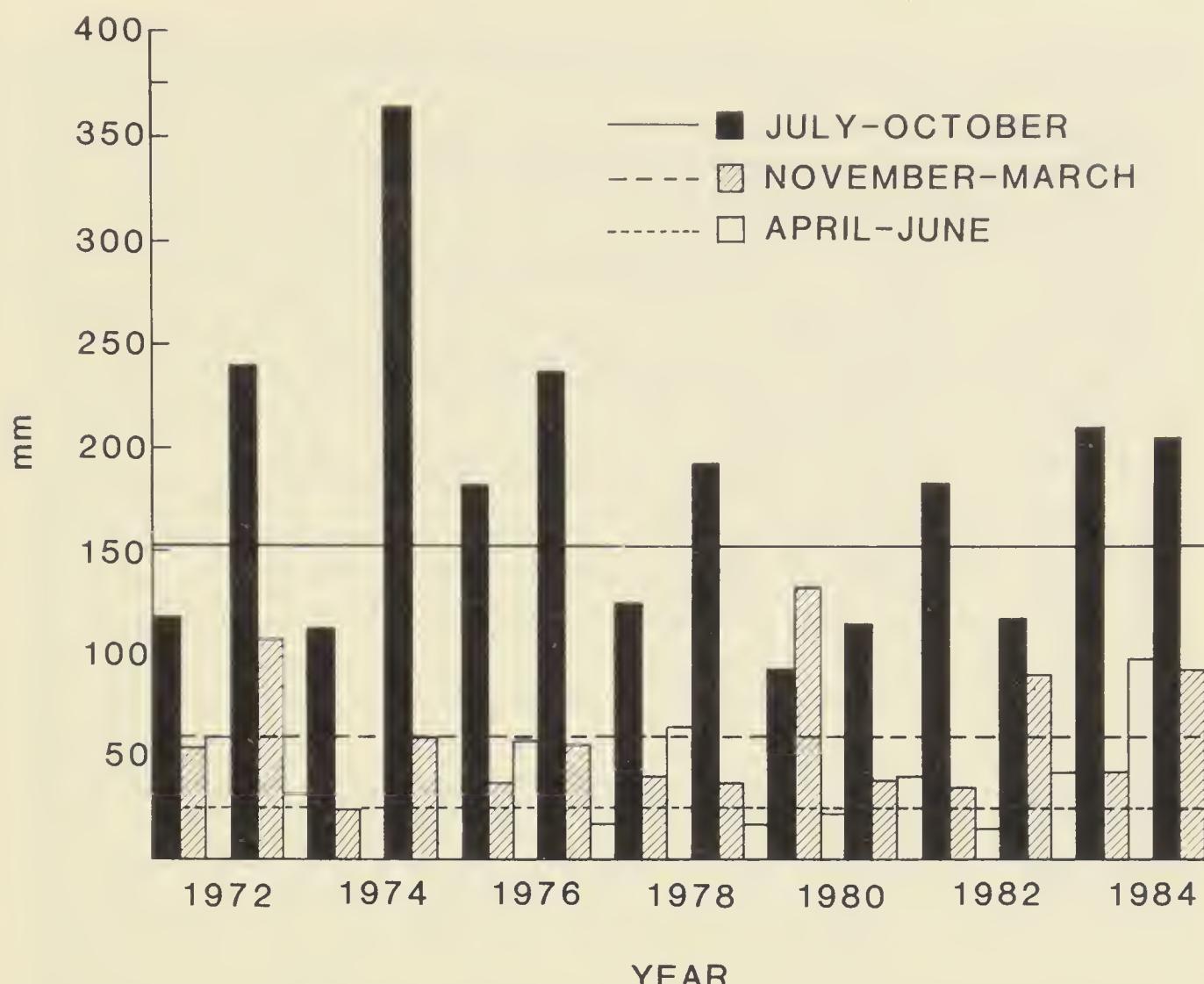
FIG. 3.—Total rainfall by season at recording stations within 10 kilometers of the study site from 1971 through March 1985. Horizontal lines indicate the long-term average precipitation for the rainfall seasons.

DISCUSSION

It was fortuitous that in the 10 years since we reported a replacement of *D. merriami* by *D. ordii* as the most numerous rodent in this community that favorable climatic conditions produced a repeat of this condition. The complete absence of *D. ordii* from the control plot during some years and the continued presence of this species in the grassier habitat supports contentions that *D. ordii* is found in grassier habitats (Shroder and Rosenzweig, 1975). Apparently, when the more typical northern Chihuahuan desert climate prevails, *D. ordii* continues to occur at low densities in the grassland habitat. The climatic conditions that allowed for large increases in *D. ordii* populations in the general area apparently included successive wet seasons and a good crop of winter annuals in the spring preceeding the "boom" or exceptionally wet summer and early autumn.

These data provide some insights into the potential competition between *D. merriami* and *D. ordii*. Schroder and Rosenzweig (1975) used a removal experiment to assess competition between these species and concluded that the interspecific alpha was zero. They cautioned this should not be

TABLE 1.—*Estimated densities of desert rodents (number · hectare⁻¹) on a herbicide treated, desert grassland, shrub removal site (T) and an adjacent untreated shrubland site (C) on sampling dates from October 1976 through July 1985.*

	1976		1977		1979		1980		1981		1984		1985	
	T	C	T	C	T	C	T	C	T	C	T	C	T	C
Dipodomys merriami	46.2	18.9	17.1	12.4	7.6	5.9	8.8	11.8	18.3	18.3	10.7	9.5	7.6	10.1
Dipodomys ordii	20.1	4.7	7.7	2.4	1.8	0.0	2.4	0.6	5.3	0.0	1.2	1.2	9.5	8.9
Perognathus flavus	5.9	0.6	0.0	0.6	0.6	0.0	0.0	1.2	1.2	1.2	0.0	1.8	0.6	3.6
Peromyscus maniculatus	0.6	0.6	0.0	0.0	0.0	0.6	0.6	1.2	1.8	2.9	0.0	2.4	2.4	5.3
Neotoma albigula	0.0	0.6	0.0	0.6	0.6	0.6	0.0	0.6	0.0	0.6	0.0	1.2	0.0	0.6
Neotoma micropus	1.2	0.0	1.2	0.0	0.6	0.0	0.6	0.0	0.6	0.6	1.2	0.6	5.3	1.2
Onychomys arenicola	4.7	0.6	3.0	0.6	0.6	0.0	0.0	0.6	0.0	2.4	0.0	0.6	2.4	3.0
Sigmodon hispidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6
Reithrodontomys megalotis	1.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dipodomys spectabilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0
Total density	80.5	26.6	29.0	16.6	11.2	7.1	12.4	16.0	27.2	25.4	13.1	17.3	29.6	33.3
Number of species	7	7	4	5	5	3	4	6	5	6	3	7	8	8

interpreted that interspecific competition is unimportant in the system and suggested that were it not for the continual threat of interspecific competition, the habitat specializations would soon disappear. These authors conducted their studies during above average wet years (1972-1973), which resulted in changes in the distribution of *D. ordii*. Considering the Shroder-Rosenzweig studies and our 10-year data set, it is plausible that the results of their removal experiments might have been different in average or dry years. Our 14-year data set (including data in Whitford *et al.*, 1978) is consistent with the arguments of Wiens (1977) that competition between co-existing species may occur primarily under conditions of resource limitation and that competition may be diluted (or nonexistent) during periods of resource abundance. During the more than 10 years of sampling in this study, *D. ordii* was more numerous in the grassier habitat only after more than one year of above-average rainfall and exceptionally high productivity, especially of the annual buckwheats, *Eriogonum* sp. (Whitford 1972, 1973, 1974, and unpublished data from the Jornada LTER Project). If grassier habitats are especially favorable to *D. ordii*, then that species should have maintained population densities close to those of *D. merriami* in that habitat during the intervening average-to-dry series of years. The marked decrease in *D. ordii* during that period suggests that *D. merriami* is behaviorally and physiologically superior to *D. ordii* and is proably out-competing *D. ordii* during the "crunch" years. However, even given that competition, *D. ordii* apparently does better in the grassier habitat than in the desert shrub habitat.

The changes in relative abundance of *D. ordii* and *D. merriami* may be examined with respect to the threshold hypothesis of Conley *et al.* (1977) (Fig. 4A). Conley *et al.* (1977) argued that fluctuations in small mammal populations are not simply a function of climatic variability but rather the result of climatic fluctuations that fall below some threshold level needed to produce the minimum resources for that species. Their graphical model presents a single threshold for a species population and does not account for habitat as a modifier of the climatic effect. The threshold level of resources for a species must be considered as the minimum value for all of the resources of the species niche. Climatic conditions that fail to produce that minimum set of resources result in reduced natality and survivorship. In our modification of the threshold hypothesis, we indicate how habitat can affect resources with respect to the thresholds of the species (Fig. 4B). In this graphical model, the climate threshold for *D. ordii* would be higher in shrub habitat and that of *D. merriami* would be higher in the grass habitat. Variation in climate affects resources such as burrows or den sites, distribution and abundance of seeds, phenology and productivity of herbaceous plants, shrubs, and grasses, and so on. The effect that variation in climate has on resources varies with habitat because vegetative structure, slope, and soil affect water infiltration, run-off, soil water storage, water extraction, nutrient distribution, seed distribution patterns, and seed species
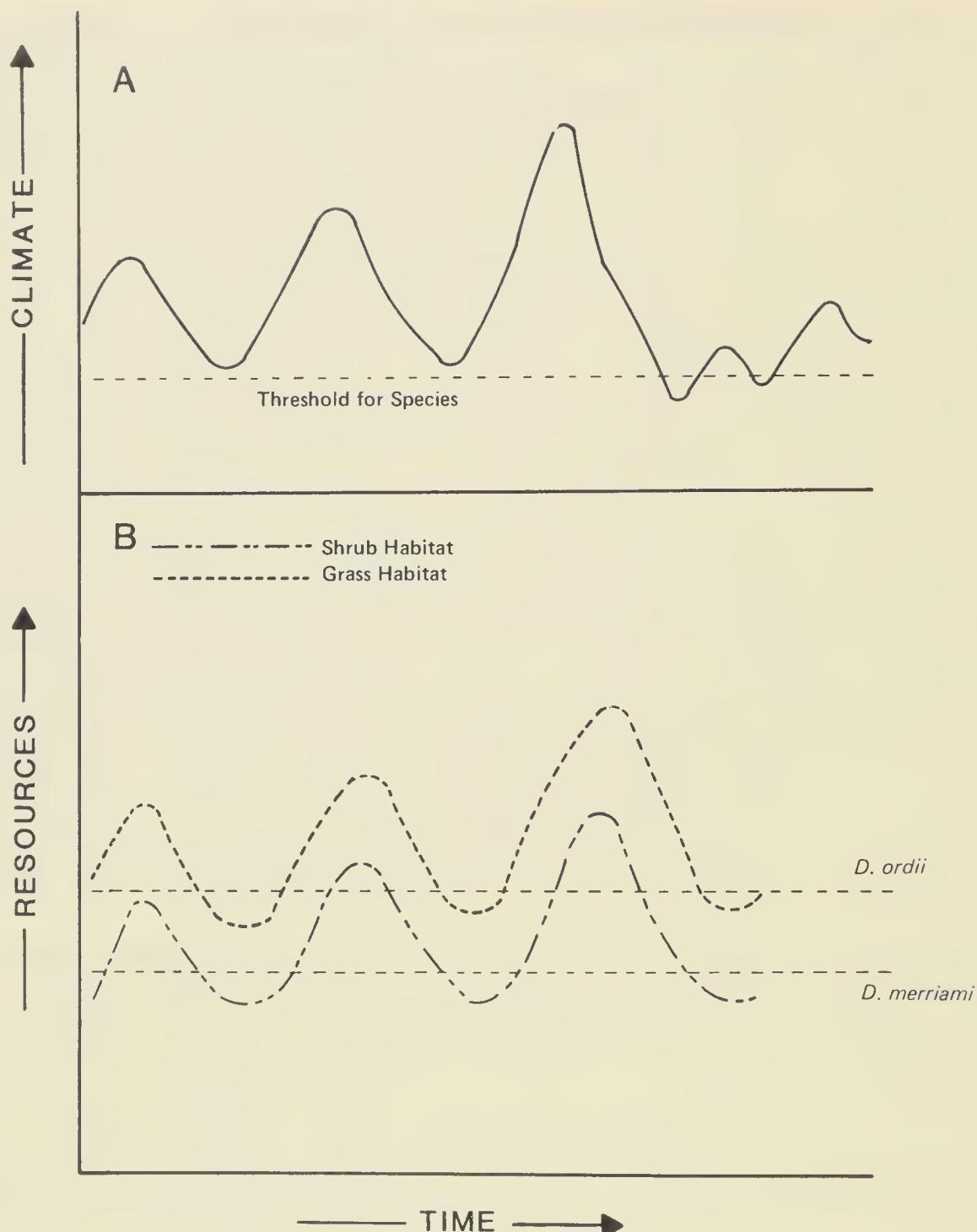
FIG. 4.—The threshold hypothesis of Conley *et al.* (1977) presented in A is compared with the variation in resources in two habitats (B) produced by the climatic fluctuation presented in A. Physiological and behavioral differences of *D. ordii* and *D. merriami* affect the minimum resource threshold for each species.

as examples of resources that are important to desert rodent species. Considering climate-resource thresholds for species and the effects that habitat can have on those resources should help us to make predictions about the structure of rodent communities through time, especially with respect to species that are potential competitors.

Applying that model to the 10-year data set from the Jornada Site provides some useful insights into the changes in rodent community structure in these habitats. If the resource threshold necessary for physiological-behavioral characteristics of *D. ordii* is higher than that of *D.*

merriami, then *D. ordii* will maintain low populations in favorable habitats and drop to zero in less favorable habitats. Under especially favorable conditions, population responses of both species will be a function of natality and survivorship. *D. ordii* has a larger mean litter size (3.16 per female) and larger range in litter size (one to six young per female) than does *D. merriami* (2.49; one to five young per female) (Conley *et al.*, 1977). Whitford (1976) reported that a portion of the females of *D. merriami* were receptive, pregnant, or lactating from February through September with less than 10 percent in reproductive condition in July through September, whereas *D. ordii* exhibited two distinct reproductive periods in May and September. Together these data suggest that under favorable conditions the natality of *D. ordii* is greater than that of *D. merriami*. If several consecutive seasons of above-average wet conditions result in greater natality of *D. ordii*, then several consecutive seasons of dry conditions would result in lower survivorship in comparison to *D. merriami* according to the threshold hypothesis. The physiological-behavior attributes of *D. merriami* that make the climate-resource threshold for that species lower than that of *D. ordii* probably gives *D. merriami* the competitive edge during relatively dry periods. The lower resource threshold of *D. merriami* should allow it to utilize scarce resources, thus further reducing the availability of common resources to *D. ordii*. The reduced availability of resources resulting from climate and competition would reduce both natality and survivorship of *D. ordii*. These relationships are consistent with the long-term data set reported here. Confirmation will require experimental studies of natality and survivorship in these habitats.

These data provide additional evidence for "resident" and "immigrant" or opportunistic species in desert rodent communities. Temporal variation in climate had some effect on population densities of *D. merriami*, *Onychomys arenicola*, *Neotoma* sp., and *Perognathus flavus*, which can be considered permanent or "resident" components of these rodent communities. *Sigmodon hispidus*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus* are occasional or opportunistic members of the community. *D. spectabilis* appears recently to have established dens in the grass habitat and may become a "resident" in that habitat. Consecutive above-average wet seasons or extremely wet summers apparently result in marked increases in certain species of this desert rodent community—*D. ordii*, *Perognathus flavus*, *Peromyscus maniculatus*. Such conditions also facilitate the spread of opportunistic species such as *S. hispidus* and *R. megalotis* into marginal habitats from habitat refugia. (Whitford, 1976).

One species that seemed to be favored by the increase in grass cover was the woodrat, *Neotoma micropus*. Wright (1973) studied the habitat distributions of *Neotoma* species in southern New Mexico and reported that *Neotoma* was not found in *Larrea tridentata* shrub habitats. Whitford (1976) reported *Neotoma* sp. in *L. tridentata* shrub lands associated with small drainages where the rats utilized *Yucca baccata* clumps as den sites. There

was no measurable change in *Yucca* sp. densities in the grass habitat during this study but the increased size of clumps of *Muhlenbergia porteri* around the *Y. baccata* seems to have made these clumps suitable den sites. By 1985, virtually every *Y. baccata* clump in the grass habitat hosted a woodrat den. In the shrub habitat, few of the *Y. baccata* clumps had woodrat dens. Brown *et al.* (1972) suggested that the capacity of a habitat to support woodrats depends upon the extent to which it affords them protection from predators. Dense clumps of *M. porteri* may indeed serve such a function in the man-induced grassland habitat.

This desert rodent community differs from that of other nearby desert rodent assemblages in that two relatively common species, *Perognathus penicillatus* and *Peromyscus eremicus*, never have been taken in this area. These are common species in similar habitats within 10 kilometers of this study site (Whitford, 1976). The absence of an intermediate size heteromyid (*P. penicillatus*) and relatively abundant congeners of virtually the same body size (*D. merriami* and *D. ordii*), makes this assemblage of heteromyids deviate from that predicted by Brown (1975) and discussed by Bowers and Brown (1982). Bowers and Brown (1982) did not include Chihuahuan desert sites in their analysis because there were insufficient localities for independent statistical analysis. Therefore, we cannot be certain that the conclusions of Bowers and Brown (1982) apply to Chihuahuan desert rodent communities. *P. penicillatus* occurs in similar habitats in other areas on the same watershed. Why should *P. penicillatus* not occur in this community? We can only speculate that some combination of habitat features and competition are responsible.

This study demonstrates the value of long-term data sets to obtain insights into community dynamics of rodents. The results of these long-term studies indicate the necessity for caution in assuming habitat specialization as the primary means of competition avoidance by rodents. Long-term studies also suggest important questions and study designs that account for the vagaries of climate. It is likely that some of the controversies and inconsistencies in results of rodent community studies may be resolved only by such long-term studies.

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POPULATION PARAMETERS, SPATIAL DIVISION, AND NICHE BREADTH IN TWO *APODEMUS* SPECIES SHARING A WOODLAND HABITAT

W. I. Montgomery

Abstract.—*Apodemus sylvaticus* and *A. flavicollis* are found together in certain areas of woodland in southern Britain. Spatial division occurred consistently but varied in its extent from barely detectable to almost complete. Many places were used by both species. This paper examines the intra- and interspecific effects of population size and structure on spatial separation. Spatial division was measured using correlation analysis. Multiple regression analyses suggested that spatial division was related to population characteristics, particularly those incorporating both species. However, at least 50 percent of the total variation in the spatial separation of *A. sylvaticus* and *A. flavicollis* was unexplained by models incorporating population characteristics. Further evidence of the role of interspecific interference in maintaining spatial division was apparent in the dynamics of spatial niche breadth of *A. sylvaticus* around or below average population densities. Spatial niche breadth of *A. sylvaticus*, the supposed poorer competitor, increased with increasing number of conspecifics but decreased with increasing numbers of supposed dominant, *A. flavicollis*. It was concluded that habitat division was maintained in part through competitive interactions and in part by other processes such as species differences in early experience and foraging behavior.

Many studies have demonstrated that where rodents occupy the same habitat, such as grassland or woodland, each species is associated with particular structural subdivisions of that habitat (see, for example, Brown, 1975; Myllymaki, 1977; Holbrook, 1978; Dueser and Shugart, 1979; Emmons, 1980; M'Closkey, 1981; Murua and Gonzalez, 1982; Morris, 1984. The basis of this division of space is viewed traditionally as the expression of past or current competitive interactions between species; among rodents, behavioral interactions or interference and possibly exploitative competition for food may be important (Grant, 1972, 1978). Evidence supporting this explanation of community structure is mostly circumstantial drawing on comparisons of abundance and distribution patterns of species in isolation from, or in close association with, supposed competitors. Limited direct evidence from experimental manipulation of rodent populations within and across habitats broadly supports the assertion that competition has occurred or is in progress (see Connell, 1983, and Schoener, 1983, for conflicting interpretations of experimental studies).

In recent years, however, the hypothesis that interspecific competition is an important determinant of community structure has been challenged with growing evidence from studies of herbivorous insect communities, where interspecific competition seems rare and community structure is better approached from an appreciation of adaptations of species to heterogeneous environments or the influence of predators (Lawton and Strong, 1981; Strong, 1983). In this context, division of space in rodent communities may,

for example, reflect differences in diet and foraging behavior or experience (see, for example, Kotler, 1984 and Price, 1984). Indeed, Morris (1984) suggested that marked differences in diet, morphology, behavior, frequent macrohabitat selection, inconsistent microhabitat selection, and lack of evidence of competitive interference indicate that spatial separation in communities of temperate-zone small mammals is unlikely to be maintained by species interactions.

The present report examines these alternative interpretations of spatial division in communities consisting of two *Apodemus* species. This is achieved through an examination of how use of space and spatial separation change with density, age structure and reproduction. The initial analysis involves linear stepwise multiple regression. Similar analyses have been carried out by Glass and Slade (1980) on *Sigmodon* and *Microtus*. In a competitive environment, an increase in the frequency of interspecific contact facilitated by greater numbers or changes in behavior during breeding may increase spatial division between species (Terman, 1974). In habitats where spatial division is not maintained by interference, demographic features of single species should have little effect on spatial associations. A further analysis is based on recent theoretical developments emphasizing the effect of density-dependence on habitat selection (Rosenzweig, 1981; Pimm and Rosenzweig, 1981). Habitat use by any species may be influenced directly by its own population size so that selectivity is apparent only at low densities (Morisita, 1969; Fretwell, 1974). This idea has been extended to encompass interspecific competition and applied to populations of hummingbirds (Pimm *et al.*, 1985) and gerbils (Rosenzweig and Abramsky, 1986). In both cases, strong interspecific effects on habitat selectivity were revealed by an association between a shift in spatial niche dimensions and the population density of the supposed competitor species.

Materials and Methods

Apodemus *Species*

Apodemus sylvaticus and *A. flavicollis* coexist in some areas of woodland in parts of western Europe (Corbet, 1978). Dietary overlap may be up to 80 percent (Holisova and Obrtel, 1980). Studies in southern England and elsewhere suggest that intrinsic differences in population dynamics, and possibly regulation, prohibit the concomitance of high densities at times other than autumn and early winter when seeds are most readily available (Judes, 1979; Montgomery, 1980a). *A. flavicollis* is more limited in its distribution both geographically and within any stand of woodland but wherever both species are present there is a consistent negative association in their distributions as revealed by trapping (Montgomery, 1980b, 1981). Hoffmeyer (1973) and Montgomery (1978) found that *A. flavicollis* is generally dominant to *A. sylvaticus* in encounters staged in small enclosures or arenas.

Study Area

The study was carried out in mixed-deciduous woodland of Woodchester Park, a steep-sided valley in the eastern escarpment of the Cotswold Hills of southwestern England. Data from four grids, M of eight rows of 12 points at 10-meter intervals, and A, B, and C each of seven rows of seven points at 10-meter intervals, were used in the present analyses. Two single-capture Longworth traps were set at each grid point for four nights every month (A, B, and C) or five nights every other month (M). The grids were set in areas of woodland chosen for the similarity of their plant communities: the dominant species included *Acer pseudoplantanus, Allium ursinum, Corylus avellana, Fagus sylvatica, Fraxinus excelsior, Mercurialis perennis, Prunus laurocerasus, Quercus robor, Ulmus glabra* (mostly diseased or dead), *Sambucus nigra,* and dense stands of English yew, *Taxus baccata.* The two species of *Apodemus* were numerically dominant throughout the study with relatively few captures of *Clethrionomys glareolus* and shrews of the genus *Sorex.* More details of the study area and trapping methods are presented in Montgomery (1980*a,* 1981).

Measurement of Association Between Species

Results of analyses of species associations depend on sample unit size in space and time (Poole, 1974). These limitations may be purely arbitrary, dictated primarily by practical considerations and the biology of the species under study. In the present study the sample unit area was always 10 by 10 meters. Interspecific association was measured using the product-moment correlation coefficient (COR). This was calculated from the number of captures of each species at grid points where any *Apodemus* were captured during a single period of trapping (four or five nights). This approach takes cognizance of the absence of both species from many trap points. Data were transformed as $\sqrt{x + 0.5}$ where x was the number of captures per trap point.

Population Criteria and Sample Size

The following were calculated for each trapping session on each grid: density of single-species populations; proportion of males, females, and juveniles in each population; proportion of males, females, and all adults in reproductive condition; mean and variance of captures and variance-mean ratio of captures per trap point of each species. Densities were based on estimates of population size using the Lincoln Index-based method of Hayne (1949) and effective trapping area was calculated after Montgomery (1980*a*). Products of population characteristics of *A. sylvaticus* and *A. flavicollis,* namely density, percentage of males, percentage of juveniles, percentage of reproductive males, percentage of reproductive adults, and variance-mean ratio, also were calculated. Data were available for 17 trapping sessions on M, 19 on A, and 12 each on B and C making a total of 60 samples in which COR and 26 population criteria were evaluated.

Multiple Regression Analyses: Organization and Presentation of Results

The relationship between spatial overlap of *A. sylvaticus* and *A. flavicollis* and population characteristics was investigated using multiple regression analysis. The analyses were broken down into regressions of the dependent variable (COR) on small groups of independent variables (population parameters). Each group of population variables constituted a possible model predicting spatial separation of *A. sylvaticus* and *A. flavicollis*. Details of these models are presented in Table 1. Isolation of strongly correlated ($r \geq 0.9$) independent variables and stepwise procedures avoid the problems of multicollinearity in multiple regression analysis (Tabachnick and Fidell, 1983). As a precaution against nonlinear trends, independent variables were subjected to arcsin or sqrt(x + 0.5) transformation. Regression analyses were carried out using the program BMDO2R, UCLA Health Sciences Computing Facility, implemented on the ICL 1900 series computer at Queen's University of Belfast. The probability associated with the F-level for inclusion was 0.01 and deletion 0.005. Tolerance level was 0.001. Residual plots against each independent variable in the regression and the computed value of the dependent variable were used to check for departures from the assumptions underlying regression models (Draper and Smith, 1968). There was no evidence of non-normality, nonlinearity, or heteroscedasticity in these plots. Nor was there any indication that autocorrelation influenced the analyses despite the collection of data at regular intervals.

Estimation of Niche Breadth and Density-Dependent Habitat Selection

Niche breadth of the weaker competitor, *A. sylvaticus*, was investigated in relation to density of that species and density of *A. flavicollis*. These analyses were conducted on the 25 samples containing the lowest densities of *A. sylvaticus*. Inter- and intraspecific effects on use of resources may be swamped by high conspecific density. These samples were distributed evenly among the four grids: seven, eight, five, and five out of 17, 19, 12, and 12 samples on M, A, B, and C, respectively. Captures of *A. sylvaticus* were associated with dense ground cover on all grids but this species also was captured at points with little or no ground cover. (See Montgomery, 1980*b* and 1981, for details of vegetation analysis and a complete presentation of results.) Spatial niche breadth was calculated from the frequency of captures in 21 cover classes ranging from zero to 100 percent ground cover. Niche breadth was evaluated using Nei and Roychoudury's (1974) unbiased estimate of the Simpson-Yule index. Following Rosenzweig and Abramsky (1986), this was inverted giving it a meaningful interpretation as "the number of equally common categories." Plots of spatial niche breadth against population density of *A. flavicollis* and *A. sylvaticus* revealed nonlinear relationships. Statistical analyses and curve fitting was carried out using the program POLYFIT (Spain, 1982) implemented on an Apple microcomputer.

Table 1.—*Groups (models) of independent variables (population criteria) and their abbreviations entered in stepwise multiple regression analyses where the dependent variable was COR a measurement of interspecific association.*

Model	Independent variable	Abbreviation
I		
Population densities	Density of *A. sylvaticus*	SDEN
	Density of *A. flavicollis*	FDEN
II		
Population structures	% Male *A. sylvaticus*	SMAL
	% Female *A. sylvaticus*	SFAL
	% Juvenile *A. sylvaticus*	SJUV
	% Male *A. flavicollis*	FMAL
	% Female *A. flavicollis*	FFAL
	% Juvenile *A. flavicollis*	FJUV
III		
Reproductive status	% Mature *A. sylvaticus*	SMR
	% Mature *A. sylvaticus*	SFR
	% Mature adult *A. sylvaticus*	SREP
	% Mature male *A. flavicollis*	FMR
	% Mature female *A. flavicollis*	FFR
	% Mature adult *A. flavicollis*	FREP
IV		
Population dispersion	Mean captures *A. sylvaticus*	SAVC
	Variance captures *A. sylvaticus*	SVARC
	Variance/mean ratio *A. sylvaticus*	SRAT
	Mean captures *A. flavicollis*	FAVC
	Variance captures *A. flavicollis*	FVARC
	Variance/mean ratio *A. flavicollis*	FRAT
V		
Interspecific interaction	SDEN × FDEN	SFA
	SMAL × FMAL	SFB
	SJUV × FJUV	SFC
	SMR × FMR	SFD
	SREP × FREP	SFE
	SRAT × FRAT	SFF

Results

Within-Habitat Spatial Segregation of A. sylvaticus *and* A. flavicollis

The dynamics of the spatial association between *A. sylvaticus* and *A. flavicollis* on grids M, A, B, and C are illustrated in Figure 1. The negative relationship in the distributions of the populations was consistent on all grids. There was no significant heterogeneity in mean spatial association between grids ($F = 0.591$; d.f. 3,56, n.s.).

Relationship Between COR and Population Characteristics

Population densities.—Both SDEN and FDEN entered the regression model giving the equation
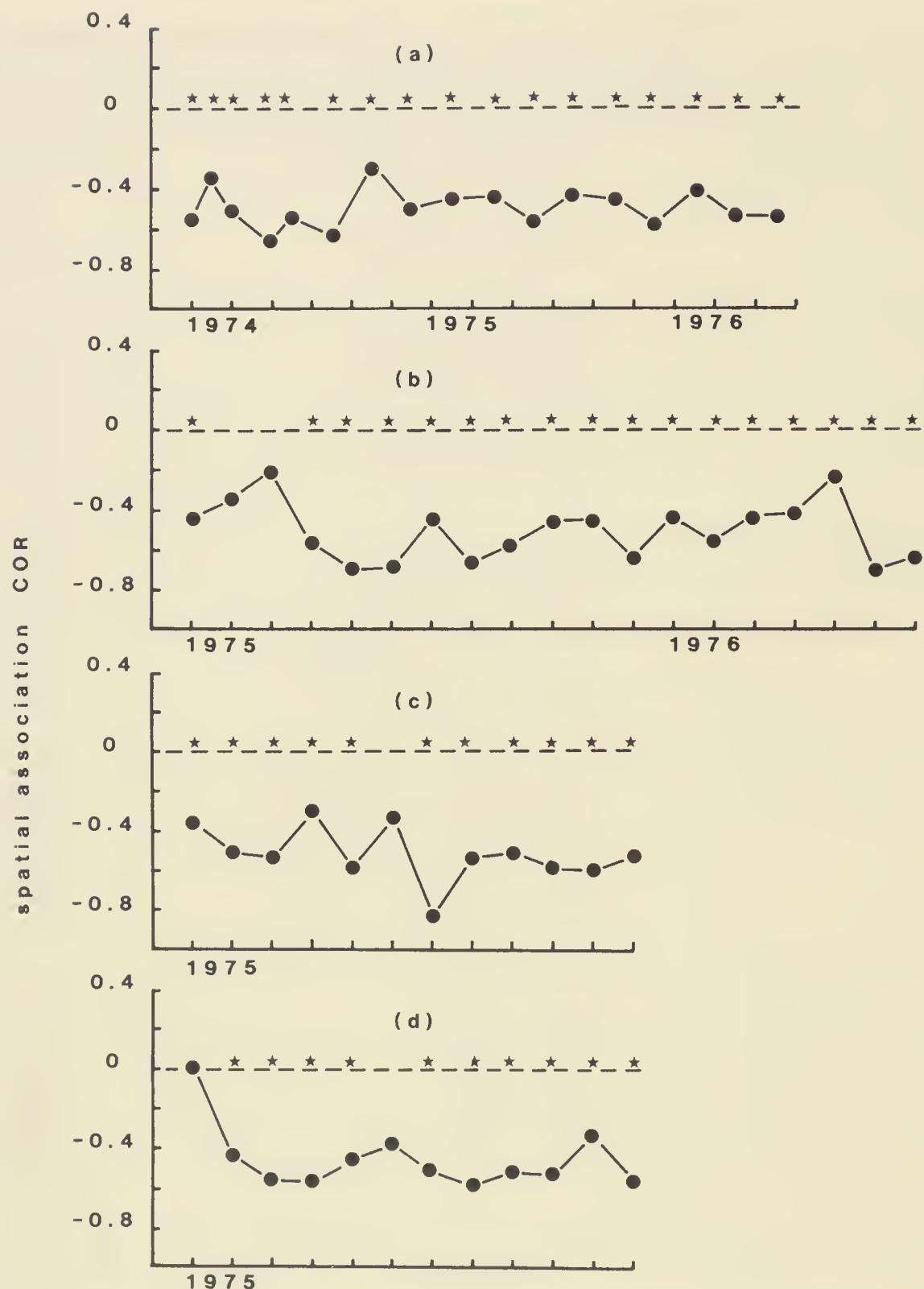
Fig. 1.—Variation in interspecific association between *A. sylvaticus* and *A. flavicollis* on grids M (a), A (b), B (c) and C (d). Solid lines indicate association measured by COR. An asterisk indicates significant departure from independence in species distribution at $P < 0.05$.

$$COR = 0.0022 \text{ SDEN} + 0.0010 \text{ FDEN} - 0.6220$$
$$(F = 4.519; \text{ d.f. } 2,57; P < 0.025).$$

The Coefficient of Determination, R^2, departed significantly from zero (F = 9.192; d.f. 1,58; $P < 0.005$) using the method described by Wesolowsky (1976). Densities of both populations were positively related to COR indicating that as population size of either species increased, spatial

separation, as measured by COR, decreased. Change in population density of *A. sylvaticus* had a greater effect on COR, accounting for 12.08 percent of the variation in the latter, than fluctuations in density of *A. flavicollis*. The addition of FDEN to the model increased the explained variation in COR by only 1.60 percent.

Population structures.—No linear model relating COR to any of the available independent variables was generated.

Reproductive status.—Again no linear model relating COR to the available independent variables was generated.

Population dispersion.—The linear model generated was

$$COR = 0.2245\ SAVC + 0.1236\ SRAT - 0.0716\ FRAT - 0.0682\ SVARC - 0.6811$$
$$(F = 4.034;\ d.f.\ 4,55;\ P < 0.01).$$

R^2 differed significantly from zero (F = 5.479; d.f. 3,56; $P < 0.005$). This four variable model accounted for 22.68 percent of the variation of COR. Increased SAVC and SRAT was associated with less interspecific spatial separation, and accounted for 11.56 percent and 5.34 percent of variation in COR respectively. Increased aggregation of *A. flavicollis* was associated with less spatial overlap between the species.

Interspecific interaction.—A three variable model for the relationship between COR and interspecific variables was obtained,

$$COR = -0.00005\ SFC + 0.00003\ SFA + 0.00001\ SFE - 0.5382$$
$$(F = 2.8163;\ d.f.\ 3,56;\ P < 0.05).$$

R^2 differed significantly from zero (F = 4.372; d.f. 2,58; $P < 0.025$) and indicated that the above model accounted for 13.3 percent of the variation in COR. An increase in the product of the proportions of juveniles in *A. sylvaticus* and *A. flavicollis* was associated with greater interspecific spatial division of the habitat. SFC accounted for 7.17 percent of the variation in COR. The product of densities, SFA, which accounted for 4.84 percent of the variation in COR, was positively related to COR so that as this value increased, spatial overlap increased.

Potential of Population Characteristics in Accounting for the Dynamics of the Negative Spatial Association of *A. sylvaticus* and *A. flavicollis*

Two further stepwise regression analyses were conducted—variation in COR was examined with respect to all single species variables (those included in Models I-IV, Table 1) and single species plus interspecific product variables (Models I-V, Table 1). These analyses involve certain statistical liberties (Wesołowsky, 1976) and detailed results will not be presented. However, the proportion of variation in the dependent variable explained by the regression, R^2 times 100, gives an indication of how good population criteria might be in predicting spatial association were more and better data available. Single species characteristics explained up to 45.09 percent of variation in COR. All population criteria, including cross product variables, explained at most 51.74 percent of variation in COR.
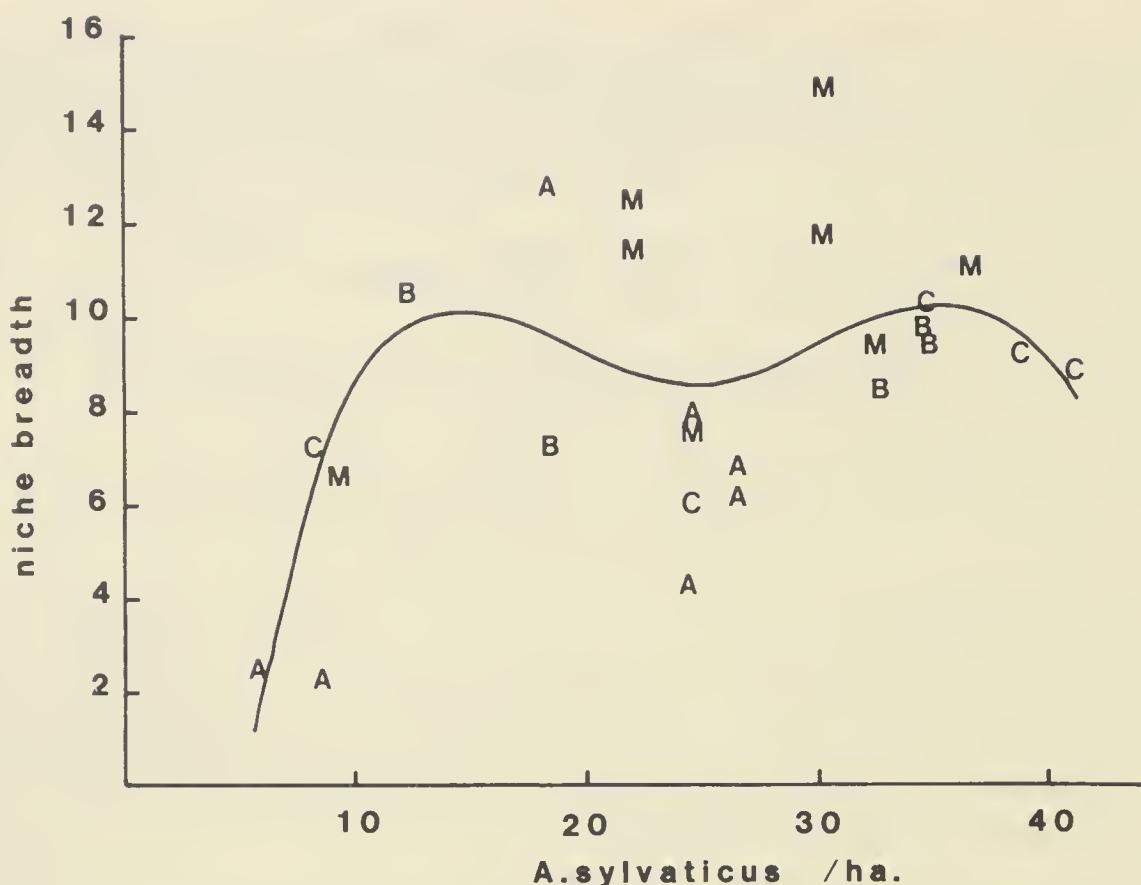
FIG. 2.—The relationship between spatial niche breadth (Nei-Roychoudury index) and population density of *A. sylvaticus* in the 25 samples with the lowest numbers of *A. sylvaticus*. Curve was fitted using the program POLYFIT giving the relationship

$$Y = -28.6 + 7.5\ X - 0.5\ X^2 + 0.01\ X^3 - 0.0001\ X^4$$
$$(F = 14.71;\ \text{d.f. } 1,19;\ P < 0.005)$$

where Y is spatial niche breadth and X is the density of *A. sylvaticus*.

Niche Breadth and Density-Dependent Habitat Selection

The relationships between spatial niche breadth of *A. sylvaticus* and population density of *A. sylvaticus* and *A. flavicollis* are illustrated in Figures 2 and 3, respectively. These data include monthly samples from each of the four grids. Although niche breadth of *A. sylvaticus* was narrower at low densities of that species, it varied erratically throughout the range of moderate population density examined (12 to 41 individuals per hectare). This suggests that *A. sylvaticus* was more selective at lower densities but there was a limit to the expansion of niche breadth as population size increased. Spatial niche breadth of *A. sylvaticus* declined with increasing densities of *A. flavicollis* over most of the range of densities of the latter species included in the analysis (4 to 46 individuals per hectare). This suggests that use of space in relatively low-density populations of *A. sylvaticus* was increasingly restricted in the presence of *A. flavicollis*. Among samples with the highest densities of *A. flavicollis* (59 to 67 individuals per hectare), however, niche breadth of *A. sylvaticus* increased. This effect may have been due to the concurrence of medium densities of *A. sylvaticus* and high densities of *A. flavicollis*.
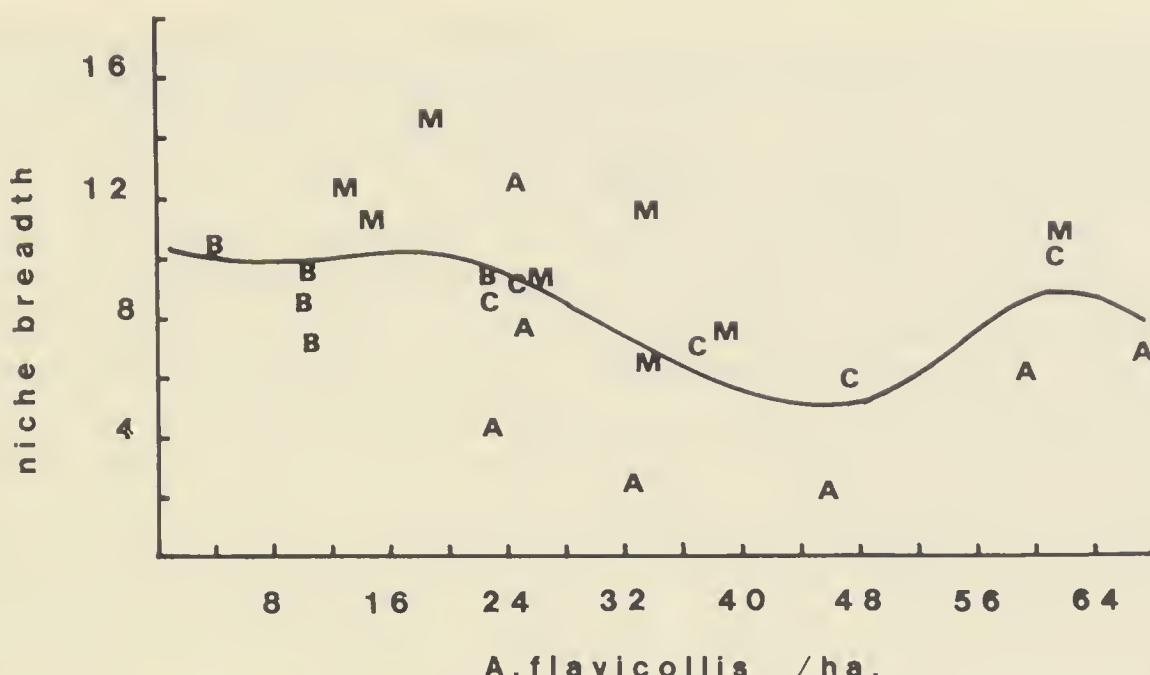
FIG. 3.—The relationship between spatial niche breadth (Nei-Roychoudury index) of *A. sylvaticus* and population density of *A. flavicollis*. Curve was fitted using the program POLYFIT giving the relationship

$$Y = 12.31 - 0.91\ X + 0.1\ X^2 - 0.005\ X^3 + 0.00008\ X^4 - 0.0001\ X^5$$
$$(F = 8.77;\ \text{d.f. } 1,19;\ P < 0.01)$$

where Y is spatial niche breadth and X is the population density of *A. flavicollis*.

Both COR and niche breadth of *A. sylvaticus* were correlated with population density of *A. sylvaticus*. Not surprisingly, therefore, there was a significant, though weak, nonlinear relationship between COR and spatial niche breadth of *A. sylvaticus* (F = 5.04; d.f. 1,19; P < 0.025). Spatial overlap was least among samples with least and greatest niche breadth.

DISCUSSION

The spatial separation of *A. sylvaticus* and *A. flavicollis* within shared habitats was consistent but quite variable (Fig. 1). The efficiency of population characteristics in predicting spatial association was limited in each of the models under test. With the exception of the relationship between COR and population dispersion where the similarity in the calculation of means, variances, and product-moment correlation coefficient may have produced a large R^2, most variation in the indices of association was explained by the interaction model incorporating several interspecific measurements of population size, reproduction, and structure. None of the models explained more than 23 percent of the variation in COR and most explained considerably less. The potential of population parameters in predicting spatial association, however, was around 40 percent for single species characteristics and 50 percent for models incorporating interspecific measurements. Glass and Slade (1980) found that between 45 and 67 percent of variation in spatial association was explained by models containing parameters related to population age structure, reproduction, or cross-product population parameters for *Sigmodon* and *Microtus*. This disparity

with the present study may originate in different methodology and analysis, or in the markedly different biology of rodent species living in old-field habitats. More information concerning the spatial and temporal dynamics of species sharing habitats is required.

Terman (1974) argued that increased "frequency of interspecific contact" in a competitive environment should increase spatial separation as numbers increase or age structure and behavior changes. This was supported by the analyses of Glass and Slade (1980). The results here are equivocal: spatial relationships between *A. sylvaticus* and *A. flavicollis* were to some extent predicted by population criteria, particularly those incorporating details of age structure and reproduction from both species. However, a substantial portion of the variation in indices of spatial overlap, 50 percent or more, was left unexplained. Although interspecific interaction may account for a component of the microhabitat separation of these species of *Apodemus*, mechanisms intrinsic to each population must have an influence on use of space. Montgomery (1981) reported a removal experiment involving *A. sylvaticus* and *A. flavicollis*. After removal of their congener, both species moved into areas of woodland previously frequented by the absent species but both retained their associations with habitat features apparent in mixed species communities. The results of the present study suggest that interspecific competition for space should not be discounted when considering rodent communities, but it is not the only cause of habitat division. Intrinsic mechanisms, such as genetic background, experience, foraging adaptations, and avoidance of predators, may be equally responsible for the maintenance of spatial separation.

The role of interspecific interference in maintaining spatial separation of *A. sylvaticus* and *A. flavicollis* also may be inferred from the mostly negative relationship between niche breadth of *A. sylvaticus* and the population density of *A. flavicollis* (Fig. 3). However, it is conceivable that this result did not originate through species interactions but through differential spatial behavior related to habitat differences on different grids (Rosenzweig and Abramsky, 1986). This explanation seems unlikely, as data were distributed evenly among all grids (see above) and the relationship between niche breadth of *A. sylvaticus* and density of *A. flavicollis* was evidently consistent among grids despite the paucity of data for any single grid (Fig. 3).

Niche breadth of *A. sylvaticus* was related positively to population density of that species (Fig. 2), indicating that intraspecific interactions also influenced spatial behavior of the lesser competitor. This result complements the earlier analysis in which spatial overlap between species increased with increasing density of *A. sylvaticus* and suggests that spatial overlap in populations of *Apodemus* was determined, at least in part, by intraspecific, density-dependent habitat selection. This presumably resulted in the rather weak, nonlinear relationship between spatial overlap and spatial niche breadth of *A. sylvaticus*. Habitat selectivity of *A. sylvaticus* was greatest

when this species was rare. This concurs with Morisita's (1969) and Fretwell's (1972) assertion that habitat preferences may be apparent only when population size is small. Rosenzweig and Abramsky (1986), following Pimm (unpublished data), argued that habitat differences in communities where species share preferred habitats or microhabitats should be less apparent when population size is small. Conversely, in communities where species have distinct habitat preferences, spatial discreteness should be enhanced when numbers are low. Populations of the two species of *Apodemus* at Woodchester Park apparently conformed to the latter pattern of community organization. *A. sylvaticus* and *A. flavicollis* exhibited distinct habitat preferences, the former for dense ground level cover and the latter for thick cover at intermediate heights, in mixed woodland (Montgomery 1980*b*, 1981).

The increase in niche breadth of *A. sylvaticus* at greater densities of *A. flavicollis* (Fig. 3) probably was due to the concurrence of greater densities of both species during autumn. Interference of *A. flavicollis* with *A. sylvaticus* was apparent over an intermediate range of densities of the former (four to 46 individuals per hectare). These samples were mostly from late spring, summer, and early autumn months when populations of *A. sylvaticus* tended to be sparse, whereas numbers of *A. flavicollis* tended to be increasingly great (Montgomery, 1980*a*). Hence, it is not possible to conclude that interspecific interference inhibits spatial behavior of *A. sylvaticus* throughout the year. The impact of *A. flavicollis* on *A. sylvaticus* was evident during late spring, summer, and early autumn, but remains uncertain for the rest of the year.

Many factors may influence the spatial distribution of any organism. The results presented here and elsewhere (Montgomery, 1980*b*, 1981) suggest that use of space by *A. sylvaticus* is determined by intrinsic habitat preferences, the presence of conspecifics and population density of *A. flavicollis*. The interaction of these processes determines population dispersion. When numbers of *A. sylvaticus* and *A. flavicollis* are small, spatial behavior may be solely the product of early experience or genetic predisposition. When *A. sylvaticus* is common but *A. flavicollis* is rare, niche breadth of the former increases. Conversely, when *A. sylvaticus* is rare and *A. flavicollis* is common, niche breadth of the former is constricted. Finally, when numbers of both species are large, niche breadth of *A. sylvaticus* increases, perhaps indicating that intraspecific interactions are ultimately more powerful than interspecific interference in molding spatial behavior. The interaction between intraspecific and interspecific effects on niche breadth will be examined more fully in a later report.

Abramsky, B. Fox, and D. W. Morris for their comments on an earlier draft of the manuscript; and Elizabeth Purdy for her assistance in the preparation of the paper.

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A COMPARISON OF BAT ASSEMBLAGES FROM PHYTOGEOGRAPHIC ZONES OF VENEZUELA

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ABSTRACT—The distributional status of Venezuelan bats was obtained from Handley (1976) and used to assess faunal relationships among the phytogeographic zones of the country. Species presence or absence from each zone was used to construct phytogeographic zone similarity matrices, whereas the inclusion or exclusion of a particular zone from the distribution of each bat species was used to construct species similarity matrices. In either case, both Jaccard's and simple matching coefficients were analyzed using UPGMA clustering algorithms. A strict concensus tree between phenograms based on the two different similarity coefficients was calculated to determine groups of phytogeographic zones with similar faunal compositions. Bats also were classified into feeding guilds for each phytogeographic zone. Trophic structure (relative number of species per guild) of zones within groups defined by the clustering procedures then were compared using Contingency Chi-square analysis. In general, bats do not have distributions limited to a particular phytogeographic zone; moreover, bat assemblages cannot be used to define Tropical, Premontane, Lower Montane, or Montane sets of life zones. Little congruence is obtained between the floral zones of phytogeographers and the distributional limits of bats. Gallery forest bat faunas that occur along the river systems in many phytogeographic zones probably contribute to this phenomenon, especially in more arid regions. Moreover, bats may not respond to environmental gradients in the same manner as the dominant floral elements. Our analyses suggest six clusters of phytogeographic zones that are taxonomically related in terms of bat composition, and for the only cluster of phytogeographic zones with sufficiently large species pools in each zone, bat trophic structure was indistinguishable for the component phytogeographic zones.

Biogeographers and ecologists have endeavored to quantify how faunal assemblages relate to each other in overall taxonomic composition. One approach, direct gradient analysis, relates faunal composition to environmental variables such as temperature, precipitation, or altitudinal relief. Two difficulties exist with this approach for bat assemblages: each species is assumed to respond linearly to measured environmental variables, and few studies of bat distribution include relevant data for location along the environmental gradient. Indirect gradient analysis, or ordination, positions assemblages in multidimensional space based upon actual species composition. The Euclidean distance between assemblages is then a measure of faunal similarity. Such an approach has been used for bats from the Antilles (Baker and Genoways, 1978) and from North Africa and the Middle East (Qumsiyeh, 1985); indirect ordination is commonly used by phytogeographers and plant community ecologists (see Kershaw, 1973, and Gauch, 1982).

Bats are frequently viewed as organisms of great vagility and wide habitat tolerance. Yet the way in which tropical bats are allocated among habitats or phytogeographic zones has not been adequately described. Neotropical bats are particularly intriguing because high species richness and trophic

diversity characterize many areas of Central and South America (see Willig and Selcer, 1988, and Willig and Sandlin, 1989). Whether particular suites of species characterize one or more of the varied phytogeographic zones of the Neotropical Region is not yet clear.

Venezuela is a country with broad habitat diversity, although contained entirely within the tropics. Lowland rain forest, tropical deciduous forest, grassland, thorn scrub, montane rain forest, and alpine scrubland characterize the country that has a diverse bat fauna of 134 species (Handley, 1976). In this paper, we examine the distribution of bat species and their allocation among the major phytogeographic zones of this tropical country, and assess whether any of these zones are characterized by particular bat species. We also examine the patterns of distribution and habitat selection of the bats, relating these patterns to the history and geography of the habitats.

Materials and Methods

Bat species lists for phytogeographic zones of Venezuela (Ewel and Madriz, 1968, and Table 1) were obtained from Handley (1976) and organized into a 14 by 134 phytogeographic zone-species matrix; phytogeographic zones in which bats were not found (Tropical scrub forest, Lower Montane dry forest, Montane dry forest, Montane humid forest, Montane very humid forest, Subalpine paramo, and Subalpine rainy paramo) were excluded from analyses. Two kinds of comparisons were performed using the above matrix. The similarity between phytogeographic zones was estimated using the presence or absence of species in the zones as classificatory variables. Two similarity indices, Jaccard's coefficient (S_j—Jaccard, 1908; Sneath, 1957) and the simple matching coefficient (S_{sm}—Sokal and Michener, 1958), were calculated for each kind of comparison. Jaccard's coefficient is given by

$$S_j = a/(a + u),$$

where a is the number of positive matches (shared species) and u is the number of mismatches (sum of the unshared species) between the two groups (phytogeographic zones). It does not consider that the absences shared by two groups contribute to overall similarity. The simple matching coefficient is given by

$$S_{sm} = m/(m + u),$$

where m (number of matches) equals a (the number of shared presences) plus the number of shared absences (species known from the fauna of Venezuela but not present in/either of the compared phytogeographic zones), and u is the number of mismatches. It does consider shared absences in assessing overall similarity. These and other similarity indices are discussed in more detail by Sneath and Sokal (1973).

Each set of similarity coefficients produced a triangular matrix, the data from which were subjected to the unweighted pair-group arithmetic

TABLE 1.—*Phytogeographic zones of Venezuela (Ewel and Madriz, 1968) in which bats have been recorded (Handley, 1976). Phytogeographic zones that are members of the same concensus cluster based upon UPGMA of Jaccard's and simple matching coefficients are indicated parenthetically by identical letters.*

Abbreviation	Phytogeographic zone
me-T	Tropical thorny forest (F)
bms-T	Tropical very dry forest (D)
bs-T	Tropical dry forest (E)
bh-T	Tropical humid forest (E)
bmh-T	Tropical very humid forest (E)
me-P	Premontane thorny forest (F)
bs-P	Premontane dry forest (D)
bh-P	Premontane humid forest (E)
bmh-P	Premontane very humid forest (E)
bp-P	Premontane rain forest (C)
bh-MB	Lower Montane humid forest (A)
bmh-MB	Lower Montane very humid forest (B)
bp-MB	Lower Montane rain forest (C)
bp-M	Montane rain forest (C)

averaging cluster algorithm (UPGMA) in order to define associations among species or phytogeographic zones (Sneath and Sokal, 1973; Rohlf *et al.*, 1974). Cophenetic correlation coefficients between the resultant phenogram and the original similarity matrix estimate the degree to which the relationships suggested by clustering are representative of the actual relations among elements in the original similarity matrix. Concensus between phenograms based upon the simple matching and Jaccard's coefficient indicate the group relationships in common to both analyses, and has been produced following the methodology of strict concensus trees used in systematic studies (Sokal and Rohlf, 1981b).

Bats from each phytogeographic zone were categorized into feeding guilds based upon the work of Wilson (1973), Gardner (1977), and Willig (1982). Eight guilds were recognized: aerial insectivores, molossid insectivores, foliage-gleaning insectivores, nectarivores, frugivores, piscivores, sanguini-vores, and omnivores. The resultant trophic structure (number of species per guild) was compared via Contingency Chi-square tests (Sokal and Rohlf, 1981a) for each concensus group that was defined from the cluster analyses.

RESULTS

In terms of bat species composition, clustering algorithms based upon Jaccard's (Fig. 1A) and simple matching (Fig. 1B) coefficients attain concensus concerning the existences of six groups of phytogeographic zones (Fig. 2A). Tropical thorny forest and Premontane thorny forest form a thorny forest cluster (group F in Fig. 2). Tropical very dry forest and Premontane dry forest form a dry forest cluster (group D in Fig. 2). Premontane rain forest, Lower Montane rain forest, and Montane rain
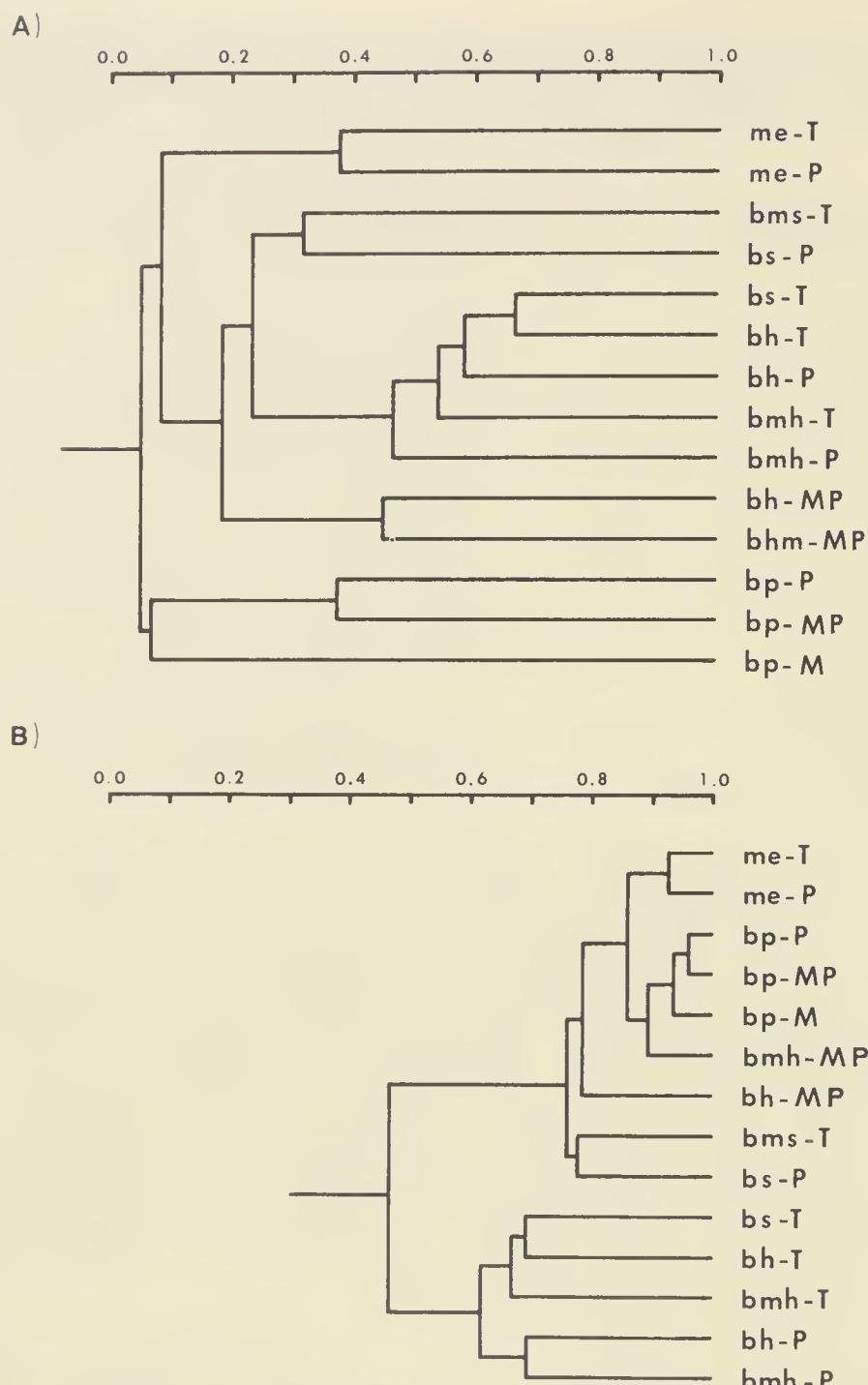
Fig. 1.—Phytogeographic zone phenograms based upon UPGMA clustering algorithms performed on Jaccard's (A) and simple matching (B) coefficients. Phytogeographic zone codes are as in Table 1. The cophenetic correlation coefficient for clustering based on the Jaccard's (0.94) and simple matching (0.88) coefficient indicate little distortion in either phenogram. The degree of similarity between zones may be obtained with reference to the scale above each phenogram.

forest constitute a rain forest cluster (group C in Fig. 2). Lower Montane humid forest (group A in Fig. 2) and Lower Montane very humid forest (group B in Fig. 2) each represents a distinct group. The final concensus cluster (group E in Fig. 2) consists of five phytogeographic zones: Tropical dry forest, Tropical humid forest, Premontane very humid forest, Tropical very humid forest, and Premontane humid forest. Differences in clustering at higher levels (compare Fig. 2B with 2C) is related to the differential sensitivity of the simple matching coefficient to shared absences wherein

A)
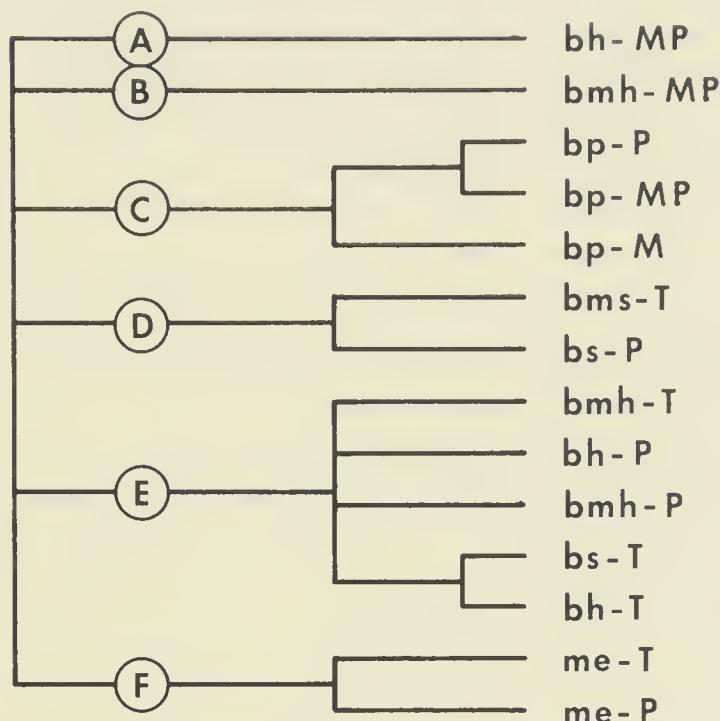
B)
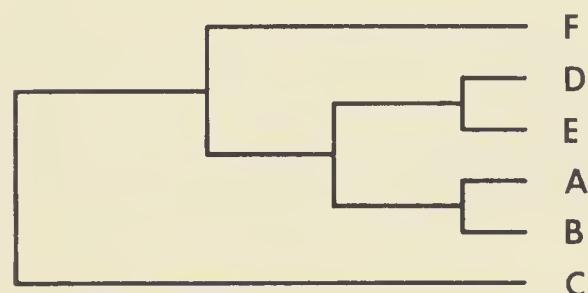
C)
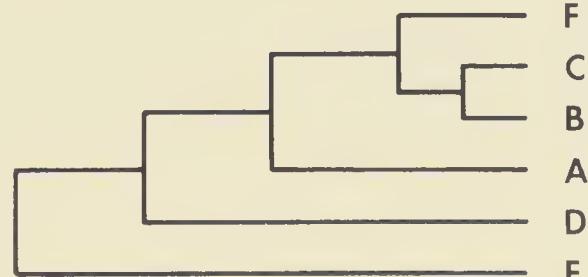
Fig. 2.—A concensus tree (A) for the phenograms in Figure 1; the single capital letters indicate concensus groups (see text for details). Phytogeographic zone codes are as in Table 1. The relationship of concensus groups (capital letters in the phenogram) based upon Jaccard's (B) and simple matching (C) coefficients cannot be further resolved based upon the method of strict concensus.

depauperate faunas will be viewed as similar because of the joint absence of many species from both zones.

Phenograms of species clusters using Jaccard's and the simple matching coefficients are complex and show little concensus beyond identifying subsets of species that in some cases link various phytogeographic zones

into groups. The thorny forest cluster (F) consists of two phytogeographic zones with depauperate faunas, linked primarily by the joint occurrence of four bat species, *Lasiurus cinereus, Rhogeesa minutilla, Leptonycteris curasoae*, and *Glossophaga longirostris. Eumops nanu* and *Myotis larensis* are species found only within the Tropical thorny zone. Within group E, Tropical dry forest and Tropical humid forest are linked by the joint occurrence of seven species, *Saccopteryx naso, Diclidurus ingens, Noctilio albiventris, Lonchorhina orinocensis, Molossops paranus, M. planirostris*, and *Molossus aztecus*. Four species, *Eptesicus dimidiatus, Eumops auripendulus, E. dabbenei*, and *Promops centralis*, have distributions restricted to Tropical dry forest. The Tropical humid forest contains nine species (*Diclidurus isabellus, Tadarida laticaudata, Eumops amazonicus, Molossops greenhalli, M. abrasus, Glyphonycteris sylvestris, Tonatia carrikeri, Lichonycteris degener*, and *Scleronycteris ega*) that only occur within that phytogeographic zone. Nonetheless, a large number of species defines links between various subsets of the entire cluster of five phytogeographic zones within group E. Seven species are uniquely found in each of these five zones; they include *Peropteryx macrotis, Trachops cirrhosus, Chrotopterus auritus, Vampyressa bidens, Chiroderma trinitatum, C. villosum*, and *Artibeus concolor*. Like the Thorny forest group, both the dry forest group (D) and the rain forest group (C) each contains phytogeographic zones that are linked by the lack of whole suites of species; no species is unique to either cluster. Neither of the Montane humid forests (A or B) contains bat species with distributions that are limited to those zones.

Reliable Chi-square tests require 1) all expected cell values to be greater than or equal to one, and 2) less than 20 percent of the expected cell values to be less than five. These requirements were only satisfied within group E (bs-T, bh-T, bmh-T, bh-P, and bmp-P) after combining omnivore, sanguinivore, and piscivore guilds into a single category. The nonsignificant statistical result (X^2 = 19.70, df = 20, $0.50 > P > 0.10$) indicates that all five phytogeographic zones within group E have indistinguishable trophic structures.

Discussion

Faunal relationships among Venezuelan phytogeographic zones are complex. In general, distinct subsets of the fauna do not characterize phytogeographic zones or concensus groups. With the exception of Tropical humid forest (nine species), Tropical dry forest (four species), and Tropical thorny forest (two species), bat species do not have distributional ranges limited to single phytogeographic zones. Interestingly, over two-thirds of the species that are phytogeographic zone specialists are insectivores. Although the New World fruit-eating bats (Phyllostomidae) reach their highest diversity in the tropics (Wilson, 1973; McCoy and Connor, 1980), few species are limited to particular phytogeographic zones. This is opposed

to the popular belief that South American mammals are stenotopic (see Mares, 1986, 1987; Patterson, 1987). Moreover, unique assemblages of bats cannot be used to define Tropical, Premontane, Lower Montane, or Montane life zones. Our analyses suggest that there is little congruence between the floral zones as defined by phytogeographers and the bat species frequenting those zones. Few of the defined zones have even one or two bat species that characterize them.

Nevertheless, as Figure 2 indicates, some distinct associations of phytogeographic zones can be obtained based upon bat species composition. The phenograms in Figure 1 can be reconciled into the concensus phenogram of Figure 2A. Each of the six clusters thus defined, although not perfectly distinct from each other, does in fact share a mix of species, and in some cases, is delimited by species that occur in all zones of the cluster. This figure may be considered as a model to determine from which zone a particular species was obtained. In most cases, a single individual cannot, with certainty, be assigned to a particular zone. But, as more species are obtained from an area, the probability of ascertaining the proper phytogeographic zone with which the area should be associated increases greatly.

The absence of bats from a number of phytogeographic zones in Venezuela may, in part, be affected by the precipitous decline of bat diversity above elevations of 1000 meters. The depauperization of high altitudes recapitulates hemispheric trends of reduced bat species richness at high latitudes (Wilson, 1973; McCoy and Connor, 1980), and may similarly involve physiological constraints associated with low temperatures and reduced food abundance (McNab, 1969, 1983).

In general, the absence of characteristic species from particular phytogeographic zones suggests that bats are not life zone specialists but rather are eurytopic. Bat distributions may fail to show patterns that reflect phytogeographic zones for a variety of reasons. Perhaps different species of bats respond in different ways to abiotic and biotic gradients such that distinct assemblages that correspond to phytogeographic zones are not obtained. In a different context, Terborgh (1970) found most of the avifauna of the Codillera Vilcabamba in Peru to have distributions that are relatively unaffected by competitive exclusion or habitat discontinuities. Over half of the bird species had distributional limits that were determined by factors in the environment that vary continuously and in parallel with the altitudinal gradient. This also resulted in the absence of pervasive avifaunal associations within floral zones because the location of the density optima of species varied randomly along the environmental gradient. The complexity of faunal relationships among phytogeographic zones also may be an artifact of using presence-absence data in lieu of species abundances. If bats have different densities in different life zones, which is a realistic assumption, then our methods may not detect life zone specialists, if they exist, because the quantitative information on abundance is not accurate.

For example, a particular species may be abundant in the Tropical dry forest but only rarely found in Tropical humid forest, Premontane dry forest, and Lower Montane rain forest. An analysis using only presence-absence information would consider the species equally characteristic of all four phytogeographic zones. Alternatively, the salient features used by phytogeographers to characterize life zones may not reflect the critical components defining the niche limitations of particular bat species. In fact, the Ewel and Madriz classification, like the Holdridge system, is primarily based upon temperature and precipitation, and does not take into account other edaphic factors. Although substantial tracts of gallery forest parallel the many rivers that occur north of the Orinoco, the land is homogeneously classified as "bosque seco." The species composition of these gallery forests shows great affinity with multistratal rain forest and substantially contributes to the species richness of areas in central Venezuela north of the Orinoco. Moreover, the extensive distribution of such riverine habitats and their associated faunas would tend to diminish the chance of detecting unique bat associations within phytogeographic zones.

ACKNOWLEDGMENTS

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THE INFLUENCE OF SPECIES INTERACTIONS

SPATIAL AND TEMPORAL VARIATION IN GUILDS OF NORTH AMERICAN GRANIVOROUS DESERT RODENTS

James H. Brown and Margaret Kurzius

ABSTRACT—Presence/absence data for species occurrences were used to assess spatial and temporal variation in species composition in granivorous rodent assemblages from the North American deserts. Our analyses showed a tremendous amount of variation on several scales: large-scale spatial variation among sites distributed across the desert region of the southwestern United States; large-scale temporal variation from late Pleistocene to Recent; small-scale spatial variation among grid stakes within plots and among plots within a local study site of desert shrub habitat; and small-scale temporal variation among monthly sampling periods within the same study area. Many different numbers and combinations of species occurred together at all of these scales, and at the larger scales each species coexisted locally with many other species and combinations of species.

All of our analyses suggest that the composition of these rodent guilds is extremely flexible and dynamic, implying an individualistic or "Gleasonian" type of community organization. This does not mean that guilds are random or unstructured assemblages. On the contrary, much of the variation probably can be explained by deterministic processes. The occurrence of individual species in both space and time appears to depend primarily on whether their unique requirements are met by the immediate enviornment and whether certain other species are present. However, our data suggest distributions of species and compositions of guilds that are not supportive of close coevolution among coexisting species in continental communities.

Any complete understanding of community organization must account for the extent and patterns of variation in assemblages of coexisting species over both space and time. Like most scientific disciplines, community ecology during its early history was more concerned with means than variances. With some conspicuous exceptions (for example, Gleason, 1926, and Whittaker, 1967), it has been only in the last decade or so that ecologists have begun to quantify the enormous variation in community composition, and to frame and test explanations for this variability. This recent trend has been stimulated in large part by the debate about the extent to which natural assemblages of species exhibit deterministic as opposed to apparently random structure (for example, Diamond, 1975; Connor and Simberloff, 1979; Bowers and Brown, 1982; Strong et al., 1984; Diamond and Case, 1986).

A major problem in resolving this question is obtaining good data on variation in community composition. Most available data sets consist of species lists, compiled by systematists and biogeographers, that simply document presence of species on a relatively large, coarse spatial scale. Accurate data on spatial and temporal variation in the composition of species on any other scale are even harder to obtain, but these are especially relevant for assessing the extent of variation and for evaluating hypotheses about the processes that determine community organization.

The granivorous desert rodents that inhabit the North American deserts are one of the most intensively studied guilds of closely related, ecologically similar species (for example, Brown, 1975, 1987; Brown and Harney, 1988). Recently we have begun to analyze data on spatial and temporal variation in this guild. Initially we focused on large-scale geographic variation in the composition of local communities using a large data set assembled from the literature (Brown and Kurzius, 1987). In the present paper, we review those results and then present new data and analyses on small-scale spatial and temporal variation in the composition of the granivorous rodent guild from our experimental studies in the Chihuahuan Desert.

Large-scale Spatial Variation

In another paper (Brown and Kurzius, 1987; see also Brown, 1987) we compiled from the literature and a few unpublished sources a large data set on the composition of granivorous rodent species in local patches of arid habitat throughout the southwestern United States (Fig. 1). The basic data consist of a presence/absence matrix documenting the distribution of 29 species among 202 sites. The species list includes all representatives of the genera *Dipodomys, Microdipodops, Chaetodipus, Perognathus, Peromyscus*, and *Reithrodontomys* that occur at one or more sites. The sites are all small, relatively homogeneous patches of desert shrub habitat that have been intensively sampled for rodents as part of an ecological study. Here we review briefly the major results of our analyses.

The most spectacular result was the enormous amount of variation that was revealed. One hundred and twenty-four different combinations of species occurred at the 202 sites. The vast majority of these (90) were observed at only one site, and the most frequently recurring combination (of two species) was found at 14 sites (Fig. 2). The number of species in a local guild varied from one to nine, but most of the sites had two to five species (Fig. 2). Most of the species were rare in the sense that they occurred infrequently. Almost half (48.3 percent) of the species were found at 10 or fewer sites, and more than half (58.6 percent) occurred at less than 30 percent of the sites within their geographic ranges. On the other hand, a few species were quite common. Two of them, *Dipodomys merriami* and *Peromyscus maniculatus* each were found at more than 40 percent of the sites and with more than 22 other species. Most species, especially the more common taxa, occurred with many other species and in many different combinations. Eighteen of the 29 species occurred with more than 50 percent of the species with which their geographic ranges overlapped.

This large-scale spatial variation suggests that a guild or community is simply an opportunistic assemblage of individual species, each distributed in response to its special requirements as proposed by Gleason (1917, 1926) for plant associations. Most of the species apparently had such narrow requirements that their geographic ranges included less than half of the southwestern desert region, and even within their ranges they were restricted
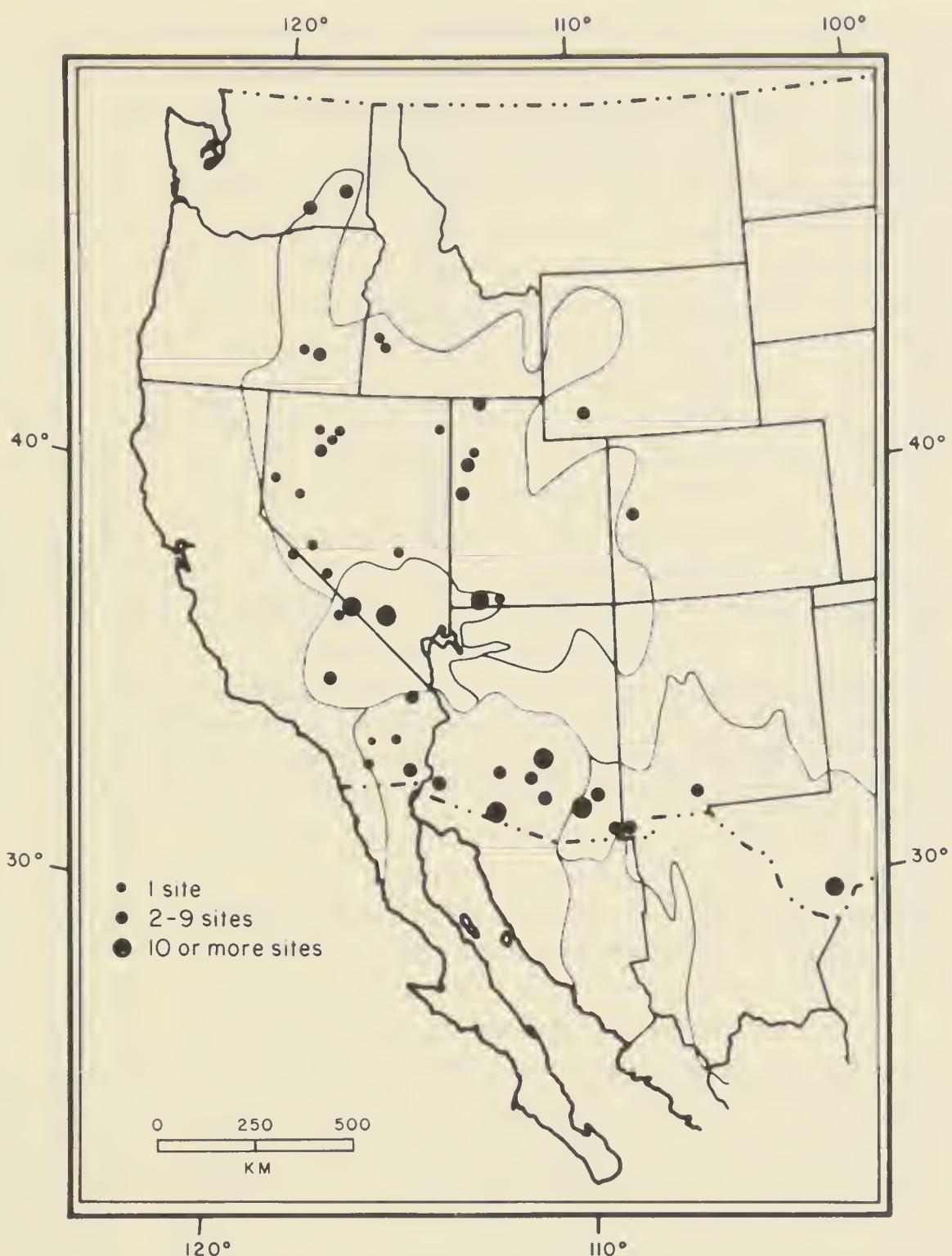
Fig. 1.—Map of the desert region of the southwestern United States, showing the distribution of sites that were used in the analysis of large-scale spatial variation in the composition of desert rodent guilds. Two or more sites that were in close proximity are indicated with larger symbols. The four major deserts (Great Basin, Mojave, Sonoran, and Chihuahuan) are outlined.

to only a small proportion of the local samples of arid habitat. Despite these limited distributions, most species co-occurred with many different species and combinations of species. Apparently in satisfying its own unique requirements, each species was distributed in space mostly independently of other species. Consequently, there was considerable variation in the size of guilds and great variation in the combinations of species that comprise the guilds. There was no indication of a small number of alternative stable
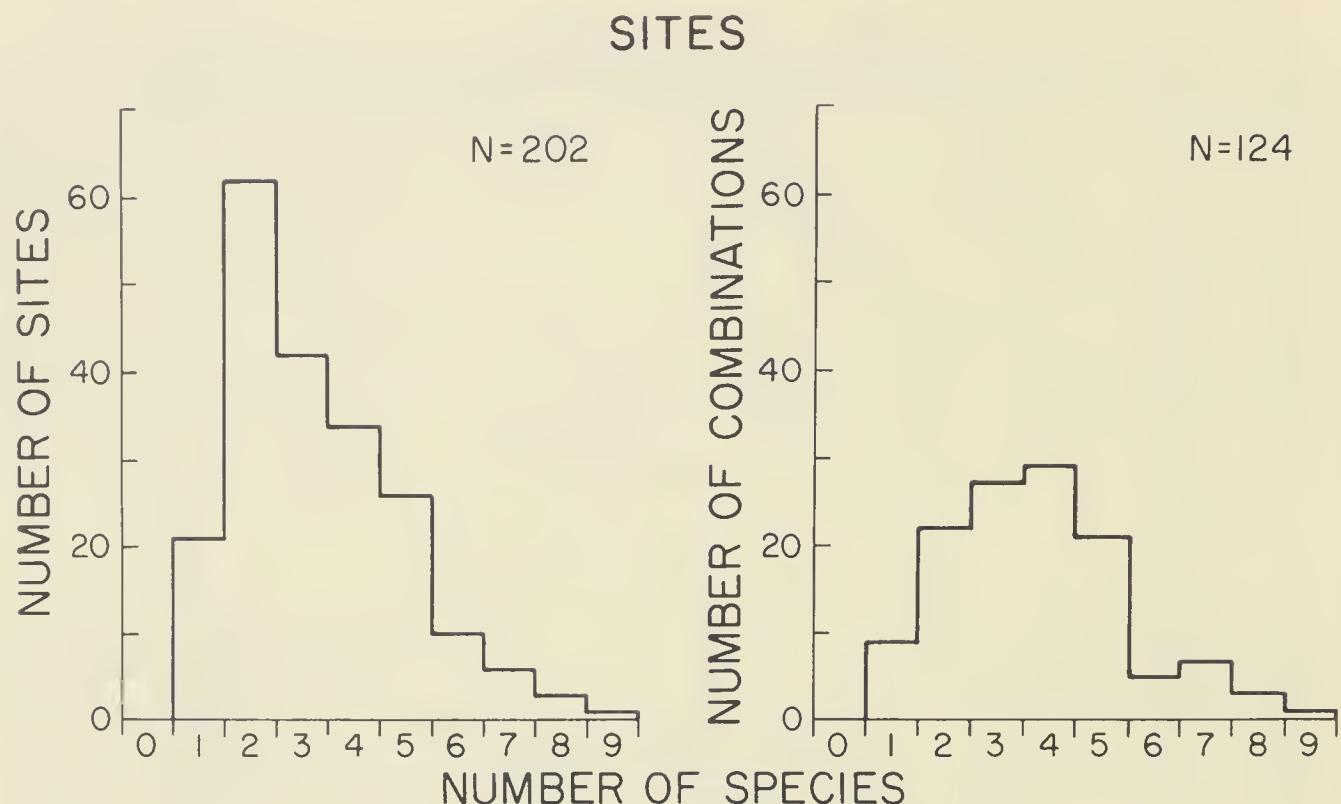
SITES

Fig. 2.—Spatial variation in the composition of guilds of granivorous desert rodents at the scale of sites distributed over the entire southwestern United States. Left, frequency distribution of the number of sites as a function of the number of species per site. Right, frequency distribution of the number of different combinations of species as a function of the number of species in the combination.

assemblages of species that occurred together frequently and replaced each other in some predictable pattern across the landscape.

Large-scale Temporal Variation

From an ecological perspective, detailed information on the co-occurrence of rodent species at particular sites over the last 20,000 years would be particularly valuable. This would permit documentation of changes in locally coexisting species during the climatic and habitat changes that accompanied the transition from the Pleistocene to the present. Harris (1985) has compiled the existing data on late Pleistocene and Holocene fossil mammals from the Southwest, but problems of identifying them to the species level and of insuring that sediments have not been been mixed or disturbed because deposition makes it difficult to determine with certainty what combinations of species actually coexisted contemporaneously in the same habitats. What is desperately needed to provide a historical account of community composition is the kind of careful, stratigraphically-controlled study that Graham (1986) has made of Pleistocene to present changes in the composition of small mammal communities in Illinois.

Although Graham's work obviously was done in different habitats and another geographic region, this, together with 1) the information that Harris (1985) has compiled, 2) the increasingly accurate reconstruction of climatic and vegetative change in the Southwest (for example, see Wells,

1983, and Van Devender, 1986), and 3) our knowledge of the ecology and biogeography of contemporary rodents, can provide the basis for informed speculation about the kinds and magnitude of historical changes in local granivore guilds. Harris' (1985) synthesis clearly shows that these changes were extensive. Virtually all of the late Pleistocene assemblages contained a large proportion of species that no longer occur at these sites today. This indicates large changes in the distribution of species and the composition of communities within the last 12,000 years. Some species that occur together frequently and over a broad area today probably were completely allopatric as recently as the latest Pleistocene 12,000 years ago. For example, assemblages currently inhabiting friable soils in the western Great Basin desert typically contain *Dipodomys deserti, D. merriami*, and either *Microdipodops pallidus* or *M. megacephalus* (Brown, 1973). Yet the evidence suggests that in the Pleistocene the two *Dipodomys* species were confined to warm desert refugia well to the south of the Great Basin, whereas the two *Microdipodops* species never occurred outside the Great Basin. There may equally well be examples of species with well-separated contemporary geographic ranges that coexisted in the same local communities in the late Pleistocene. Graham (1986) and others have found species with contemporary geographic ranges separated by hundreds of kilometers occurring together in the same late Pleistocene fossil strata. Harris (1985) presented several possible examples of this in the Southwest (for example, the co-occurrence of fossils of *Dipodomys spectabilis* with those of *Cryptotis parva, Neotoma cinerea*, and *Microtus* sp.), but these should be treated with caution until more accurate dating and stratigraphy are available.

Thus it appears that on a large scale guilds are extremely variable in time as well as in space. Species that occur together today may not have a long history of coexistence, and species may have long histories of co-occurrence with species that they no longer encounter. This historical perspective also is consistent with an extremely individualistic or "Gleasonian" view of community organization. The unique requirements of each species define the ecological variables that limit abundance and distribution in local habitats within their geographic range. Because the geographic range is the aggregate of the local distribution, these same limiting factors determine the boundaries of the geographic range and the barriers to dispersal. Although species certainly can evolve and alter their requirements, we suspect that effects of such endogenous changes on abundance, distribution, and community composition during the last 20,000 years have been relatively slight compared to the enormous changes caused by variation in climate and vegetation.

Small-scale Spatial Variation

We have described above the large variation in the composition of granivore guilds on a spatial scale as small as adjacent patches of different habitat type. Now we consider spatial variation on an even smaller scale. To

TABLE 1.—*Spatial variation: mean density per plot, variance over mean density, plots with highest and lowest densities.*

Species	Mean density	Variance/mean	Highest	Lowest
D. merriami	198.1	29.0	12>11=14	8<22
D. ordii	47.9	22.0	8>1	4=13<18
D. spectabilis	123.6	18.1	9>4	14<2
P. flavus	15.9	6.8	8>4	17<12
C. penicillatus	9.6	7.3	11>12	17<14
P. eremicus	9.6	12.9	2>6=20	1=9<4
P. maniculatus	2.6	2.9	18>11	4=13<8=20=22
R. megalotis	9.2	8.0	12>17	4=13<1=6

*Two other granivores (*Chaetodipus hispidus* and *Reithrodontomys flavescens*) that were captured fewer than 12 times at the site were not included in this analysis.

do this we analyzed spatial distribution of species and combinations of species on our experimental study area in extreme southeastern Arizona. The 20-hectare site is covered with relatively homogeneous, upper elevation Chihuahuan desert shrub vegetation. From July 1977 to June 1986 we sampled rodents on 24 fenced plots, each 0.25 hectares in area and containing 49 permanent grid stakes spaced 6.5 meters apart. Rodents were live-trapped at approximately monthly intervals, setting one trap at each grid stake for a single night. Here we present data on the captures on each of the 14 plots to which all rodent species had free access through 16 holes (3.7 by 5.7 centimeters) in the fences. These plots have been subjected in pairs to experimental manipulations in which selected ant species were removed, exogeneous millet seed was added, or no changes have been made (for a more detailed description of the study site, trapping protocol, and experimental treatments, see Brown and Munger, 1985).

We can analyze the spatial distribution of species and combinations of species on two scales: among individual grid stakes and among different plots. In both cases, we summed trapping records over 100 sample periods separated by intervals of approximately one month. We have used presence/absence data to analyze species composition. The pool of species available to be sampled on both of these scales can be estimated conservatively from the total sample, which contained 10 species of granivores of widely varying abundance (Table 1).

For the smallest scale (individual grid stakes), we have 100 monthly samples of one trap night for each of 686 microsites. The number of individuals captured per stake ranged from zero to 31, with a mean of 8.5 and a variance-to-mean ratio of 2.41, significantly different from a random (Poisson) distribution ($P < 0.001$—Table 2). Figure 3 shows the patterns of variation in the numbers and combinations of species in these samples. The number of species captured varied from zero to six with a mean of 2.8. The number of different combinations of species was 91, and most of these were of two to four species. The most frequently observed combination of species

TABLE 2.—*Spatial variation: percent of all stakes at which each species was captured, variance over the mean density per stake per plot, plots with highest and lowest variance over mean density.*

Species	Percent of stakes	S^2/X /stake/plot	Highest S^2/X (within) plot	Lowest S^2/X (within) plot
D. merriami	89	2.11	11>12	6=8<2
D. ordii	47	1.46	17>20	1=13=14=18<9
D. spectabilis	73	3.46	12>8	14<18
P. flavus	25	1.08	11=13>2=8=9	1<6=22
C. penicillatus	16	1.21	12>1	20=22<2=8=13
P. eremicus	13	2.43	6>2	20<12
P. maniculatus	5	1.12	1=8=12=14=20=22>6	18<2
R. megalotis	14	1.40	11>12	14<1=6

(two species—*Dipodomys merriami* and *D. spectabilis*) was captured at 120 stakes, whereas 35 different combinations were observed at only one stake.

For the larger scale we have 100 monthly samples of 49 trap nights for 14 plots, each 0.25 hectares in area and separated by a minimum distance of 25 meters. Number of individuals captured per plot per trapping period ranged from 3.18 to 5.99, with a mean of 4.17 and a variance-to-mean ratio of 15.3 (highly significantly different from a Poisson distribution $P < 0.001$—Table 1). Figure 4 shows the extent of variation in numbers and combinations of species. The number of species per plot varied from six to nine with a mean of 7.5. There were seven different combinations of species. The most frequent combination (eight species—*Dipodomys merriami, D. ordii, D. spectabilis, Chaetodipus penicillatus, Perognathus flavus, Peromyscus eremicus, P. maniculatus,* and *Reithrodontomys megalotis*) was observed seven times, and five combinations were observed only once.

These data indicate the enormous microspatial variation in community composition that occurs even within a small patch of relatively homogeneous habitat. Undoubtedly much of this variability is due to chance. At the scale of grid stakes, the number of individuals captured is small. Consequently, sampling error results in substantial variation in the number of species and number of different combinations of species observed. This kind of random sampling error also contributes to variability at the level of plots, even though plots have been intensively sampled (4900 trap nights resulting in an average catch of 419 individuals per plot). The reason for this sampling effect is that some species were rare (for example, two species had fewer than 12 individuals captured—Table 1). Consequently, these rarities formed unique combinations, even at the level of entire plots. Additional variation could have been caused by our experimental treatments of different plots, but the evidence suggests that these had small effects. The only statistically significant response of rodents to these manipulations that we have been able to detect was an increase in the density of *D. spectabilis* and a decrease in the densities of *D. merriami* and *D. ordii* on the eight
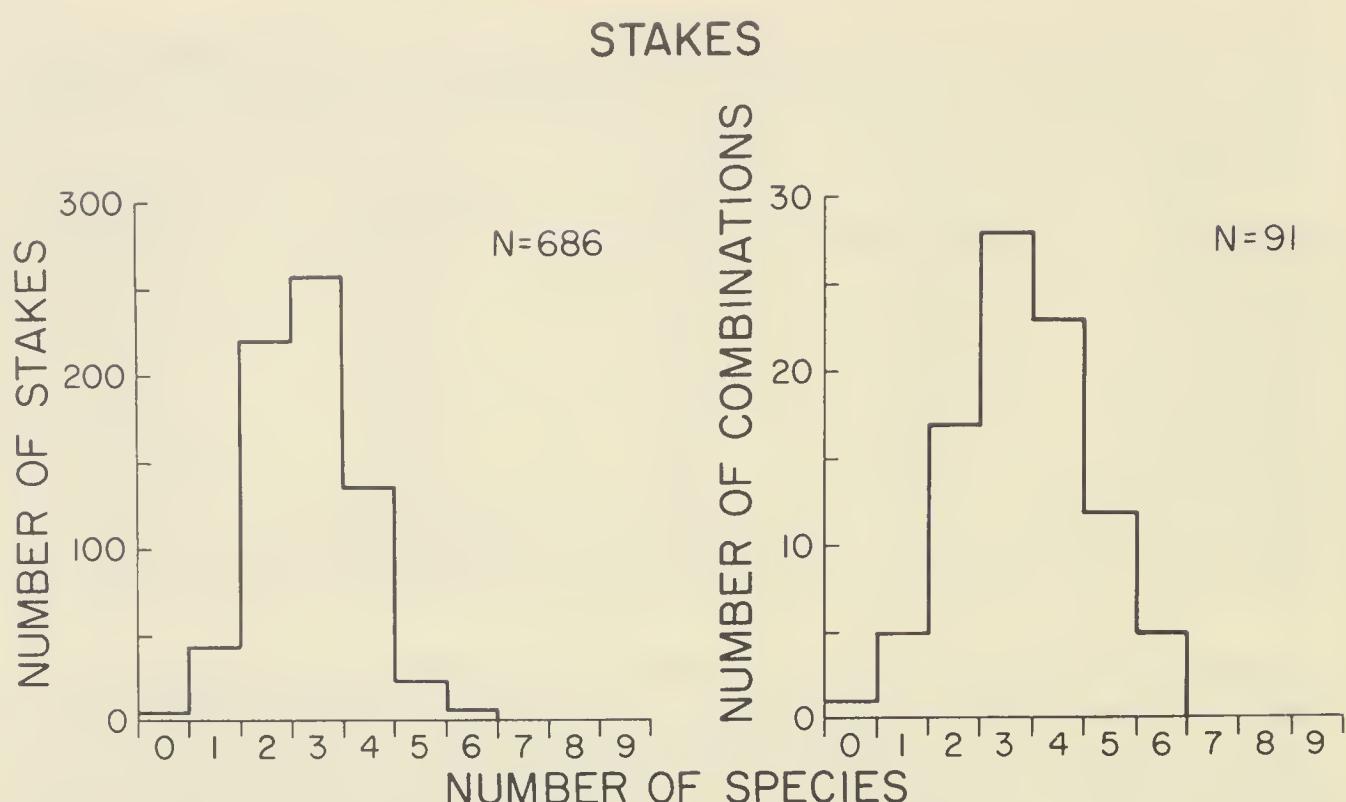
STAKES

FIG. 3.—Spatial variation in the composition of guilds of granivorous desert rodents in the Chihuahuan Desert of southeastern Arizona at the scale of grid stakes within experimental plots. Left, frequency distribution of the number of stakes as a function of the number of species captured per stake. Right, frequency distribution of the number of different combinations of species as a function of the number of species per combination.

plots where we added millet seeds (Brown and Munger, 1985). Because these were three of the most common species and they were present on all plots, changes in their abundance did not affect our measures of guild composition. However, we did not include in this analysis those plots from which we experimentally excluded *Dipodomys*. Four species of small granivorous rodents increased dramatically in response to this manipulation (see Munger and Brown, 1981; Brown and Munger, 1985; Brown, 1987), and they would have shown much more heterogeneous distributions at the scale of plots had these data been included.

There appeared to be much microspatial variation that could not be attributed either to chance or to our experimental treatments, but was due instead to differences in the way rodent individuals and species perceived and responded to their local environment. Certainly the distribution of individuals among stakes was highly nonrandom. Other studies (for example, Brown and Lieberman, 1973; Rosenzweig, 1973; Brown, 1975; Lemen and Rosenzweig, 1978; Price, 1978; Bowers, 1982; Thompson, 1982; Kotler, 1984; Larsen, 1986; Bowers *et al.*, 1987) have shown that individual species of these granivorous rodents differentially use open and vegetated microhabitats, and they change these patterns in response to the presence of other rodent species and perceived risk of predation. It also is well known that species are differentially distributed among local habitat types distinguished by modest differences in vegetation and soil type (see
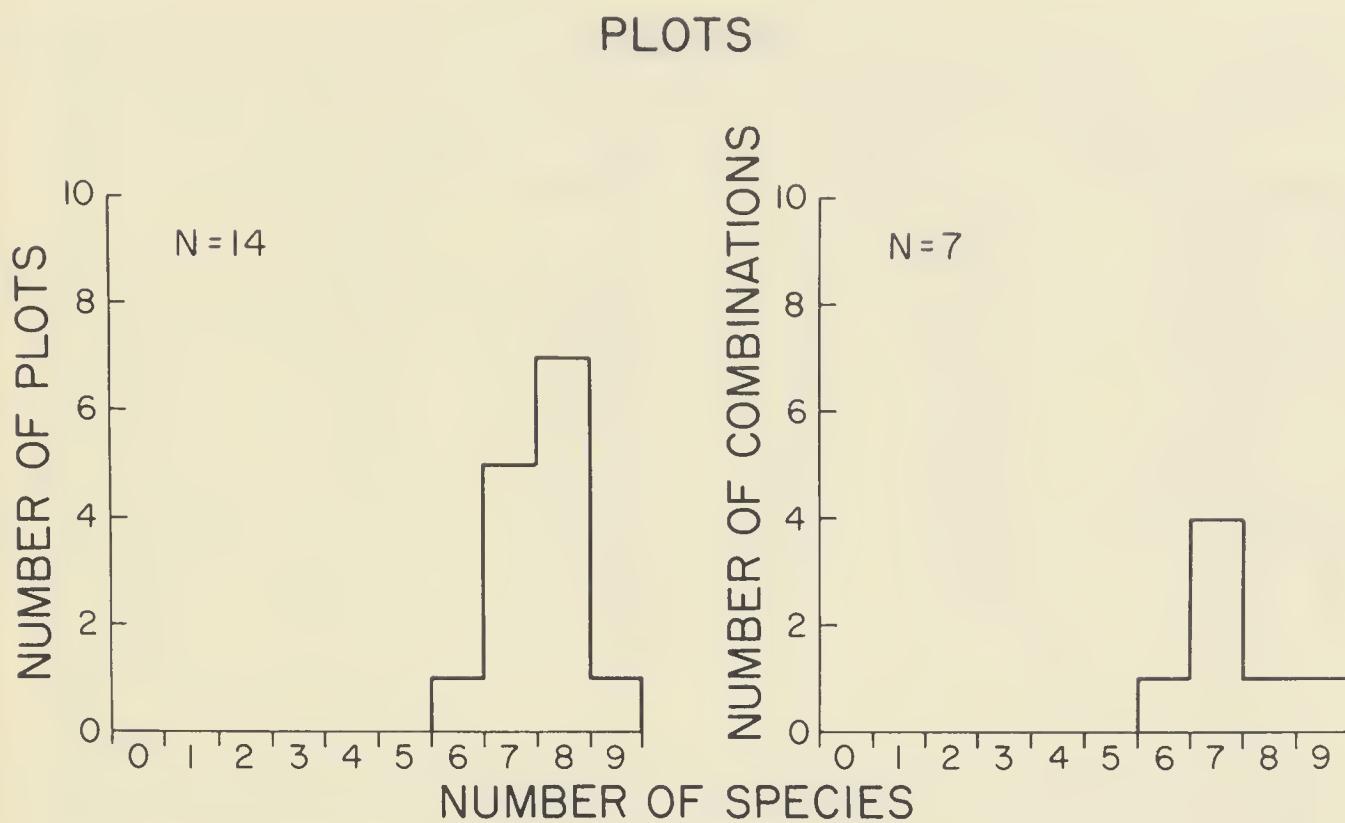
PLOTS

Fig. 4.—Spatial variation in the composition of guilds of granivorous desert rodents in the Chihuahuan Desert of southeastern Arizona at the scale of 0.25-hectare experimental plots within a 20-hectare study area. Left, frequency distribution of the number of plots as a function of the number of species per plot. Right, frequency distribution of the number of different combinations of species as a function of the number of species per combination.

Rosenzweig and Winakur, 1969; Rosenzweig *et al.*, 1975; Price, 1978; M'Closkey, 1981).

Almost certainly much of the microspatial variation in species composition that we have observed was due to habitat selection on these small spatial scales. Evidence for this comes from variance-to-mean ratios for the distributions of individuals of the different species with respect to both plots and stakes (Tables 1 and 2). All of these values were greater than one, indicating nonrandom aggregation of individuals at certain stakes or plots. At the scale of stakes, it might be supposed that some of this clumping simply reflects the proximity of some traps to permanent burrows, but in the one species in which we can evaluate this possibility, it does not appear to account for most of the variation. *Dipodomys spectabilis* constructs large, long-lasting burrows, but the stakes with the most frequent captures were not necessarily those nearest burrows. All species show markedly nonrandom and clumped distributions especially at the scale of plots (Table 1). This suggests that each species responded to subtle differences in habitat structure and resource availability (perhaps influenced to some extent by our experimental manipulations, but see above). Different species attained their highest and lowest densities on different plots (Table 1), indicating that they responded to different environmental variables.

Thus there was great variation in the number and identity of species that actually used small patches of habitat. Some of this variability may be
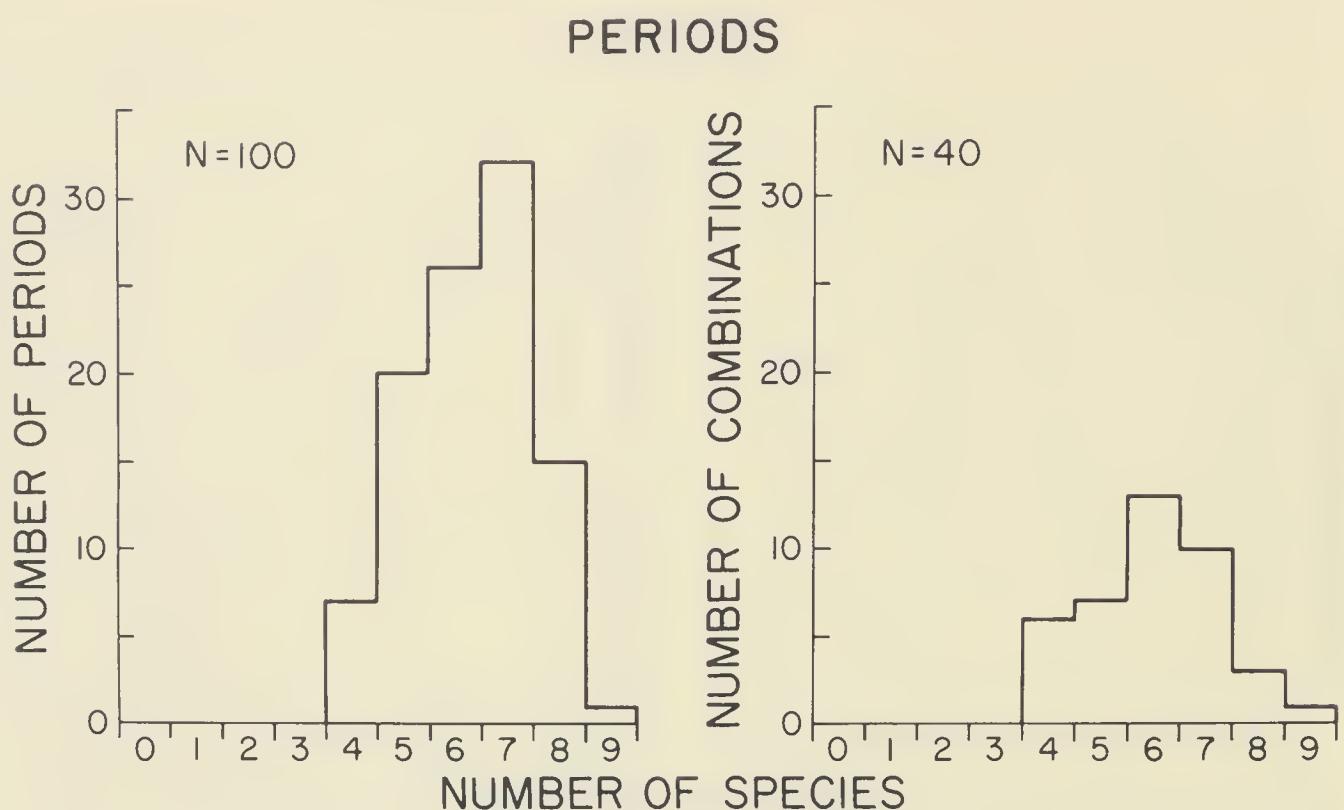
PERIODS

FIG. 5.—Temporal variation in the composition of guilds of granivorous desert rodents in the Chihuahuan Desert of southeastern Arizona at the scale of monthly sampling periods over a 10-year interval. Left, frequency distribution of the number of periods as a function of the number of species captured per period. Right, frequency distribution of the number of different combinations of species as a function of the number of species per combination.

attributed to sampling error and other random processes, but most of it reflects deterministic differences in the requirements and tolerances of individual species. Like the large-scale patterns, the microspatial variation seems to reflect primarily the individualistic distribution of each species in response to different combinations of variables.

SMALL-SCALE TEMPORAL VARIATION

We can use our 100 monthly samples to examine small-scale temporal variation in the composition of the granivore guild. We did this by combining captures at all stakes and plots to obtain a sample for the study area as a whole based on 686 trap nights per month. The number of individuals captured per month ranged from 29 to 146 with a mean of 73.9. Figure 5 shows the temporal patterns of variation in species composition. The number of species varied from four to nine with a mean of 6.4. There were 37 different combinations of species. The most frequent (eight species—*Dipodomys merriami, D. ordii, D. spectabilis, Chaetodipus penicillatus, Perognathus flavus, Peromyscus maniculatus, P. eremicus,* and *Reithrodontomys megalotis*) was observed 17 times, and 19 different combinations were found in only one period. Variance-to-mean ratios much greater than one for all the common species (Table 3) indicate that the temporal distributions were highly clumped. This pattern should be interpreted with caution, because such time series data clearly do not

TABLE 3.—*Temporal variation: density, variance over mean density, high and low density periods of Portal granivores by month. Numbers in parentheses are based on number of captures from April through October only.*

Species	Percent of months captured	X density	S^2/X	Highest density period	Lowest density period
D. merriami	100 (100)	34.02 (31.02)	5.33 (4.49)	8/82-3/83	2/79-10/79
D. ordii	96 (95)	7.57 (6.43)	4.17 (3.12)	1/85-3/85	7/77-4/78
D. spectabilis	99 (98)	18.19 (19.34)	5.75 (6.67)	4/80-6/80	5/84-12/85
P. flavus	75 (75)	4.62 (4.46)	6.21 (6.40)	6/82-6/83	12/83-6/86
C. penicillatus	67 (95)	2.09 (3.23)	2.20 (1.23)	8/85-9/85	10/77-4/78*
P. eremicus	77 (75)	2.46 (2.15)	3.18 (2.36)	11/81-5/82	5/78-7/78; 7/81-9/81
P. maniculatus	49 (47)	1.34 (1.36)	2.91 (3.11)	3/82-1/83	3/79-5/81
R. megalotis	58 (46)	3.55 (1.46)	9.96 (3.46)	2/82-3/82	7/77-10/79

*Chaetodipus penicillatus was seldom captured during the winter months of any year.

represent independent observations. At the moment, we cannot rule out the possibility that each species population fluctuated essentially at random. However, we think that this is unlikely, and we have anecdotal information relating some of the peaks and troughs with environmental variation, especially in rainfall. The fact that different species attained their highest and lowest densities at different times (Table 3), shows at a minimum that all species did not respond similarly to the same environmental fluctuations.

Two additional aspects of this temporal variation should be addressed. First, our presentation of the data does not do justice to the magnitude of the fluctuations. Some species, even relatively common taxa such as *P. flavus, R. megalotis*, and *P. eremicus*, have been totally absent from the site for several months in succession. Such species can be said to have become locally extinct and then to have recolonized. Second, some of the variability may be due to the inactivity of species in hibernation or aestivation. We have no evidence that any of the species aestivated, but two pocket mice, *P. flavus* and *C. penicillatus*, certainly hibernated. Shifts in species composition due to differences in seasonal activity should not be discounted, however, because they indicate ecologically important temporal changes in the species that were actively foraging and potentially interacting. It also may be of interest to assess to what extent hibernation contributed to the magnitude of temporal variation in these species. One way to do this is to exclude the winter months when some individuals may have been in hibernation, and ascertain what effect this has on the variance-to-mean ratio in population density. When this was done (Table 3), *C. penicillatus* was distributed much more evenly over time, but *P. flavus* remained highly clumped.

Despite the large samples and the inherent tendency of time series population data to be autocorrelated, the montly samples of a local guild reveal enormous variation in species composition. Many different numbers and combinations of species occur together at the same local site within a

period of a few years. Although some species are present continuously or nearly so, others exhibit repeated episodes of local extinction followed by recolonization from surrounding areas. Although a certain proportion of this variation may be indistinguishable from random fluctuations, the patterns are consistent with the general interpretation that most of the variability reflects the response of the individual species to fluctuations in the environmental conditions required for survival and reproduction.

DISCUSSION

Our analyses reveal great variability in the composition of granivorous desert rodent guilds in both time and space over a wide range of scales. These results have several important implications for the way we think about the "structure" or "organization" of communities.

Sampling

It might be claimed that much of the variation we observed is an artifact of sampling processes. It is true that we have analyzed small- to medium-sized samples of individuals from larger assemblages, but for a number of reasons we believe these samples are representative of temporal and spatial variation in the combinations of species that actually occur together. First, although it might be suspected that the use of presence/absence data instead of relative abundances of species might exaggerate the apparent variation, this is not the case. We have shown elsewhere (Brown and Kurzius, 1987) that using presence/absence data actually gives a conservative estimate of variation in guild structure, because assemblages with the same species present typically exhibit great variation in the relative abundances of these species.

Second, it might be objected to that the use of presence/absence data overestimates the importance of rare species in communities. The above comment on variation in relative abundances is relevant here; species that are rare in some samples are common in others. In addition, we note that most of the species in all communities are relatively uncommon (for example, Preston, 1962; Williams, 1964; May, 1975; Sugihara, 1980). Because of difficulties in acquiring sufficient data on these rarities, many ecological studies may underestimate their importance in communities. Certainly an important feature of community organization is the ability of these numerous uncommon species to coexist with the numerically dominant forms.

Third, one might think that much of the variability we have shown is a consequence of the small and finite size of our samples. To a certain extent this is true. Sampling larger spatial areas or for longer time periods would tend to increase the apparent number of species in the guild and to reduce apparent variation in guild composition by combining samples that would otherwise have contained different numbers and combinations of species. But the extent of this effect is limited. Brown and Kurzius (1987) showed

that neither sampling effort nor number of individuals captured explained a substantial proportion of the macrospatial variation among guilds.

Finally, there is an important element of biological realism about our small, finite samples. The organization of granivorous desert rodent guilds has been attributed in part to interactions among the member species (see Brown, 1987, and Brown and Harney, 1988, and included references). In order for species to interact, individual members of those species must occur in sufficient proximity in time and space to affect each other. Although we cannot be certain of the exact number of individuals that have impacts on each other, the limited lifespans and home ranges of these rodents dictate that it is a modest number. We believe that our samples are representative of the numbers of individuals and combinations of species that are likely to interact frequently in the field.

The Individualistic Nature of Species and Communities

All of our analyses are consistent with an individualistic or Gleasonian view of species distributions and community organization. The distribution of individual species in both time and space suggests that each one responds to its own unique set of limits and requirements; each is also relatively independent of the effects of other species. As a consequence, local communities are assemblages of species that are able to live together because all members are able to satisfy their requirements. These are essentially the concepts of species distribution and community organization proposed by Gleason (1917, 1926) and supported by subsequent authors (for example, Whittaker, 1956, 1960; Hutchinson, 1958; Cole, 1982; Brown, 1984, 1987). It contrasts with Clements' (1916) concept of communities as combinations of closely integrated species with complementary functional roles. This "Clementsian" view is similar to those of subsequent authors (for example, MacArthur, 1972; Diamond, 1975, 1986; Roughgarden, 1979; Roughgarden et al., 1983; Grant, 1986), who have suggested that predictable patterns of species distribution and guild composition reflect the close coevolution of species in response to interspecific competition. The modern equivalents of Gleasonian and Clementsian concepts of community organization might be characterized as individualistic and coadjusted.

These views are not so much alternatives as extremes of a continuum. Most species and communities probably lie somewhere between these two extremes, so that the spatial and temporal distributions of all species depend to a certain extent on the effects of other species, but a high level of coevolved integration among coexisting species occurs infrequently. Here we shall confine our discussion to guild structure and to interactions among species within a guild defined both taxonomically and functionally. It may be no accident that most of the guilds that have been claimed to fall toward the coadjusted end of the spectrum occur on islands, whereas those that have been described as more individualistic occur primarily on continents. On islands, where species diversity is low and the habitat amplitude of

species is often high, the same combination of species may occur together repeatedly and predictably over large areas and long periods of time. One or a few other species in the same guild may be one of the most predictable and important environmental factors affecting the availability of essential resources and hence limiting the abundance and distribution of a species. There might often be strong, consistent selection for coevolutionary adjustments to reduce the intensity of interspecific competition. Thus, it is not surprising that the best examples of character displacement in apparent response to interspecific competition occur within insular guilds, such as Antillean *Anolis* lizards or Galapagos ground finches (see Schoener, 1970; Roughgarden *et al.*, 1983; Grant, 1986).

Our analyses of variation in desert rodent guilds and studies of terrestrial plant assemblages (for example, Shreve, 1914; Gleason, 1917, 1926; Whittaker, 1956, 1960, 1967; Cole, 1982) suggest that the distribution of species and the composition of guilds may be much farther toward the individualistic end of the spectrum in continental regions. In comparison to islands, continents have many more species and these have narrower habitat distributions but much larger geographic ranges. The result is that there is much more temporal and spatial heterogeneity in the distribution of species and the composition of guilds. Because species have broad geographic ranges, they could potentially occur with many other species, but because each species has unique requirements for habitat and other biotic and physical conditions, its distribution within its range is patchy. Each species occurs with many other species and many different combinations of species over its range (Brown and Kurzius, 1987). A similar pattern is seen at a microspatial scale. The distribution of each species is clumped, apparently in response to availability of resources. But because different species require different conditions, many different combinations of species can be found together at the smallest-scale unit that can be sampled, an individual grid stake.

This spatial heterogeneity is compounded by temporal heterogeneity. Continental communities are open systems (Brown, 1987). Each local patch of habitat is constantly susceptible to immigration of new species from nearby areas. Because the environment is constantly changing, invading species become established and existing species disappear as the conditions that they require wax and wane. Consequently, the numbers and combinations of species change on all time scales, from the thousands of years of Pleistocene-Holocene transition to the days or weeks of local ecological fluctuations. There must be some kind of coupling between the temporal and spatial changes in guilds. At least at certain scales, temporal fluctuations tend to be autocorrelated over space and vice versa. As climatic and vegetational changes occur over long time scales, species shift their geographic ranges and different combinations of species come into contact. As weather and resources change on shorter time scales, species expand and contract their habitat distributions and occur together with different combinations of species.

Perhaps the most surprising result of our analyses is not that such variation occurs, but that its magnitude is so great. The colonizations and extinctions of species that occurred at geographic spatial scales since the end of the Pleistocene and the local extinctions and recolonizations that occurred at our experimental study site within a single decade suggest a dynamic kind of community organization that is more often associated with insects than with endothermic terrestrial vertebrates. Admittedly desert environments are among the most widely and unpredictably fluctuating on earth, but desert rodent guilds hardly maintain any kind of constant organization, nor do they vary between some small number of alternative stable configurations.

Structure Versus Randomness: Patterns and Processes

A logical response to all of this variability would be to suggest that desert rodent guilds have little deterministic organization. Such an inference, however, would be unjustified and incorrect. Despite the enormous variation in both space and time, the species composition of guilds does not vary randomly as if the identity of coexisting species were the result of stochastic sampling from some larger species pool. Although the number of observed combinations of species is large, it is much smaller than the number of possible combinations of species that could occur together. The observed combinations are highly nonrandom (for macrospatial variation see Brown and Kurzius, 1987).

The nature of the deterministic structure in these assemblages depends to some extent on the scale. At a macrospatial scale, the local guilds are comprised of species that are more different in body size and other traits than expected on the basis of chance. Several different kinds of analyses clearly have shown that the body-size ratios between coexisting species are more different and more evenly spaced than expected from appropriate null models (Brown, 1973; Bowers and Brown, 1982; Hopf and Brown, 1986). If the granivorous desert rodents are divided into three functional groups on the basis of morphology and taxonomy (bipedal heteromyid, quadrupedal heteromyid, and quadrupedal murid), then guilds tend to be comprised of species from different functional groups significantly more frequently than expected by chance (Brown and Harney, 1988; B. J. Fox and J. H. Brown, manuscript in preparation). These patterns are consistent with the idea that competitive exclusion, which tends to be strongest between closely related species of similar morphology, has played an important role in determining which of the species in the available pool are actually able to coexist at the same local sites.

Within our experimental study site, the pattern of coexistence is different from the larger scale, but also nonrandom. There is a pronounced tendency for abundant species to occur in most of the samples, both in time (months) and in space (stakes or plots), whereas rare species are much more irregular and patchy in distribution. This is similar to the pattern of core and

satellite species noted by Hanski (1982). Tests of this pattern against null models are just beginning (Fox and Brown manuscript in preparation), but preliminary results suggest a significant degree of nonrandom organization. Apparently the presence or absence of species in these samples does not reflect stochastic variation in local abundance over time or space as suggested by Hanski (1982), but instead is a response to the deterministic dependence of local populations on the availability of essential resources (Brown, 1984). This interpretation is consistent with the observed tendency of the "core" and "satellite" species to belong to different functional groups; that is, the widespread, abundant species are mostly bipedal heteromyids, whereas the rare, patchy species tend to be quadrupedal heteromyids and murids (Tables 1-3). This suggests that at these small scales the availability of resources has at least as much influence on the combinations of species that occur together as does interspecific competition for these resources. Or in other words, once species are able to coexist within a patch of habitat, the probability that they will actually be found together in the same microtemporal or microspatial sample depends primarily on whether essential resources are available in sufficient supply. Species with similar requirements for resources often tend to covary in time and space, even though they may compete.

There may appear to be some inconsistency between the degree of deterministic structure in granivorous desert rodent guilds that we have reported and the individualistic or Gleasonian concept of species distribution and community organization that we advocated earlier. We do not think that this is the case. We believe that each species has unique requirements, and it tends to occur wherever those requirements are met and its population densities are determined primarily by local conditions. Local communities are comprised of those species that are able to coexist because the local environment satisfies their requirements. Interspecific competition among guild members is one process that can affect the availability of resources and hence the probability that certain combinations of species will occur together. But interspecific competition is only one factor that affects the suitability of the local environment. Therefore, it is not surprising that species of granivorous desert rodents exhibit highly individualistic distributions and local guilds show great variation in composition in both time and space, and yet, at the time, the distribution of these species and the structure of these guilds is limited to some extent by the availability of resources and competition among guild members for these resources.

Conclusions

We found enormous variation in the composition of guilds of granivorous desert rodents at all spatial and temporal scales that we were able to analyze. If the existence of such variation is not surprising, its magnitude is—at least it was to us. It raises two obvious questions. What is the pattern and magnitude of this variation in other kinds of organisms and in different

kinds of environments? What are the consequences of such variability for developing and testing general theories of community structure and function? Neither question is easy to answer.

We suspect that this kind of variation in community composition is widespread, perhaps even universal. This is not to deny that certain combinations of species, such as mutualists, predators and prey, and parasites and hosts, may occur together frequently and predictably. But within guilds of taxonomically and ecologically similar species, wide temporal and spatial variation in species composition is probably the rule, because the distribution of the component species is a consequence of their individualistic response to different combinations of several environmental variables. Comparative data for other organisms or habitats are hard to obtain, because ecologists have been concerned primarily with trying to characterize average conditions and general trends rather than the extent of variation. But other studies have documented comparable variability, especially over time. For example, enormous Pleistocene to Recent changes that apparently reflect the individualistic response of different species to environmental change (see Davis, 1986, and Graham, 1986) have been documented in assemblages of everything from trees to small mammals. At a smaller scale, Diamond and May (1977) documented great year-to-year changes in terrestrial bird assemblages inhabitating small islands in the British Isles. O'Connor (1981) has shown patterns of spatial and temporal variability in land birds in Britain comparable to those we have observed in desert rodents. From these and other examples, it is apparent that high levels of temporal and spatial variation are not confined to a few groups of organisms such as desert rodents and temperate insects. However, more studies that focus explicitly on variability clearly are warranted.

Such variation and the underlying individualistic nature of species distribution and community composition have important implications for attempts to develop and test general theories of community organization. On the one hand, such variation is intimidating, because it requires that any complete theory account for the great variety of observed combinations in addition to the average trends. On the other hand, the variation is helpful because it provides a great number of systems to test the predictions of alternative theories. One saving grace may be that the number of observed combinations, although often large, usually is much less than the almost astronomical number of possible combinations of even modest numbers of species. Therefore, it is possible to use tests of null hypotheses to detect patterns of association. Once nonrandom structures have been identified, they provide the basis for erecting and testing hypotheses about the underlying mechanistic processes that simultaneously maintain and limit variation in community organization.

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SMALL-MAMMAL COMMUNITY PATTERN IN AUSTRALIAN HEATHLAND: A TAXONOMICALLY-BASED RULE FOR SPECIES ASSEMBLY

Barry J. Fox

Abstract—An assembly rule is derived empirically for a small-mammal community from coastal heathlands in eastern Australia. The rule is based on the spatial niche overlap and niche separation observed for this community in which interspecific competition and diffuse competition have been experimentally verified. The rule can be stated in its simplest form as follows: there is a much higher probability that each species entering a community will be drawn from a genus, a guild, or a taxonomically related group of species with similar diets, until each group is represented. The rule is repeated in species-rich communities and is an extension of the niche compression hypothesis and of previously derived assembly rules. Combinations of species that lack a member from one group while having two or more species from any other group occupy "forbidden" or "unfavored" states, as this implies the existence of underutilized resources and will be susceptible to invasion. When assemblages of species observed from 52 heathland sites from eastern Australia (20°S to 43°S) were compared to expected values calculated from neutral-model Monte-Carlo simulations, "unfavored" states had significantly fewer sites than expected for any chance assembly of species ($P < 0.01$), whereas "favored" states had significantly more ($P < 0.001$). The rule should have wider applicability to other mammal communities and indeed to other taxa.

Diamond (1975) first proposed a series of assembly rules, based on interspecific competition, to provide insight into bird community structure. The role of interspecific competition as an important factor influencing the patterns observed in the structure of communities had already been recognized for rodents (Brown, 1973, 1975), lizards (Pianka, 1973), and birds (Cody, 1974). Diamond based his assembly rules on matching the resource utilization functions of individual species to the resource production curves for the habitat supporting each community. Permissible combinations were those that left fewest resources unused, combinations of species with amounts of unused resources were incompatible as they were subject to invasion and were hence unstable.

A detailed assembly rule to explain the structure of communities of seed-eating desert rodents was devised by M'Closkey (1978). He demonstrated that his empirical assembly rule produced a similar minimization of unused resources as did those of Diamond (1975). M'Closkey used niche axes of seed size and habitat use to show that niche separation increased with species richness, for relatively low-diversity communities, as predicted by May and MacArthur (1972). In addition, he was able to show mean ecological overlap to be a negative function of species diversity, thus supporting Pianka's (1972) niche overlap hypothesis.

M'Closkey (1978) measured the mean niche separation for all possible combinations of two-, three-, and four-species assemblies from the pool of four rodent species encountered. Of the 11 combinations possible only four were observed—those assemblies showing the closest packing of niches (minimum separation). The observed assemblies were saturated, whereas "imaginary assemblies," those not observed, showed greater niche separation and were regarded as under-saturated because all available resources were not used. This supported Diamond's (1975) proposal that observed assemblies match resource production curves better than "imaginary assemblies."

Simberloff and Connor (1981) have questioned both Diamond's (1975) assembly rules and M'Closkey's (1978) application of similar competition-based rules to mammal assemblages. In particular, Simberloff and Connor questioned whether M'Closkey had a single species pool of four species, or two separate pools of two and four species. Recently, M'Closkey (1985) clearly has demonstrated the existence of a single four-species pool, thus supporting his earlier conclusions and his application of assembly rules.

This paper proceeds from a detailed analysis of the structure of the small-mammal community on a series of abutting patches of discrete habitat, to reveal an empirically-derived, taxonomically-based assembly rule for the species comprising the assemblage in each habitat. The rule is an extension of the niche compression hypothesis of MacArthur and Wilson (1967), but without their restriction to an ecological time scale, and uses the ideas suggested by M'Closkey (1978) and the basic precept proposed by Diamond (1975). Previous studies of simulation experiments (Fox, 1981) and manipulation experiments (Fox and Pople, 1984) support the use of such competition-based models and the applicability of similar assembly rules to this small-mammal community. The model for species assembly derived from this rule then was tested against small-mammal assemblages in eastern Australian heathlands, as determined from the literature (Fox, 1985), to compare the expected and observed community structure.

The Study Area and the Community

The major study area was in the Myall Lakes National Park (32°28′S, 152°24′E), and is a mosaic of patches of swamp, wet heath, dry heath, tree heath (or woodland), and forest. The vegetation, the small mammals, and their spatial distribution on this seven-hectare site have been described (Fox, 1981, 1983), as has the long-term response of the community to wildfire (Fox, 1982a). The seven species of small mammals present have significantly nonrandom spatial distributions and a set of hierarchical simulations show that interspecific interactions influence community structure (Fox, 1981). Subsequent analyses of ecological separation (Fox, 1982b), resource sharing (Fox and Archer, 1984), and manipulation experiments (Fox and Pople, 1984) have confirmed that interspecific competition does play an important role in this community.
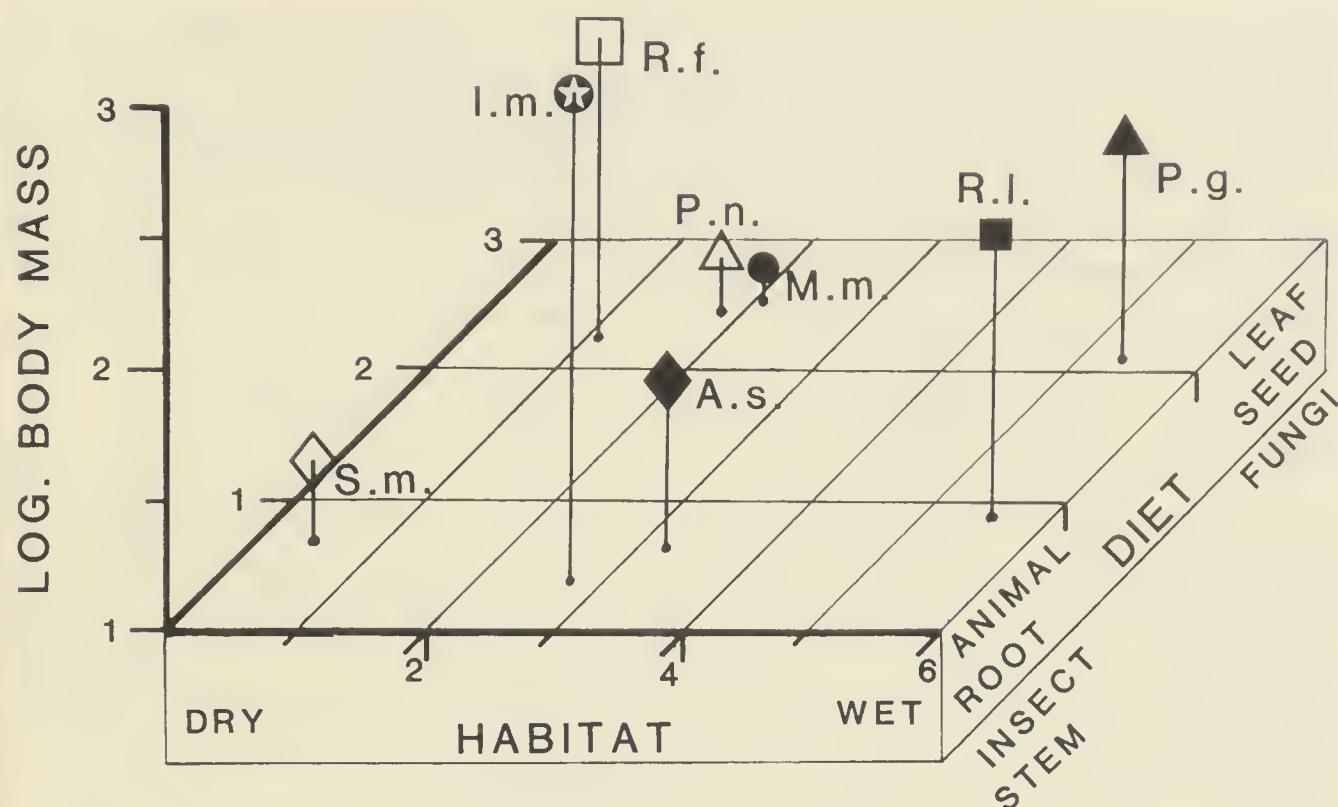
Fig 1.—Niche separation shown for the eight most common species of small mammals in the Myall Lakes community. The axes are: the logarithm of body mass (in grams); the first factor from a principal component analysis of diet; and the first factor from a similar analysis of habitat use. The species shown are the marsupials: *Sminthopsis murina* (*S.m.*), *Antechinus stuartii* (*A.s.*), *Isoodon macrourus* (*I.m.*); and the rodents: *Pseudomys gracilicaudatus* (*P.g.*), *Rattus fuscipes* (*R.f.*), *R. lutreolus* (*R.l.*), *Mus musculus* (*M.m.*).

The structure of the small-mammal community occupying this site is illustrated in three dimensions—habitat, diet, and body size (Fig. 1); body size is used rather than the more usual temporal dimension as all species show similar nocturnal activity patterns (Fox, 1978). The axis of body size on a logarithmic scale is self-explanatory but the other axes need explanation. The proportional use by each species of the seven habitats available to it (Fox, 1983) was used as the raw data for a principal component analysis to establish the score for each species on the first principal component, explaining 43 percent of the variance, which was then used as the habitat axis. A similar procedure was used for the diet categories: leaf, stem, root, seed, fungi, insect, and animal to provide scores for each species on the diet axis, taken from the first principal component, which explained 55 percent of the variance.

Taxonomic Groupings

The small mammals present belong to the families Dasyuridae (*Antechinus stuartii* and *Sminthopsis murina*, insectivores) or Muridae, which is subdivided into the "old endemic" conilurine rodents (*Pseudomys novaehollandiae* and *P. gracilicaudatus*, granivores-omnivores) and the "new endemics" *Rattus* (*R. fuscipes* and *R. lutreolus*, herbivores). The introduced *Mus musculus* (omnivore) and the larger peramelid *Isoodon*

macrourus (insectivore-omnivore) complete the common members of this fauna. The two dasyurid species, although from different genera, have been treated as one group as there are no biologically significant differences in their diets (Fox and Archer, 1984). This demonstrates a trophic base that in most cases parallels the taxonomic groupings but may overrule them in some circumstances. The assembly rule, therefore, may be more appropriately termed a guild rule rather than a taxonomic one.

Niche Parameters and Observed Species Assembly

The effect of increasing species richness on niche parameters in this community has been studied (Fox, 1981). Spatial niche overlap decreases as predicted by Pianka's (1972) niche overlap hypothesis, whereas spatial niche separation increases as predicted by May and MacArthur (1972) for relatively low-diversity communities. Spatial niche separation increases at a significantly greater rate than for randomly assembled communities; this and the associated decrease in spatial niche overlap provide the empirical basis for the assembly rule proposed here.

The assembly of species into the communities occupying different habitat patches (Fig. 2) illustrates the operation of an interesting assembly rule, with entry based on the presence or absence of species from the other taxonomic groups available. For three wet habitats, the least rich has two species, one *Rattus* (*R. lutreolus*) and one dasyurid (*A. stuartii*); the three-species habitat patch has added one *Pseudomys* (*P. gracilicaudatus*); the four-species habitat patch has added a second species of *Pseudomys* (*P. novaehollandiae*). The least rich dry habitat has four species, one each from the dasyurids (*S. murina*), *Pseudomys* (*P. novaehollandiae*), and *Rattus* (*R. fuscipes*), in addition to the introduced *M. musculus* found in all the dry habitats. To this is added a second dasyurid (*A. stuartii*) in the five-species patch; then follows a second *Pseudomys* (*P. gracilicaudatus*) and a second *Rattus* (*R. lutreolus*), respectively, in the six- and seven-species habitat patches.

The Assembly Rule

The rule suggested by Figure 2 is expressed in terms of the three groups of native small mammals used above, *Pseudomys, Rattus*, and dasyurid, and can be stated in a probabilistic manner as follows. There is a much higher probability that each species entering a community will be drawn from a genus, a guild, or a taxonomically related group of species with similar diets, until each group is represented. The rule is viewed as operating at a generic level reflecting the organization of the community from which it was empirically derived. However, there may be other cases in which the operational groups, in the sense of a guild, are suprageneric or subgeneric. Henceforth, I will use the term "group" in this wider sense. Generally, there will be sufficient diversity and abundance of resources to accommodate
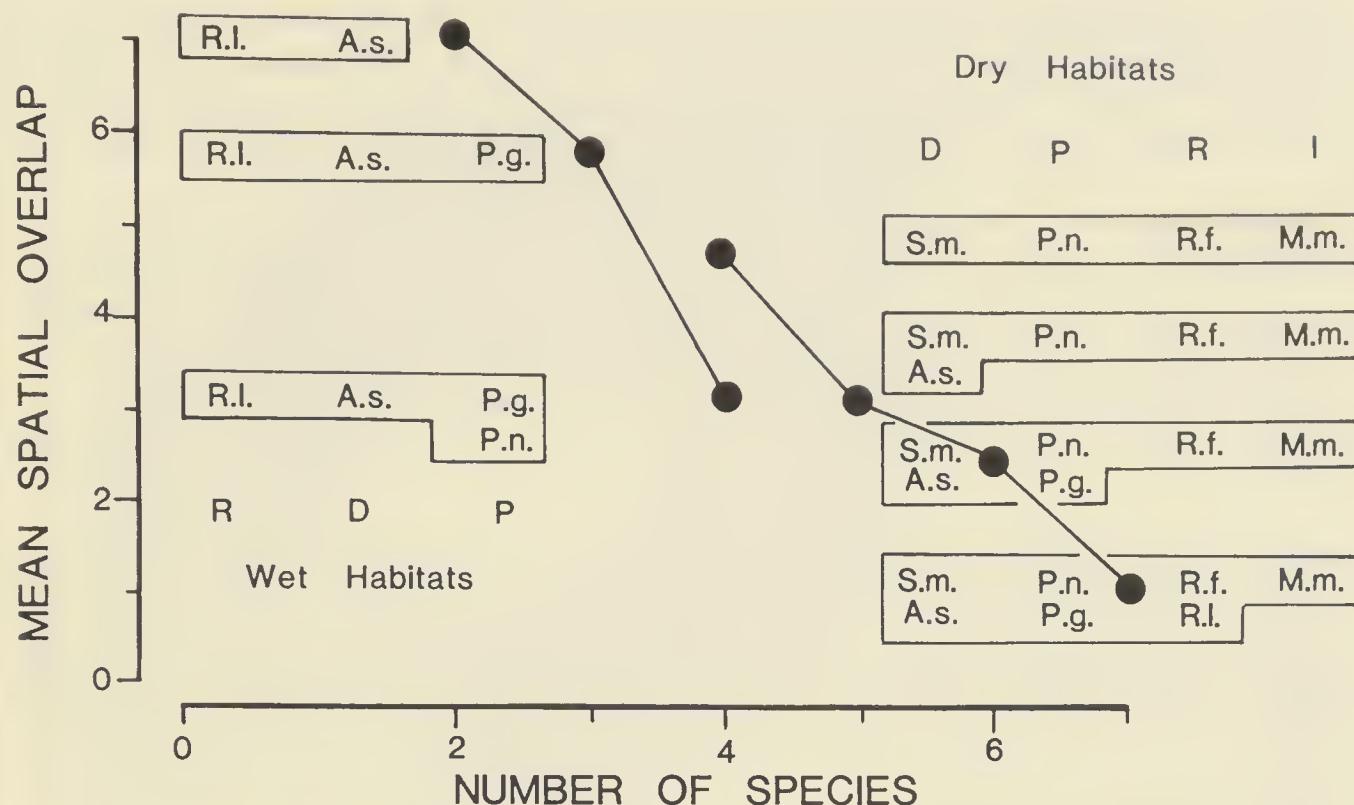
Fig 2.—Mean spatial niche overlap as a function of species richness for seven habitat patches (three wet and four dry). The structure and order of species packing is shown for species from the groups *Pseudomys* (P), *Rattus* (R), and dasyurid (D), with the introduced (I) *Mus musculus* shown in all four dry habitats. Species abbreviations as for Figure 1 and the numbers refer to habitat patches in Fox (1981).

one member from each major group before a second member from any one group can be accommodated as the rule repeats.

The Rationale

This rule is in part an extension of MacArthur and Wilson's (1967) niche compression hypothesis, which states that whereas a species habitat niche may be compressed to accommodate more species in that habitat, the diet niche will suffer little compression.

The data presented in Table 1 illustrate the diet and habitat niche separation for species pairs in this community and is based on the first principal component scores for these axes. The within-group mean value for diet niche separation (0.55) is below the 95 percent confidence interval for the mean of between-group pairs (0.69-1.57), whereas the within-group mean for habitat niche separation (1.80) exceeds the 95 percent confidence interval for mean value from between-group pairs (0.69-1.75).

Within any group, speciation has ensured that there are genetically based morphological constraints operating on characters, such as dental morphology and digestive physiology, which means that pairs of species within the group will have a higher probability of less diet niche separation (and hence greater overlap) than between-group species pairs. Conversely sympatric, within-group species pairs will have a higher probability of greater habitat niche separation (and hence less overlap) than sympatric between-group

TABLE 1.—*Mean values for habitat and diet niche separation for congeneric or within-group pairs (S.E.) and confidence intervals for the mean values for all between-group pairs. Data are for six native species of small-mammals (from Fig. 1), based on the first principal component scores for each resource axis. The bandicoot* (Isoodon macrourus) *is excluded because of its differential trappability (Fox, 1981).*

Species pairs	Mean niche separation	
	Habitat	Diet
All between-group pairs 95% confidence interval for the mean (N=12)	0.69-1.75	0.69-1.57
Within-group pairs mean value followed by S.E. in parentheses (N=3)	1.80 (0.27)	0.55 (0.40)

species pairs. Another possible example may be found in the morphological stasis of the plethodontid salamanders, coupled with their behavioral plasticity, which has allowed compensation for environmental change (Wake *et al.*, 1983). This would extend the niche compression hypothesis (MacArthur and Wilson, 1967) from an ecological to an evolutionary time scale.

It follows that within any given habitat, at low species richness, the community will comprise one member only from each group. The species in this community will have greater diet niche separation (and less overlap) than would additional species from the same group. As the diversity of available resources increases, sufficient resources become available to support a second species from one group and the rule continues to operate at this second tier so that a second species from another group is accommodated (rather than a third species from the first group). Although Tilman's (1982) productivity-diversity curves have been shown to be applicable to small mammals (Abramsky and Rosenzweig, 1984), I have not addressed that question here. However, I can see no reason why this rule should not work for species richness decreasing, as well as increasing, as a function of increasing productivity.

It should be noted that these predictions do not specify the order in which species will enter but rather which genera (or species groups) are "forbidden" to enter. This introduces the notion of "forbidden states" that can be illustrated in the three-dimensional model shown in Figure 3. Such states are not "forbidden" in the sense that they cannot physically occur, rather they might be called "unfavored" states, with a low probability of occurrence, because if they do occur there will be unused resources and the community will contain an "empty niche" for the group not represented. The assembly will be subject to invasion and hence unstable. When more detailed information is available on the species present and their resource use, it may be possible to make additional predictions such as: in wet habitats the first *Rattus* will be *R. lutreolus*, whereas in dry habitats it will be *R. fuscipes*.

The mechanism proposed for the rule is similar to that outlined by Diamond (1975:425). If one considers a single complex resource axis (for

A MODEL FOR SPECIES ASSEMBLY
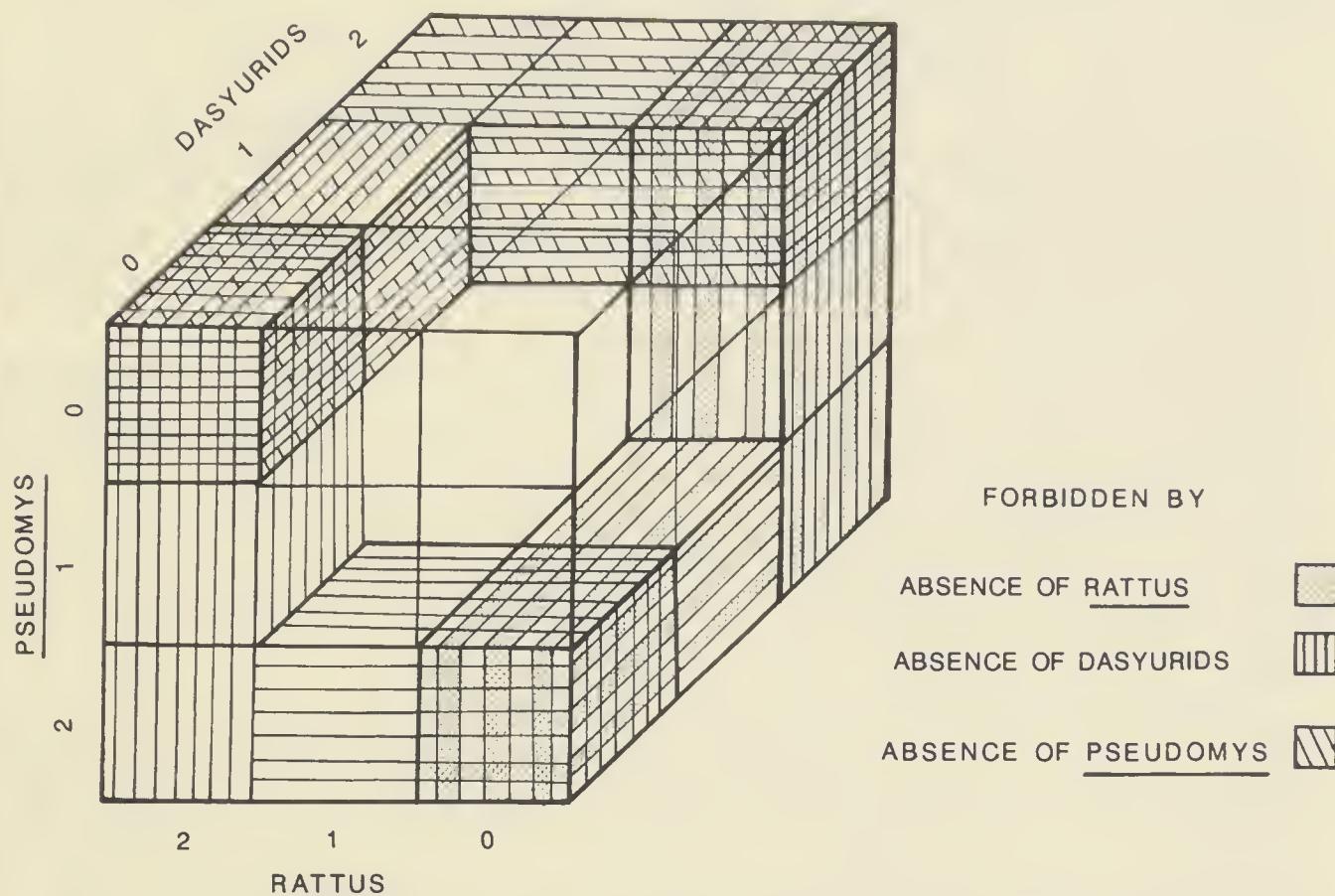
FIG 3.—A model for species assembly, showing for each cell the number of species (none, one, or two) from the three groups *Pseudomys, Rattus*, and dasyurids. Cells with one species group absent and more than one species present from a second group are "forbidden" as their existence implies an "empty" niche from the absent group. "Forbidden" states are shown coded for the absent group.

example, a principal component axis) with positions marked H, O, and I as the notional centers of resource use for each of the three species groups or guilds (herbivores, omnivores, and insectivores), progression through "allowed" or "favored" states occurs, with the community increasing in richness, as the available resources increase in abundance and diversity. A "forbidden state" can occur in two ways: it can result from the unavailability of members of one taxonomic group (as seen for the disjunct distributions of *Pseudomys* sp. explained below), thus creating an empty niche; or because of some super abundance of one particular type of resource, caused by an asymmetric resource availability curve. The dietary resources available to these three trophic groups are not independent, because their relative abundances are linked. The manner in which these resources are linked differs in different habitats so that the exact distribution and availability of resources is site-specific and determines which of the three trophic groups first is able to enter that habitat and the order that follows. In this simplest case, the omnivore is placed between the extremes of insectivore and herbivore. A detailed analysis of the theoretical basis for the rule has been published recently (Fox, 1987), including a possible

operational mechanism and a step-by-step worked example of the simulation used for the neutral model.

A Test of the Model

If such a model has any wider applicability to communities other than the one from which it was derived, then a survey of a large number of small-mammal communities should show this pattern. A set of 52 heath sites from eastern Australia have been collated from the literature (Fox, 1985) and provide the basis for such a test.

In Figure 3 each cell is labelled according to the number of species of *Pseudomys*, *Rattus*, and dasyurids in the community so that the bottom, back, right-hand cell represents no *Pseudomys*, two *Rattus*, and two dasyurids (P0 R2 D2) or in matrix notation X(022). The bottom, front, left-hand cell then becomes X(000), representing sites where no animals were caught. Those cells representing states "forbidden" by an unfilled niche are indicated by heavy outlines.

The results of the survey are shown in Figure 4 where each slice of the model is shown separately and cell entries represent the frequency of occurrence for communities with that particular structure. The values for the above two examples for heath sites can be seen in Figure 4—X(002) = 0 and X(000) = 3. A common community of one member from each group X(111) can be seen to have occurred six times in heathland (Fig. 4).

Equal Probability Case

Expected values for the number of sites occupying each state were determined using neutral-model, Monte-Carlo simulations (n = 500) of the distribution of the 52 heath assemblages into the 27 cells. Each simulation was constrained to have the same number of sites with one, two, three, four, five, or six species as was observed. In this first simple model, a probability of 1/3 was used to allocate each species drawn to one of the three groups shown.

The favored and unfavored states were analyzed separately using the log-likelihood ratio test to compare observed and expected values. The results of this simple model are summarized in Table 2A, unfavored states contained significantly fewer sites than expected (G = −6.67, $P < 0.01$), whereas favored states contained significantly more (G = +25.36, $P < 0.001$).

Fractional Contribution Case

The main difficulty in the null-model simulation is in assessing the actual probability of belonging to each group, as there is no common pool of species available to all sites. This is a function of the 16 degrees of latitude included in the study. To overcome this problem, the contribution that each species makes to the pool of species (available on average to each site) is determined by the number of locations that fall within the
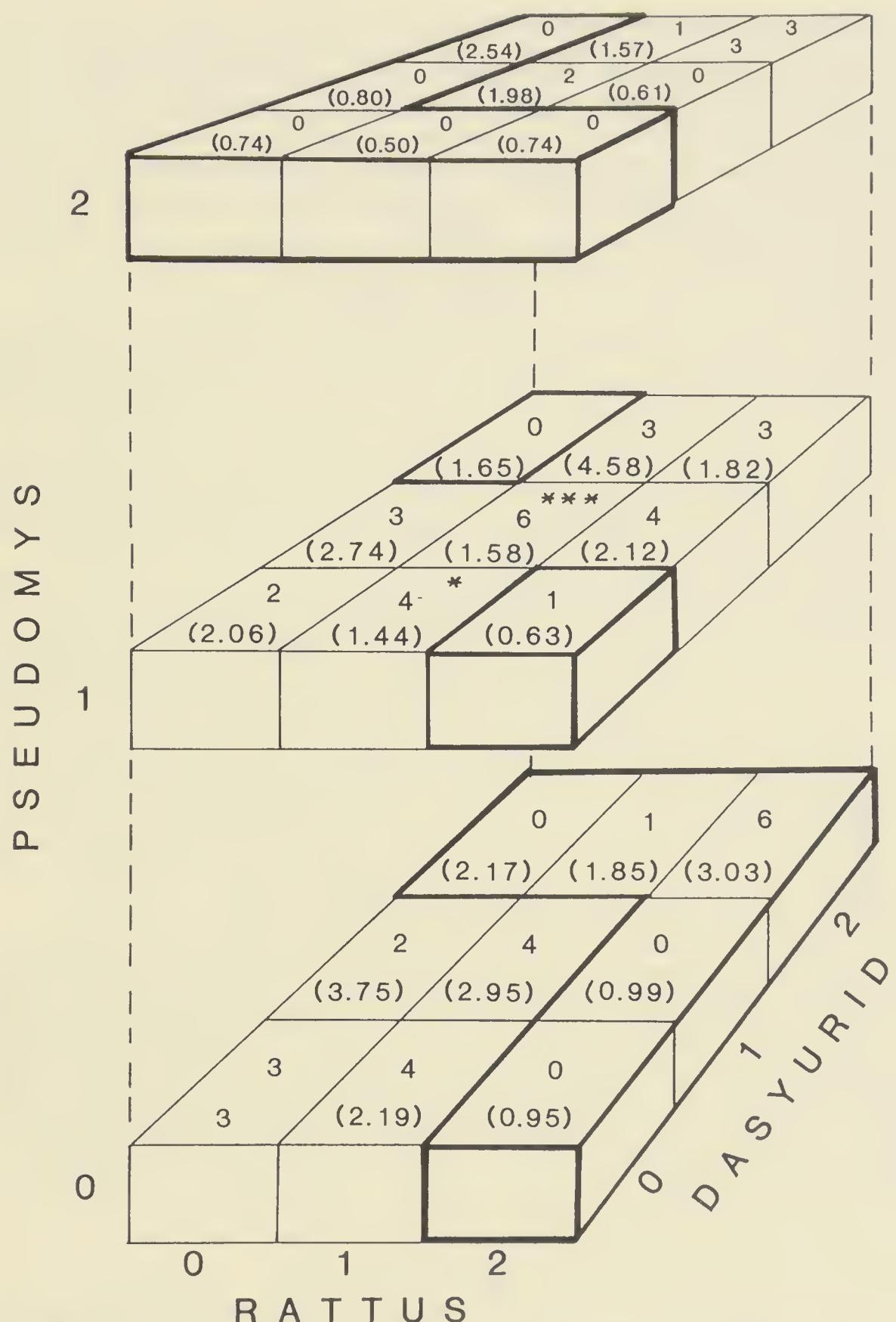
FIG 4.—An analysis of the distribution of observed communities on the model for community structure shown in Figure 3 where the model is represented as three slices with none, one, or two species of *Pseudomys* present, covering the 52 heath sites from Tasmania, Victoria, New South Wales, and southeastern Queensland. The heavy borders represent "forbidden" or "unfavored" states shown in Figure 3. The data are derived from Fox (1985) which incorporates sites in the literature. Shown in parentheses are the expected values for each state using a neutral-model Monte-Carlo simulation constrained to match the observed number of sites with 1,2,3,4,5 or 6 species assemblages, see text for further detail (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

geographic distribution of species (Strahan, 1983) divided by the total of 33 heath locations shown in Fox (1985). These 33 locations contain 52 heath sites (plus two additional sites, see Table 2B and text below), as one geographic location often had more than one site. The fractional contribution from each species in the group then is summed to give the average number of species from that group that is available to each site. These were *Pseudomys* = 1.82, *Rattus* = 1.97, and dasyurids = 3.24, giving probabilities of 0.2586 : 0.2802 : 0.4612, respectively.

The results of this more realistic model are displayed in Figure 4, showing the observed and expected values for the frequency of sites in each of the 27 cells. Expected values were obtained from 10 sets of neutral-model, Monte-Carlo simulations, each with 30 iterations. For each set, an expectation value and 95 percent confidence interval were calculated and mean values from the 10 sets were used in Figure 4. In two favored states, observed frequencies significantly exceeded the expectation, for (1,1,1) this was highly significant ($P < 0.001$).

The statistical analysis of these results is shown in Table 2B. In favored states, observed frequencies were significantly greater than expected (G = 20.76, $P < 0.001$), whereas for unfavored states they were significantly less (G = −9.98, $P < 0.01$). Two additional sites had three species of dasyurid and, hence, were not included in the simulation, but they can be included in the remaining analysis. These sites occupied cells (0,2,3) and (1,2,3), both unfavored. It is possible to set limits on the expected values for these cells by inspection of the surrounding cells in Figure 4. For the first cell, the minimum, estimated, and maximum frequencies likely are 0, 2.0, and 6.0, whereas for the second cell they are 0, 1.3, and 3.0.

The influence of these two additional unfavored states can be seen from the entries in parentheses in Table 2B. Here, the observed and expected frequencies are shown, together with the amended G-values for unfavored states, spanning the minimum, estimated, and maximum range indicated above. The effect is minimal, in the limiting case where the expected frequencies are taken as zero the G-value decreases marginally, but still remains highly significant [G = −7.35, $P < 0.01$]. In all other cases, the significance is increased.

Discussion

For the 52 heath sites (Fig. 4), only eight were found to occupy any of the 12 unfavored states. Seven of these sites were unfavored because no *Pseudomys* was present; however, in each case the introduced *Mus musculus* was present, filling the otherwise vacant *Pseudomys* niche (granivore-omnivore). At both of the additional sites, *M. musculus* also was reported present and at the (0,2,3) site *P. novaehollandiae* had been reported in the recent past but no longer was present. The role played by the introduced *M. musculus* is important, because *Pseudomys* sp. now have disjunct distributions and often are rare (Strahan, 1983), whereas subfossil deposits

TABLE 2.—*The frequency of occurrence of 52 heath sites for 27 cells, pooled into three categories determined by the number of species of dasyurids present, analyzed separately for favored and unfavored states. A)—A simplistic model with equal probabilities of entry (1/3), mean of 500 simulations. B)—A more realistic model with probabilities determined by species geographic distributions (see Fig. 4 and text), mean of 10 sets of 30 iterations. Included in parentheses are values for two additional sites not able to be included in the simulation (see text). (A double asterisk = P < 0.01, a triple asterisk = P < 0.001). Amalgamated cells are shown in italics.*

A)		Number of species of dasyurids					G-value total
States		0	1	2			
Unfavored	observed	1	0	7			
	expected	7.58	*3.15*	8.03			**
	G-value		(−4.75)	+	(−1.92)	=	−6.67
Favored	observed	13	21	10			
	expected	8.06	16.45	8.75			***
	G-value	(12.43)	+	(10.26)	+	(2.67) =	+25.36

B)		Number of species of dasyurids				G-value total
States		0	1	2	[3]	
Unfavored	observed	1	0	7	[2]	
	expected	*3.56*	*1.79*	11.24	[0/3.3/7]	**
	G-value		(−3.35) +	(−6.63) =	−9.98	
					[−7.35/−11.98/−16.0] ** *** ***	
Favored	observed	13	21	10		
	expected	8.69	15.73	10.97		
	G-value	(10.47) +	(12.14) +	(−1.85)	=	+20.76 ***

indicate that they once were abundant and more widely dispersed in eastern Australia (Wakefield, 1972).

This rule is complementary to that of M'Closkey (1978); it is more general in that it does not require the detailed information of niche separation for all species pairs, yet at the same time it does not identify individual assemblages, only the groups from which the species should come. It should be possible to combine both rules, this rule determines favored and unfavored states from the genera or groups involved so ensuring sufficient niche separation to allow coexistence. If the relevant information is available, M'Closkey's (1978) rule provides the detailed predictions on which species combinations can occupy the favored states in order to maximize species packing. In this way, the two rules establish both a lower and an upper limit for allowable niche separation between species.

The model presented here still requires refinement, most obviously the introduction of information on the availability of different resource categories to determine the shape of the resource production curve (Diamond, 1975) at each site. Collection of such data is both time- and labour-intensive, but is underway. If this information were to be combined

with a better understanding of resource utilization curves for each species, it would be possible to predict the species that should form an assemblage rather than just the genus or group from which they should come. M'Closkey's (1978) rule provides one method of including this information.

Another obvious problem is determining the level at which groups are defined. Although a generic-level grouping is desirable, it may not always be practical, indeed that point is well demonstrated by the dasyurids (*A. stuartii* and *S. murina*) in this example. Rather the groupings should be determined by the degree of sharing or overlap of diet resources to be consistent with the theoretical justification for this assembly rule. The problem in fact becomes one of defining guilds (see Adams, 1985). This point emphasizes that the real basis for the rule is a trophic one, which is reflected in most cases by taxonomic groupings, and the mechanism is one of reducing diet overlap in communities occupying the one habitat. As habitat (and hence resource) diversity increases, additional species from each group can be added as greater diet overlap then can be tolerated. The important point is to recognize the resource components that are in short supply and hence the subject of competition within groups. Where such resources are not limiting this assembly rule may not operate in the same way.

With a better understanding of how to identify guilds, to determine species groups, I see no reason why this rule should not have a wider applicability to other mammal communities, and indeed, to communities of other taxa.

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DIRECT TESTS FOR COMPETITION IN NORTH AMERICAN RODENT COMMUNITIES: SYNTHESIS AND PROGNOSIS

RAYMOND D. DUESER, JOHN H. PORTER, AND JAMES L. DOOLEY, JR.

ABSTRACT—Manipulative experiments frequently are used to test for the species-wise effects of interspecific competition in North American rodent communities. Evidence for ongoing competition has been reported for 80 percent of 25 studies, 68 percent of 50 experiments, and 38 percent of 138 tested effects. Competition experiments have differed in degree of replication, type and timing of controls, type of experimental units, duration and timing of treatments, prevailing population densities, and dependent (response) variables. Most experiments, however, have involved short-term (less than two generations) tests for numerical responses, or habitat shifts, or both, by open-grid populations. Numerical responses are observed less often than habitat shifts, but neither response is observed frequently. The most conspicuous responses are exhibited by partially- or fully-enclosed populations. The results of these experiments suggest that interspecific competition is neither so strong nor so pervasive that it can be casually invoked as the active organizing force in any given rodent community. Nevertheless, only a few of the studies in which an absence of competitive effects has been reported lend themselves to a statistical power analysis by which we might weigh confidence in this "negative" conclusion. The results of *post hoc* power analyses for eight replicated, fully-reported experiments reveal that only one produced unambiguous results vis-à-vis the occurrence of competition—and this was an experiment in which competition was actually observed. Examination of statistical power curves for simulated removal experiments incorporating practical levels of replication confirms that the detection of subtle competitive effects will be statistically difficult with populations exhibiting typical levels of variation in abundance.

Recent reviews by Schoener (1983) and Hurlbert (1984) graphically illustrate both the importance and the difficulty of performing manipulative field experiments with small mammal populations. Schoener (1983) summarized 164 experimental field studies in which tests were reported on the occurrence, effects, and significance of interspecific competition. Rodents were the subject of 19 studies, representing 12 percent of all studies, 40 percent of studies involving vertebrates, and 95 percent of studies involving mammals. Seventeen (89 percent) of these 19 studies reported evidence for competitive effects on at least one species (Schoener, 1983:table 1). Schoener interpreted these studies as providing evidence for the importance of competition in natural communities. Hurlbert (1984) subsequently examined the statistical experimental designs of 176 manipulative ecological field experiments. He described five of the rodent competition studies cited by Schoener as containing serious statistical-analytical flaws. All five incorporated pseudoreplication (that is, no replication of treatments or a lack of independence between replicates) in one form or another, prompting Hurlbert (1984:199) to conclude: "Where

TABLE 1.—*Summary of 25 studies that have reported manipulative field experiments to test for the occurrence and consequences of interspecific competition in North American small mammal communities.*

Reference	Location[1]/ habitat[2]	Grids/ controls[3]	Number experiments	Species removed[4]/ remaining[5]	Number grids[6]	Grid traps/ area (ha)[7]	Months/ trap-nights[8]	Effects tested[9, 10]
Abramsky et al., 1979	CO/G	O/S	1	Moc, Rm/Pmm	1/1	118/1.00	8/5488	DENS
Blaustein, 1980	CA/G	O/S	1	Mc/Rm	1/1	50/0.10	2/2300	CAPS, ARBO, imig
Brown and Munger, 1985	AZ/DS	P/B	2	Dm, Do, Ds/ Ol, Ot, Pgf, Pgp, Pme, Pmm, Rm	4/4	49/0.25	60/23520	caps, repr, rest, pres, bwgt, DENS[15], ROEC
				Ds/Dm, Do, Pgf, Pgp, Pmm, Pme, Rm, Ol, Ot	2/2	49/0.25	36/7056	dens
Caldwell and Gentry, 1965	SC/G	E/N	1	Pmp/Mum	1/1	43/0.68	19/?	XCLU
Cameron 1977; Cameron and Kincaid 1982	TX/CP	O/S	2[11]	Rf/Sh	2/2	81/1.60	36/26244	imig, dens, ages, repr, bwgt, move, tire, sexr, recr, surv, arbo
				Sh/Rf	2/2	81/1.60	36/26244	imig, dens, ages, repr, BWGT, MOVE, TIRE, sexr, RECR, surv, ARBO

TABLE 1.—Continued.

Reference	Location[1]/habitat[2]	Grids/controls[3]	Number experiments	Species removed[4]/remaining[5]	Number grids[6]	Grid traps/area (ha)[7]	Months/trap-nights[8]	Effects tested[9, 10]
Cameron et al., 1979	TX/CP	O/S	2[11]	Sh/Rf	1/1	81/1.60	12/?	caps, dens
				Rf/Sh	1/1	81/1.60	12/?	caps, dens
Chappell, 1978	CA/SW	O/S	2[11]	Ea/Em	1/1	55/8.80	6/?	HABS, life
				Em/Ea	1/1	55/8.80	6/?	habs, life
DeLong, 1966	CA/G	P/S	1	Mc/Mum	1/1	?/0.54	8/?	bgro, DENS, repr, emig, RECR, surv
Galindo and Krebs, 1985a	YU/MW	O/B	2	Mp/Pmm	1/1	120/1.20	5/4800	HABS, dens, repr, recr, SURV
				Mp/Pmm	1/3	120/1.20	5/7920	habs, dens, repr, RECR, SURV
Galindo and Krebs, 1985b	YU/T	O/S	1	Moe/Mmi	1/1	102/1.00	4/1508	habs, dens
Grant, 1969	QU/GW	E/S	2[11]	Mp/Cg	1/1	50/0.47	4/3400	HABS
				Cg/Mp	1/1	50/0.47	4/3400	habs, recr
Grant, 1971	QU/GW	E/S	3	Mp/Pmm[12]	1/1	50/0.40	4/8550	MOVE, HABS, imig, SPAT
				Mp/Pmm[12]	1/1	50/0.40	4/8550	IMIG, HABS, recr, SPAT
				Mp/Pmm[12]	1/1	50/0.40	5/9975	recr, HABS, MOVE, SPAT

TABLE 1.—Continued.

Reference	Location[1]/ habitat[2]	Grids/ controls[3]	Number experiments	Species removed[4]/ remaining[5]	Number grids[6]	Grid traps/ area (ha)[7]	Months/ trap-nights[8]	Effects tested[9, 10]
Holbrook, 1979	AZ/SW	O/B	4[11]	Ns/Pmb	1/1	100/1.50	3/2200	HABS, arbo, life, spat, dens
				Pmb/Ns, Pmm[12]	1/1	100/1.50	3/2800	life, ARBO, HABS, spat
				Pmb/Ns, Pmm[12]	1/1	100/1.50	3/2800	habs, ARBO, LIFE, spat
				Pmb, Ns/Pmm[12]	1/1	100/1.50	3/3800	ARBO, LIFE, habs, spat
Joule and Jameson, 1972	TX/CP	O/S	2[11]	Orp, Rf/Sh	3/3	54/1.20	4/4749	caps, BWGT, SEXR
				Sh/Orp, Rf	3/3	54/1.20	4/4749	caps, bwgt, sexr
Kincaid and Cameron, 1982	TX/CP	O/S	2[11]	Rf/Sh	1/1	81/1.60	14/6804	habs, diet
				Sh/Rf	1/1	81/1.60	14/6804	habs, diet
Koplin and Hoffmann, 1968	MT/G	O/B	1	Mp/Mmo	1/1	200/1.01	11/4709	HABS, move
Morris and Grant, 1972	SA/GW	E/N	2	Cg/Mp	1/1	60/0.80	2/1080	HABS
				Cg/Mp	1/1	131/0.80	7/13000	HABS
Munger and Brown, 1981	AZ/DS	P/S	1	Dm, Do, Ds/ Pgf, Pgp, Pmm, Rm	4/4	49/0.25	36/?	CAPS, DENS
Petersen, 1973	DU/DG	O/S	1	Sf/Sh	2/1	49/0.81	13/8575	DENS, SPAT, move, surv
Price, 1978	AZ/DS	E/B	6	Dm/Pmb[12]	1/1	32/0.31	2/448	None[14]
				Dm/Pgp[12]	1/1	32/0.26	2/448	

TABLE 1.—Continued.

Reference	Location/habitat[2]	Grids/controls[3]	Number experiments	Species removed[4]/remaining[5]	Number grids[6]	Grid traps/area (ha)[7]	Months/trap-nights[8]	Effects tested[9,10]
Rebar and Conley, 1983	NM/DG	E/S	2[11]	Dm/Pgb[12]	1/1	32/0.34	2/448	habs
				Dm/Pmb[12]	1/1	32/0.31	2/448	HABS
				Dm/Pgp[12]	1/1	32/0.26	2/448	
				Dm/Pgb[12]	1/1	32/0.34	2/448	
				Do/Ol	1/1	36/0.40	2/1440	DENS, XCLU
				Ol/Do	1/1	36/0.40	2/1440	DENS, xclu, RECR
Redfield et al., 1977	BC/G	O/S	3	Mt/Pmm	1/1	100/0.64	39/31200	DENS, REPR, SURV
				Mor, Mt/Pmm[12]	1/1	100/0.64	37/29600	
				Mor, Mt/Pmm[12]	1/1	100/0.64	24/19200	
Schroder and Rosenzweig, 1975	NM/DG	O/S	4[11]	Dm/Do[12]	2/2	331/16.20	8/10000	dens, imig, habs
				Dm/Do[12]	2/2	331/16.20	5/5900[13]	dens, imig, habs
				Do/Dm[12]	2/2	331/16.20	5/6620	dens, imig, habs
				Do/Dm[12]	2/2	331/16.20	5/6620[13]	dens, imig, habs
Stoecker, 1972	MT/G	O/N	1	Mmo/Mp	1/1	4/0.10	1/60	HABS
Wolff and Dueser, 1988	VA/W	O/N	1	Pml, Pmm/Cg	1/1	36/0.36	1/720	dens, habs

[1]Locations are AZ (Arizona), BC (British Columbia), DU (Durango, Mexico), CA (California), CO (Colorado), MT (Montana), NM (New Mexico), QU (Quebec), SA (Saskatchewan), SC (South Carolina), TX (Texas), VA (Virginia), and YU (Yukon).

TABLE 1.—*Continued.*

[2]Habitats are CP (coastal prairie), DG (desert grassland), DS (desert shrubland), G (grassland), GW (grassland-woodland), MW (sedge meadow-woodland), SW (shrubland-woodland), T (tundra), and W (woodland).

[3]Grid types are O (open grids), E (enclosures), and P (partial enclosures). Control types are S (synchronous with treatment), N (nonsynchronous), and B (both synchronous and nonsynchronous).

[4]Species are Cg (*Clethrionomys gapperi*), Dm (*Dipodomys merriami*), Do (*Dipodomys ordii*), Ds (*Dipodomys spectabilis*), Ea (*Eutamias amoenus*), Em (*Eutamias minimus*), Mc (*Microtus californicus*), Mmi (*Microtus miurus*), Mmo (*Microtus montanus*), Moc (*Microtus ochrogaster*), Moe (*Microtus oeconomus*), Mor (*Microtus oregoni*), Mp (*Microtus pennsylvanicus*), Mt (*Microtus townsendii*), Mum (*Mus musculus*), Ns (*Neotoma stephensi*), Ol (*Onychomys leucogaster*), Ot (*Onychomys torridus*), Orp (*Oryzomys palustris*), Pga (*Perognathus amplus*), Pgb (*Perognathus baileyi*), Pgf (*Perognathus flavus*), Pgp (*Perognathus penicillatus*), Pmb (*Peromyscus boylii*), Pme (*Peromyscus eremicus*), Pml (*Peromyscus leucopus*), Pmm (*Peromyscus maniculatus*), Pmp (*Peromyscus polionotus*), Rf (*Reithrodontomys fulvescens*), Rm (*Reithrodontomys megalotis*), Sf (*Sigmodon fulviventer*), and Sh (*Sigmodon hispidus*).

[5]"Remaining species" often include both the indicator (target) species and one or more secondary species. For enclosure studies involving an "added" species, the added species is listed here as a "removed" species.

[6]Number of experimental grids/number of control grids.

[7]Grid areas are approximate for many experimental treatments.

[8]Duration of experiment (in months), including pretreatment period for those treatments employing nonsynchronous controls. Number of trap nights is approximate for most experimental treatments.

[9]Tested effects for the remaining species are AGES (altered age structure), ARBO (change in arboreal activity), BGRO (increased body growth rate), BWGT (increased body weight), CAPS (increased number of captures), DENS (increased population density), DIET (altered diet composition), EMIG (decreased emigration rate), HABS (altered habitat use or "habitat shift"), IMIG (increased immigration rate), LIFE (increased lifespan and expectation of future life), MOVE (altered patterns of movement), PRES (percent residents in population), RECR (increased recruitment), REPR (increased reproductive activity), REST (increased residence time on grid), ROEC (rate of energy consumption), SEXR (altered sex ratio), SURV (increased survival), SPAT (altered spatial distribution), TIRE (altered timing of reproduction), and XCLU (exclusion of population).

[10]Uppercase effects were reported to be observed by the authors of the original study. Lower case effects were reported to be tested but not observed.

[11]Reciprocal experiments designed to test for asymmetry.

[12]Treatment similar to another treatment reported in the same study. For example, two similar treatments might involve the same removed and remaining species, but differ in the proportion removed.

[13]Only that portion of the experiment preceding the change of treatments is included.

[14]These six experiments were pooled for analysis. No effects were tested for any individual experiment.

[15]Effect observed for at least some individual remaining species and for remaining species collectively.

field experiments confront great logistical difficulties (small mammals), pseudoreplication is not only common but dominant.''

Two conclusions are apparent from these reviews. On the one hand, mammalian ecologists have been particularly responsive to the call for increased field experimentation in ecology. Experimental studies of rodent competition now occupy a central position in community ecology. On the other hand, interpretation of the results of much of this experimentation is problematical. Even some of the most frequently cited studies contain potentially serious flaws in aspects of their design or analysis, or both. The result is that we are less certain than it would appear, given the substantial effort expended, about the operation (*sensu* Grant, 1978) of competition in rodent communities.

Our objective was to determine the principal sources of experimental evidence for the importance of ongoing interspecific competition in rodent communities. Which experimental protocols have provided evidence for and against the importance of competition? Which locations, habitats, and species? Because experimental results can be evaluated on three levels, we have summarized the rodent competition literature by study, by experiment within study, and by treatment effect within experiment. Two points became evident during this review. On the one hand, there is considerable experimental evidence both for and against the importance of competition in rodent communities. On the other hand, much of this evidence—both for and against—comes from experiments with unreplicated treatments. The reliability and generality of this evidence is thus unknowable but suspect. With the objective of reducing the number of ambiguous results from future experiments, we illustrate how statistical power calculations might be routinely incorporated into the design of field tests for competition in small mammal communities.

DATA BASE

This review is restricted to studies of North American rodent communities that satisfy four criteria. 1) The study reports an intentional manipulation (that is, removal or addition) of one or more populations. This criterion excluded nonmanipulative (that is, "natural") experiments, many of which were reviewed by Grant (1972, 1978). 2) The experiment was conducted in the field, in the usual habitat(s) of the species. This criterion excluded laboratory studies but not studies of populations introduced to outdoor enclosures. Experimental units were classified as open grids, enclosures, or partial (that is, "semipermeable") enclosures. 3) There was one or more nearby control units (that is, grids or enclosures) by which the results of the experimental treatment could be judged. Control units were observed during experimental periods (synchronous), immediately before or after experimental periods (nonsynchronous), or both. We adopted this liberal requirement for experimental control in the interest of inclusiveness. In fact, this criterion admitted only two of the early studies excluded by Schoener (1983),

presumably because of the absence of synchronous controls. 4) The authors report no reason to question the interpretation of the experiment as a test for competition. This criterion eliminated the apparent demonstration of competition between extremely dense, enclosed populations of *Microtus pennsylvanicus* and *M. ochrogaster* reported by Krebs *et al.* (1969) and the *Clethrionomys gapperi* reintroduction treatment reported by Morris and Grant (1972). Of the North American studies reviewed by Schoener (1983), Sheppe (1967) is excluded here because the experiment was conducted in farm buildings.

Table 1 summarizes the study locations, habitats, experimental protocols, species, and principal findings of the 25 published studies that satisfied these criteria. Multiple papers by the same author(s) might share a study area, species, and experimental treatment but still qualify as separate studies if they reported different experimental periods and different data (for example, Munger and Brown, 1981, and Brown and Munger, 1985). Conversely, the papers by Cameron (1977) and Cameron and Kincaid (1982) are treated as a single study because they merely report different aspects of the same data. Interpretation of this summary information is subject to four caveats. First, as indicated by Schoener (1983), preparing such detailed summaries inevitably involves an element of subjectivity. Nonetheless, we assume full responsibility for any errors of fact that may be contained in Table 1. Second, our intention was to summarize these 25 studies as reported by the investigators, not to reanalyze or reinterpret their results. We have therefore implicitly accepted each author's claims about treatment effects tested and observed with each experiment. Third, this review concerns only the results of field experiments involving population manipulations. Collateral lines of evidence that supplemented the findings of several field experiments (for example, behavioral trials) are not considered here. Finally, the studies reviewed here represent only a few study locations, habitats, species, and experimental protocols. Each study reports only one or two experiments conducted with one set of species at one location. Comparisons between locations, habitats, species, and protocols are, therefore, not independent of one another.

Study Summaries

Locations, Habitats, and Species

These 25 studies were conducted in eight states of the United States, the Mexican state of Durango, and four Canadian provinces. Thirteen studies were conducted in the Southwest, three in the Rocky Mountain states, and two in the eastern United States. As described by the authors, study habitats have included grassland (seven studies), coastal prairie (four), desert grassland (three), grassland-woodland (three), desert shrubland (three), shrubland-wodland (two), woodland (one), sedge meadow-woodland (one), and tundra (one). Many studies used ecotonal or coarse-mosaic habitats in tests for habitat shifts.
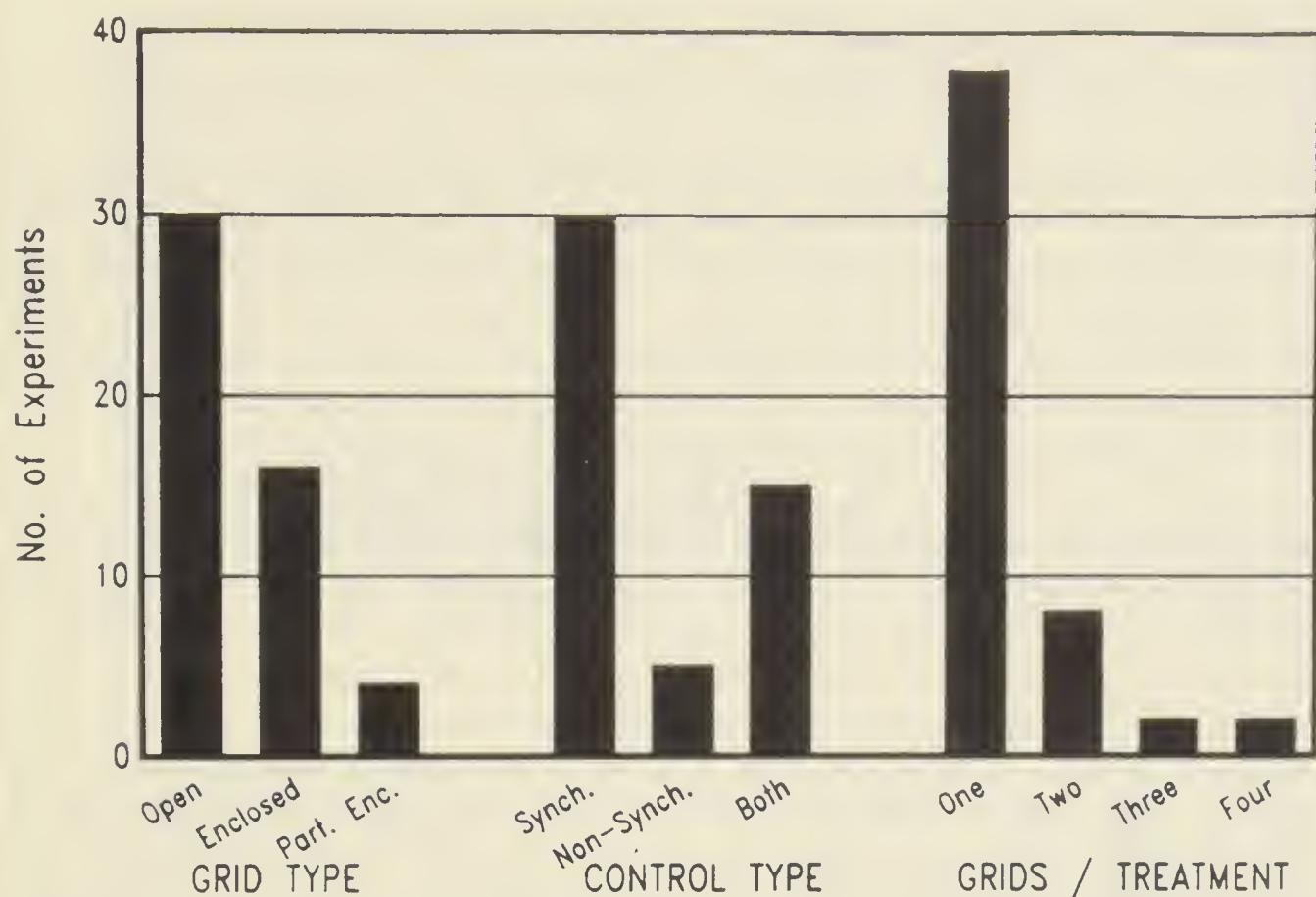
Fig. 1.—Experimental protocols that have been used in 50 manipulative field experiments designed to test for the occurrence and consequences of interspecific competition in North American rodent communities. Grid types are open, enclosed (that is, fenced), and partially enclosed. Control types are synchronous with experimental treatment, nonsynchronous (that is, before or after treatment period), and both.

These studies directly involved 12 rodent genera and 32 species. The six most frequently removed species include *Sigmodon hispidus* (four studies, one location), *Microtus pennsylvanicus* (four, four), *Dipodomys ordii* (four, three), *D. merriami* (four, three), *Reithrodontomys fulvescens* (three, one), and *Clethrionomys gapperi* (two, two). Twenty-two species were observed as the indicator (that is, remaining) species in one or more experiments. The seven most frequently studied indicator species included *Peromyscus maniculatus* (seven studies, six locations), *S. hispidus* (five, two), *R. fulvescens* (four, one), *M. pennsylvanicus* (three, three), *D. ordii* (three, two), *C. gapperi* (two, two), and *Mus musculus* (two, two). Eighteen studies reported single-species responses to single-species removals and seven studies involved multiple removed or remaining species, or both, in the same experiments.

Experimental Protocols

These 25 studies report the results from 50 experiments. The number of experiments per study ranged from one to six (median, two). Experimental protocols varied according to grid type, control type, and replication (Fig. 1). Most experiments employed open grids (60 percent), synchronous (or both) controls (90 percent), and only one grid per treatment and control (74

percent). Only 11 (22 percent) experiments employed replicate ($N > 1$) experimental and control grids, and only four of those (eight percent) employed more than two grids per treatment. The most frequently used protocol, representing 36 percent of all experiments, employed a combination of one open experimental grid and one open, synchronous (or both) control grid. Another 26 percent used one enclosed experimental grid and one enclosed, synchronous (or both) control grid. Of the 20 experiments conducted in full or partial enclosures, only three incorporated replication. Only nine studies reported reciprocal experimental treatments designed to test for asymmetry in species interactions.

These 50 experiments also varied greatly in duration, sampling effort, and effectiveness in implementing the planned treatment. Including pretreatment and treatment periods, study duration ranged from one to 60 months (median, five). Treatment periods ranged from one to 48 months (median, five). Grid (or enclosure) area ranged from 0.1 to 16.2 hectares (median, 0.8). The number of traps per grid ranged from four to 331 (median, 55). Trapping effort ranged from 60 to 31,200 trap nights (median, 4749 trap nights). Few authors reported the effectiveness with which they were able to implement open-grid treatments such as removals, but several indicated that even intensive trapping produced only incomplete removals (50-80 percent reductions) of one or more species (Schroder and Rosenzweig, 1975, Cameron, 1977, Chappell, 1978, Abramsky *et al.*, 1979, Holbrook, 1979).

Effects

These 50 experiments tested for 138 treatment effects. Twenty-two different but nonexclusive types of effects were described, representing the potential effects of competition on both the individual and the population (Fig. 2A). Sixteen of these 22 types were "observed" (that is, judged to be significant) at least once. Overall, 38 percent (53 of 138) of the tested effects were judged significant. The two most frequently tested and observed effects were habitat shifts (HABS) and density responses (DENS), representing 20 percent and 16 percent, respectively, of all effects tested and 25 percent and 15 percent, respectively, of all observed effects. Effects that were tested more than once and observed in at least half of all tests include change in spatial distribution (SPAT, 50 percent), increased movement (MOVE, 50 percent), altered timing of reproduction (TIRE, 50 percent), population exclusion (XCLU, 67 percent), and change in arboreal activity (ARBO, 71 percent).

Treatment effects were observed in 80 percent (20 of 25) of the studies and 68 percent (34 of 50) of the experiments. The evidence for competition varied substantially among experimental protocols. The percentage of experiments producing at least one observed effect increased from 57 percent (17 of 30) for open grids to 75 percent (three of four) for partial enclosures and 88 percent (14 of 16) for full enclosures. Similarly, this percentage increased from 53 percent (16 of 30) for synchronous controls to 80 percent (four of five) for nonsynchronous controls and 93 percent (14 of 15) for both
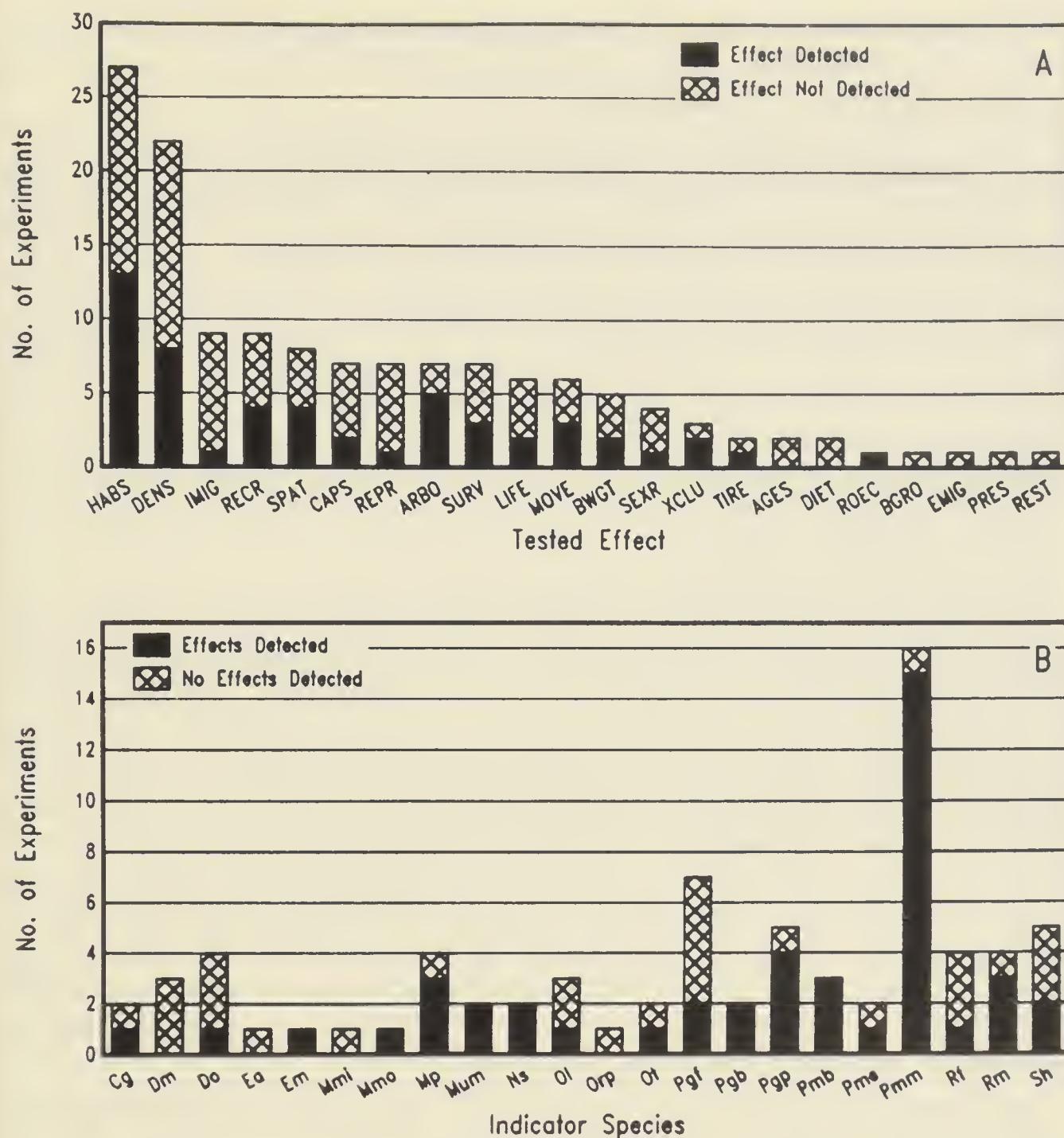
FIG. 2.—A. Experimental effects tested and observed (that is, judged significant) with 50 experimental field tests for competitive effects. B. Experimental effects tested and observed for 22 indicator species. See Table 1 for effects and species mnemonics.

types of controls used together. Finally, the percentage of experiments producing at least one observed effect was 76 percent (29 of 38) for unreplicated experiments but only 42 percent (five of 12) for replicated experiments. These experiment-level summaries include six experiments that were interpreted as providing evidence for competition but for which no specific effects were actually tested—Price, 1978. If these are excluded, the percentage of experiments producing at least one significant effect drops to 64 percent and the percentage of unreplicated experiments producing at least one significant effect drops to 72 percent. There was no apparent difference between experiments that did and did not reveal the occurrence of competition in the number of effects tested ($\bar{X} \pm$ S.E., 2.7 $\pm$ 0.38 as opposed

to 2.6 ± 0.46 effects per experiment), treatment duration in months (9.7 ±
2.26 as opposed to 10.4 ± 2.71), or sampling effort in total trap nights (7622
± 1669 as opposed to 6759 ± 1788).

The proportion of experiments producing evidence for competition varied
greatly among habitat types, ranging from zero percent (none of one) each
for eastern woodland and tundra to 100 percent each for grassland (nine of
nine) and sedgemeadow-woodland (two of two). Although 58 percent of the
"grassland" experiments (that is, those experiments conducted in the coastal
prairie, grassland, desert grassland, and grassland-woodland categories)
produced evidence for competition, there was substantial variation among
"grassland" habitat types. For example, 100 percent (nine of nine) of the
grassland (G) experiments yielded at least one observed effect, whereas only
25 percent (two of eight) of the coastal prairie (CP) experiments did so.
Overall, 76 percent of tested and 77 percent observed effects represent some
form of "grassland" habitat.

The proportion of experiments producing evidence for competition also
varied greatly among indicator species. One or more observed effects were
reported for 78 percent of the 22 indicator species (Fig. 2B). Among the most
frequently studied genera, *Dipodomys* species exhibited a significant effect
in 14 percent (one of seven), *Sigmodon* in 40 percent (two of five),
Reithrodontomys in 43 percent (three of seven), *Perognathus* in 57 percent
(eight of 14—including Price, 1978), *Microtus* in 66 percent (four of six), and
Peromyscus in 90 percent (18 of 20—including Price, 1978) of the
experiments in which they served as the indicator species. Removal resulted
in an observed effect by the indicator species in 57 percent (eight of 14) of
the *Dipodomys* removal experiments, 40 percent (two of five) of the
Reithrodontomys experiments, 40 percent (two of five) of the *Sigmodon*
experiments, 80 percent (four of five) of the *Peromyscus* experiments, and 93
percent (14 of 15) of the *Microtus* experiments.

There were 14 experiments in which the removed and remaining species
were congeners. One or more effects were observed in 50 percent of these
experiments, as compared with 58 percent of the experiments that did not
involve congeners. Four of the seven pairs of congeners employed in these
experiments provided evidence for competition. Of the reciprocal experi-
ments involving congeners, *Microtus ochrogaster* and *M. pennsylvanicus*
each responded to the removal of the other, *Eutamias minimus* responded to
the removal of *E. amoenus* but not vice versa, and neither *Dipodomys ordii*
nor *D. merriami* responded to the removal of the other.

Of the nine studies reporting reciprocal experimental treatments designed
to test for asymmetrical interactions, five reported asymmetrical results in
which the effects of competition were apparent for one species but not the
other. Four studies reported symmetrical results, with three of these four
reporting no evidence for ongoing competition. In general, when
competition was evident, its effects were felt more strongly by one species
than by the other.

Discussion

The Available Data

Interspecific competition was reported for 76 percent of the indicator species and 90 percent of the studies included in Schoener's (1983) review of competition experiments. Comparable values for our less inclusive review are 81 percent of the indicator species and 80 percent of the studies. At another level, however, competition was reported for 68 percent of the experiments (64 percent—without Price, 1978) but only 38 percent of the tested effects. Based on the frequency of experiments in which one or more tested effects were observed, the evidence for competition varied greatly among treatment protocols: 1) competition was more apparent between enclosed populations of rodents (88 percent) than between free-ranging populations on open grids (57 percent); 2) competition was more apparent with nonsynchronous controls (80 percent) than with synchronous controls (53 percent); 3) competition was more apparent with unreplicated treatments (76 percent) than with replicated treatments (42 percent). This last point illustrates Hurlbert's (1984) concern about pseudoreplication. Replication should increase the sensitivity of experiments, and yet experiments employing replicated treatments detected competition only 55 percent as often as those using unreplicated treatments. This suggests that differences arising from factors other than competition existed between the control and treatment grids in experiments not employing replication, and that in some cases their effects were incorrectly attributed to competition.

There is thus considerable evidence both for and against the importance of competition in North American rodent communities. Unfortunately however, much of this evidence—both for and against—comes from incomplete (that is, nonreciprocal), poorly controlled or unreplicated treatments (or both). Little of it comes from well-controlled, replicated treatments applied over a period of more than one generation for the indicator species. The generality of this evidence thus is unknowable but suspect. Furthermore, if the limitations in this mammalian data base also characterize a comparable fraction of the nonmammalian studies summarized by Schoener (1983), then we know less about the operation of competition in general than Schoener's review would suggest.

The results of replicated treatments that produce evidence for competitive effects are unambiguously interpretable. The generality of the reported result may be limited, depending on the experimental design and protocol, but the result itself is interpretable as evidence for the occurrence of ongoing competition. More ambiguous are those experiments that produce no significant effects. Ambiguity arises when an effect may be judged nonsignificant either because it truly did not occur or because the experimental design lacked sufficient statistical power to be able to detect the effect against background variation even when it did occur (Toft and Shea, 1983). These reasons for nonsignificance lead to quite different

conclusions about the occurrence and consequences of competition and have different implications for future research.

Experimental Design

Statistical power analysis provides a way to reduce the frequency of ambiguous experimental results (Winer, 1971). "Power" is the probability that a statistical test will detect a difference between treatment and control values for a variable when that difference actually exists. The power of a test thus provides a measure of "certainty" for an observed outcome. Power depends on the specific test statistic and significance level (α) used to compare treatment and control values for the response variable, the amount of within-treatment variation for that variable, the effect size, and the number of replicate experimental units (for example, grids) per treatment.

Analytical methods for calculating power exist for a number of test statistics (Cohen, 1977). Monte Carlo techniques may be applied where analytical solutions are not available. Just as the appropriate test statistic varies from case to case, so do the details of power analysis, ranging from simple (for example, t-test) to complex (for example, repeated-measures analysis of variance).

Effect size is the magnitude of the expected difference between treatment and control values for the response variable (that is, the alternative hypothesis). The difficulty in selecting an appropriate effect size varies with both the type of experiment and the type of response variable, but is relatively straightforward for a removal experiment designed to test for a density response by the indicator species. The maximum expected effect size can be estimated reasonably, for instance, as the increase in density exhibited by the indicator species if it completely compensates for the reduction in density of the removed species. An experimental design that does not have power to detect such a relatively large response (that is, such a large difference between treatment and control values) cannot provide a strong test for competition.

The amount of variation expected among grids or other experimental units within a treatment depends on the similarity of the grids and on the extent to which they are affected by extraneous factors not under experimental control. Usually this information is obtainable from preliminary trapping on the grids in question. The selection of an appropriate number of replicates for each experimental treatment is a primary reason to undertake power analysis.

The application of power analysis in experimental design is best illustrated by reference to an example. Two potential competitors coexist, with the density of species A (10 individuals per hectare) double that of species B (five per hectare). A removal experiment is designed to determine the competitive effect(s) of A on the less abundant B. The density response of B to the complete removal of A is the response variable. How many replicate treatment and control grids should be employed in this
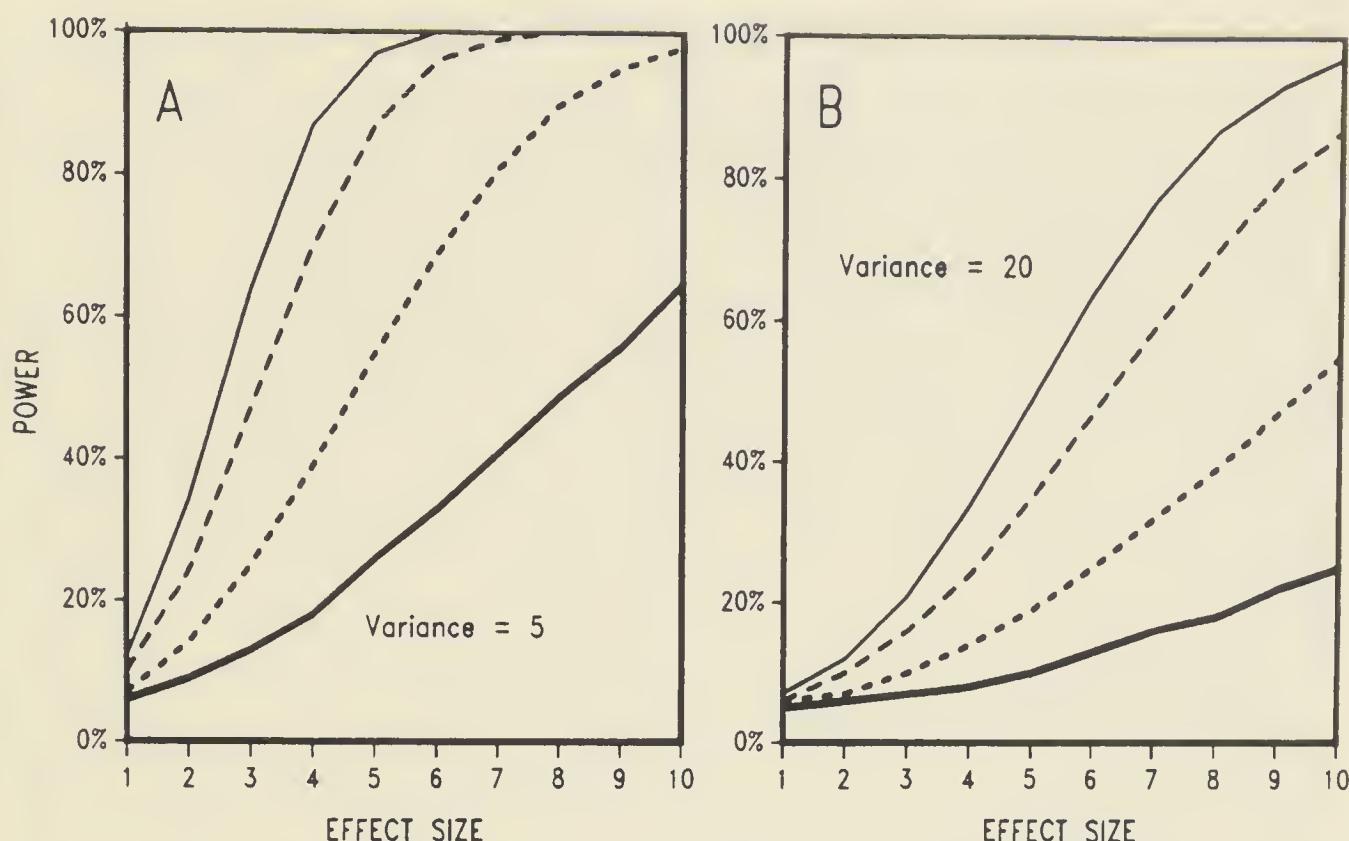
Fig. 3.—Statistical power curves for hypothetical removal experiment to test for pairwise interspecific competition. Power was estimated for density effect sizes ranging from one to 10, grid number of two (heavy solid line), three (dotted line), five (dashed line), and seven (light solid line), and within-treatment variances of five (A) and 20 (B).

experiment? Using a two-tailed t-test with $\alpha = 0.05$ and within-treatment variance in the density of B equal to five, we use the method of Winer (1971) to estimate power for a range of potential effect sizes, from a small density response by B (for example, +1 individual per hectare) up to complete density compensation (that is, +10 individuals per hectare).

The minimum replication having adequate power to detect even complete density compensation is three (Fig. 3A). With $N = 3$ treatment and control grids, power equals 97 percent for a change of 10 individuals of B per hectare. The result could be interpreted unambiguously vis-à-vis strong competition regardless of the outcome of the experiment. On the other hand, any experiment incorporating fewer replicates would have little chance of producing an unambiguous result. For example, the power to detect an effect size of 10 would be only 65 percent with $N = 2$ replicate grids. Also, if density compensation were incomplete, even three replicates might not be sufficient. For example, if each two removed individuals were replaced by only one, power would drop to 55 percent with $N = 3$ grids. This probability increases to only 85 percent with $N = 5$ grids. Similarly, three replicates might not be sufficient if the within-treatment variance were greater. For example, with variance equal to 20, the minimum replication required to detect even complete compensation would be $N = 7$ grids (Fig. 3B). Power for three grids would be only 50 percent. The number of replicates required thus depends on the circumstances under which the experiment is performed.

Post hoc *Power Calculations*

Power calculations are most useful when employed in designing and planning experiments. *Post hoc* calculations nevertheless may be used to reduce the ambiguity inherent in interpreting nonsignificant (that is, "negative") results. Such calculations require knowledge of both the magnitude of the expected change in the response variable and either the within-treatment variance for the response variable or the values for the individual replicates so that a variance may be estimated. Surprisingly, most published studies of rodent competition do not report this information or even the data necessary for its computation. Of the replicated studies reported here only Petersen (1973), Schroder and Rosenzweig (1975), Munger and Brown (1981), Brown and Munger (1985), and Galindo and Krebs (1985a) provide the data required for a *post hoc* power analysis of their tests for density responses. Each of these studies reported an experimental test for a numerical response by at least one indicator species, but only Petersen (1973), Munger and Brown (1981), and Brown and Munger (1985) reported an observed effect. How much "excess replication" was incorporated into these experimental designs? Conversely, how should we interpret the negative results of Schroder and Rosenzweig (1975) and Galindo and Krebs (1985a)?

Estimates of statistical power were computed for four of these studies using a standard procedure. For simplicity and uniformity, a *t*-test was employed as the test statistic, with a two-tailed significance level of 0.05. Standard deviations for the density response variable were estimated, usually as the average across time of the individual standard deviations obtained from replicate censuses within same treatment and time period. Such a procedure allows the maximum use of time-series population data, without confounding the variability between time periods with the variability within time periods. Expected effect sizes were estimated as the average density of the removed species on the control grids during the period of the experiment. Estimated in this way, effect size assumes effective removals and complete density compensation. Following Winer (1971:34), the noncentrality parameter of the *t*-distribution (δ) was computed as

$$\delta = \frac{\text{Expected density change}}{\sigma \sqrt{1/n_a + 1/n_b}},$$

where: σ is the hypothesized standard deviation; n_a is the number of replicates in treatment a; and n_b is the number of replicates in treatment b. Power values then were obtained from tables in Winer (1971), with $\alpha = 0.025$ (for a two-tailed α of 0.05—Cohen, 1977:5) and degrees of freedom (f) equal to $n_a + n_b - 2$. These *t*-test based power estimates may be minimal; more complex analyses (for example, repeated-measures analysis of variance) potentially could yield higher estimates.

The procedure is illustrated by reference to the first experimental treatment listed for Brown and Munger (1985). They excluded three large

granivorous rodent species (*Dipodomys ordii*, *D. merriami*, and *D. spectabilis*) from four 0.25-hectare partial enclosures and observed the density responses of several small granivorous and omnivorous rodent species over a five-year period. Four standard deviations (control-year one, experimental-year one, control-years two to five and experimental-years two to five) were computed from information in Brown and Munger (1985:table 3, ignoring the ant removal). The average of the standard deviations in abundance for small granivores is 0.150. An average of 3.87 large granivores per month were captured on the control grids during the study (Brown and Munger, 1985:table 2). Assuming that the density of small granivores compensates completely for the removed large granivores, the noncentrality parameter was computed as $\delta = 3.87/(.150 \sqrt{1/4 + 1/4}) = 36.49$. From table C.13 of Winer (1971), with $\alpha = 0.025$ and $f = 4 + 4 - 2 = 6$, this experiment had greater than 99 percent power to detect an effect of this size. Given the prevailing conditions, replication of $N = 4$ was more than sufficient to detect a reasonable expected effect if the abundance of small granivores were reduced by the presence of large granivores.

Two conclusions are immediately apparent from inspection of the calculated power values for these studies (Table 2). First, the experiment with high power, the three-species *Dipodomys* removal of Munger and Brown (1985), did detect competition. Even had it not done so, this experiment would have been unambiguously interpretable. Of the experiments with low power, only Petersen (1973) contended to have observed effects of competition, based on a graphical appraisal of the data. It is unlikely that Petersen would have detected competition had a statistical criterion been used. Second, those experiments for which no significant density response was reported had modest statistical power. These experiments incorporated insufficient replication to be able to detect complete density compensation under the prevailing conditions. (The single experiment with adequate power for which no effect was observed, that is, the *Dipodomys ordii* 2/3 removal of Schroder and Rosenzweig, 1975, failed to achieve the levels of removal postulated in the power analysis. Indeed, the average density of the species being removed in this experiment was higher on the removal grids than on the controls.) It is, therefore, most prudent to interpret the results of these experiments as being inconclusive vis-à-vis the occurrence of interspecific competition, at least as it affects population density (Brown and Munger 1985). To interpret these results as conclusive evidence for the absence or unimportance of competition (Schroder and Rosenzweig, 1975; Galindo and Krebs, 1985a) is to run a substantial risk of making a Type II error and misrepresenting the true state of nature.

These power values reflect the influence of a number of factors (Table 2). A major reason for the high level of power for the first experiment of Brown and Munger (1985) is the extremely large expected effect. The expected density response represents a 955 percent increase in the captures of

TABLE 2.—Post hoc *power analysis for replicated experimental tests for density responses.*

Study	Removed/ remaining[1]	σ	Effect size[2]	δ[3]	f[4]	Power[5]	N_s[6]
Brown and Munger, 1985	Dm, Do, Ds/ Pgf, Pgp, Pmm, Pme, Rm[7]	0.150[8]	3.87[9]	36.49	6	> 99%	2
	Ds/Dm, Do[7]	0.407[8]	0.95[9]	2.33	2	27%	5
Galindo and Krebs, 1985*a*[10]	Mp/Pmm	2.314[11]	3[12]	1.12	2	10%	11
Petersen, 1973	Sf/Sh	2.352[13]	28[14]	9.72	1	55%	2
Schroder and Rosenzweig, 1975	Do/Dm	2.297[15]	14.3[16]	6.22	2	85%	2
	Do/Dm	2.297[15]	10.4[17]	4.52	2	65%	3
	Dm/Do	38.042[15]	11.9[16]	0.31	2	<<10%	>100
	Dm/Do	38.042[15]	5.9[17]	0.16	2	<<10%	>100

[1]Species abbreviations are as given in Table 1.

[2]Effect size estimated as expected density response by the indicator species, assuming complete density compensation.

[3]Noncentrality parameter required for power calculations, computed as in text.

[4]Degrees of freedom for noncentrality parameter, computed as in text.

[5]Approximate power for a two-tailed t-test, interpolated from Winer (1971:table C.13, for one-tailed α = 0.025).

[6]Number of replicates in each treatment required to yield a power of 80 percent given the observed standard deviation and expected effect size. Found by iteratively computing δ for different numbers of replicates and comparing with tabled values (Winer 1971).

[7]Species were considered as groups.

[8]Estimated as the average standard deviation between replicates within each year/treatment combination (Brown and Munger, 1985:table 3 and fig. 4B, ignoring the ant removal).

[9]Estimated as the average number of captures of the removed species per census period on the control grids during the experimental period (Brown and Munger, 1985:fig. 2).

[10]Due to naturally low density of the removed species (*Microtus pennsylvanicus*) on two of the three control grids, Galindo and Krebs regarded them as additional removal grids. As per our criterion that actual removals must have taken place, these grids were treated as control grids for this analysis.

[11]Estimated as the average monthly standard deviation for two of the control grids for May through September 1982 (Galindo and Krebs, 1985*a*:fig. 6).

[12]Estimated as the average minimum number alive of *Microtus pennsylvanicus* on grid B.82 during 1982 (Galindo and Krebs, 1985*a*:fig. 3).

[13]Estimated as the average standard deviation for the two experimental grids taken monthly during the period December 1967-June 1968 (Petersen, 1973:fig. 3).

[14]Estimated as the average control density of *Sigmodon fulviventer* (Petersen, 1973:fig. 3).

[15]Estimated as the average standard deviation between grids within the control and experimental treatments when they were trapped within four weeks of one another (Schroder and Rosenzweig, 1975:figs. 4, 5).

[16]Estimated as two-thirds of the density of the removed species on the control grids during the experiment.

[17]Estimated as one-third of the density of the removed species on the control grids during the experiment.

small granivores! The power of this experiment drops to 53 percent for a postulated doubling—still a 100 percent increase—of the small granivores to 0.405 individuals per month. The low power of the Galindo and Krebs (1985a) experiment is due largely to the small number of *Microtus pennsylvanicus* available for removal, that is, the small expected effect. Had *Microtus* been present during the experiment at the density observed the previous year (approximately 39 individuals per grid), the power of the experiment would have been greater than 99 percent, even with the same level of replication. As it was, however, even $N = 11$ replicates would have had power of only about 80 percent to detect complete density compensation. For Schroder and Rosenzweig (1975), the much lower power of the *Dipodomys merriami* removal, relative to the *D. ordii* removal, reflects both the greater variability in the abundance of *D. ordii* and the smaller expected effect size. The application of power analysis in the design and planning of these experiments would have facilitated more efficient allocation of replication and sampling effort and, where competition was not observed, might have yielded less ambiguous results. We reiterate, however, that these particular studies are analyzed here not because of their shortcomings, but rather because they represent some of the best of the rodent competition studies from the viewpoint of statistical experimental design.

Consideration of statistical power suggests four ways to increase the probability of observing unambiguous experimental results.

1. Increase replication. The gain in power associated with increased replication is largest for a small number of replicates. Thus, the gain in power in going from two to three grids is much greater than the gain realized in going from five to seven.

2. Reduce within-treatment variation, perhaps by selection of study sites to assure homogeneity or by manipulations such as predator removal, habitat alterations, or pre-treatment population adjustments (that is, additions or removals). Unfortunately, because such steps also may reduce the generality of the experimental results, they must be used with caution.

3. Use more powerful test statistics, such as one-tailed tests and repeated-measures analysis of variance. One-tailed tests well may be justified in tests for "competitive release" in which it is hypothesized that the indicator species will exhibit a directional response (that is, a numerical increase).

4. Test for "large" effect sizes. This may be achieved either by selecting a relatively abundant species as the species to be manipulated or by conducting simultaneous removal and addition treatments that maximize between-treatment differences in density. Unfortunately, the removal of a relatively rare species inevitably results in a small effect size. If sufficient replication is not possible for grid-based population manipulations, alternative protocols may be appropriate.

There are, of course, other questions that can influence the design of manipulative experiments. For example, how large should the grids or

other experimental units be? Should the experiments be conducted in enclosures? Although these and other practical considerations may influence tremendously the outcome and interpretation of an experiment, their implications are less amenable to objective appraisal. Statistical experimental design is inherently one of the more straightforward, objective aspects of research planning.

As indicated by Schoener (1983), mammalian ecologists have been particularly responsive to the general call for increased experimentation in ecology. Experimental studies of rodent competition now occupy a central position in community ecology. Greater attention paid to the fine points of statistical experimental design can only increase the contribution of this research in the future.

Acknowledgments

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TEMPORAL VARIATION IN THE STRUCTURE OF A DESERT RODENT COMMUNITY

BURT P. KOTLER

ABSTRACT—Microhabitat selection differences among nocturnal, seed-eating desert rodents are believed to promote species coexistence. In order to better understand what interactions determine community structure, two factors effecting microhabitat selection (seed resources, predatory risk) were examined in two sequential years for a community of North American desert rodents. Species composition in this community changed during the study. Mortality from long-eared owls (*Asio otus*) also was monitored by collecting owl spit pellets from which rodent skulls were removed and counted. In both years, predatory risk as affected by illumination altered rodent foraging behavior. Resource distribution also affected foraging behavior, but within constraints set by predatory risk as affected by animal morphology. Habitat selection of a species was correlated to the degree of development of its antipredator morphology. Also, owls showed significant selectivity for quadrupedal species, although selectivity changed with rodent density. Despite similarities in animal behavior and community organization from year to year, rodent species composition changed greatly. The reason for such volatility is unclear, but may be due to two important ecological tradeoffs: 1) antipredator specialization versus efficient foraging in the absence of predation mediated through morphology, and 2) foraging speed as opposed to efficient foraging mediated through body size.

A goal of community ecology is to find organizing principles for biotic communities. It is of further interest to know if there are predictable aspects of these organizing principles. For example, can we predict *a priori* how a given type of community will be organized? Do these mechanisms hold over time? In this paper, I examine the second question for a community of desert rodents. Few attempts have been made to answer this question. In one example, Pullium and co-workers (Pullium, 1975, 1983; Pullium and Mills, 1977) found that winter flocks of sparrows in Arizona vary from one year to the next in the number of species, their relative abundance, and the way in which they partition space or resources. For sparrow communities, the organization of the community appears to differ greatly over time, depending on bird density and resource abundance, which are determined independently.

The community ecology of seed-eating North American desert rodents has been studied intensively (for example, Brown, 1973; Rosenzweig, 1973; Price, 1978; Stamp and Ohmart, 1978; Kotler, 1984a). Three important patterns have emerged. Any explanation of desert rodents communities must be able to account for them. They are as follows.

First, significant differences among coexisting species in the use of habitats or microhabitats have been found repeatedly (for example, Rosenzweig, 1973; Brown, 1975; Rosenzweig *et al.*, 1975; Schroder and Rosenzweig, 1975; Lemen and Rosenzweig, 1978; Stamp and Ohmart, 1978;

Wondolleck, 1978; Kotler, 1984a). In general, kangaroo rats (*Dipodomys*) and kangaroo mice (*Microdipodops*) forage in open areas, whereas pocket mice (*Perognathus*) and deer mice (*Peromyscus*) restrict their foraging to shrubs. Such differences are believed to promote species coexistence. Second, the various habitat selection behaviors are associated with distinct morphologies. Kangaroo rats and kangaroo mice, which forage in the open, have hyperinflated auditory bullae that increase auditory acuity (Webster, 1962) and elongated hind legs for bipedal locomotion that aid in escape from predators (Bartholomew and Caswell, 1951; Eisenberg, 1963). Pocket mice and deer mice, which forage near bushes, mostly lack these features. Third, coexisting species of rodents are of dissimilar body size (Brown, 1973, 1975; Simberloff and Boecklen, 1981; Bowers and Brown, 1982). In this paper, I will concentrate on the pattern of habitat use, but the experimental results also will shed light on the other patterns.

Habitat partitioning appears to be a widespread mechanism of species coexistence for desert rodents. Many hypotheses have been proposed to explain it. For example, one suggests that foraging efficiency based on the microhabitat specific foraging costs and locomotor capabilities of a species, along with the distribution of seeds in and among microhabitats, determine microhabitat use (Reichman and Oberstein, 1977; Hutto, 1978; Price, 1978, 1983; Bowers, 1982; Price and Waser, 1984). Another proposes that habitat selection is enforced by predatory risk. There is an ecological tradeoff between the ability to forage safely in the risky microhabitat, and to forage efficiently when predatory risk is low or absent (Kotler, 1984a).

In this paper, I will examine a desert rodent community in which species composition fluctuates over time, and attempt to assess if the same mechanisms of coexistence appear to be affecting community organization from one year to the next. To assess the effect of predation and competition on the coexistence of desert rodents, similar experiments were performed on a particular desert rodent community in sequential years. The effects of predatory risk and seed resources on the microhabitat selection behavior of the coexisting species were observed. Also, changes in rodent densities were examined in the light of mortality from avian predators.

METHODS

The study was conducted on stabilized sand dune habitat in the Great Basin Desert at Tonopah Junction, 12 km. S Mina, in Mineral Co., Nevada (elevation 1343 meters). Rodent species present on the dunes included Merriam's kangaroo rat (*Dipodomys merriami*), Ord's kangaroo rat (*D. ordii*), Great Basin kangaroo rat (*D. microps*), desert kangaroo rat (*D. deserti*), pallid kangaroo mouse (*Microdipodops pallidus*), little pocket mouse (*Perognathus longimembris*), deer mouse (*Peromyscus maniculatus*), and western harvest mouse (*Reithrodontomys megalotis*). The major predators at the site were long-eared owls (*Asio otus*). Other predators included coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), and gopher

snakes (*Pituophis melanoleucus*). With the exception of gopher snakes, these predators hunt prey by pursuit, and the location of prey is aided by vision. These predator attributes help produce a gradient of increasing predatory risk from under shrub canopies to open microhabitats.

To assess fluctuations in species density and relative abundance, rodent populations were censused regularly (July, November, 1979; March, July, November, 1980; May, 1981). Two parallel census lines with three assessment lines were established in 1979 (O'Farrell *et al.*, 1977), and censuses were performed regularly through 1981. Census lines were 460 meters long, contained 23 stations spaced 20 meters apart, and were separated by 42.5 meters. Assessment lines, each with 15 stations, cut the census lines at 45° angles. Each station contained four live-traps, one in each of four microhabitats (Brown and Lieberman, 1973). At each census period, census lines were trapped for three to five nights, and all captured animals marked and released. Then assessment lines were trapped for two or three nights. All density estimates in this paper are based on data collected on the census lines.

Two one-hectare live-trapping grids were established in 1980 for performing experimental manipulations. Each grid contained 25 trap stations; stations were 20 meters apart. At each station, two traps were placed in the open microhabitat five to eight meters from a bush, and two traps were placed under bushes. Standard mark and recapture techniques were used. The proportion of captures in the open were used as a measure of microhabitat use and the number of captures as a measure of foraging activity. In 1980, one grid served as the control and the other as the experimental grid. In 1981, experiments were rotated randomly from one grid to the other. Both grids always were trapped simultaneously.

The experiments were designed to manipulate predatory risk and the distribution of food resources, and to note the effect of these manipulations on the foraging behavior of rodents. Because microhabitat partitioning among species appears to promote species coexistence in this community (Brown and Lieberman, 1973), the experiments were designed to measure the effects of resources and predatory risk on microhabitat use. Predatory risk was manipulated by altering illumination. Important predators in deserts, such as owls, have been shown to be more dangerous under levels of illumination equivalent to moonlight than under starlight levels (Dice, 1945, 1947; Clarke, 1983). Also, rates of predation by barn owls (*Tyto alba*) on desert rodents in a seminatural enclosure have been shown to be higher for moonlight levels of illumination than for starlight levels, and to be higher in open microhabitat than in bush microhabitat (Kotler, Brown, Smith, and Wirtz, in press). Light was augmented using four camp lanterns to illuminate the grid (L), creating levels of illumination similar to moonlight over most of the grid (Kotler, 1984b). Shadow was added by shading traps in the open at each station with parachute canopies hung from wooden scaffolding (P). Resources were manipulated by scattering 15

TABLE 1.—*Densities and habitat selection behavior of the common rodent species at Tonopah Junction, Nevada, in 1980 and 1981. Habitat selection behavior is measured by the percent of captures occurring in the open microhabitats.*

Species	Body mass grams	Density (no./ha.) 1980	Density (no./ha.) 1981	Habitat selection (percentage of captures in the open) 1980	Habitat selection (percentage of captures in the open) 1981
Dipodomys merriami	42	12.09	5.88	53.65	56.0
Dipodomys ordii	47	1.43	0.79	44.01	—
Dipodomys microps	65	1.39	2.62	69.88	59.0
Dipodomys deserti	100	4.89	1.63	77.50	95.0
Microdipodops pallidus	12	7.23	3.65	50.73	63.0
Perognathus longimembris	7	5.09	3.59	16.24	40.0
Peromyscus maniculatus	18	0	13.89	—	23.0
Total		32.12	32.05		

grams of bird seed at each station over a two to three square meter area around either the traps in the bush (S_b) or the traps in the open (S_o). In 1980, the following treatments were performed; L, P, S_o, L+P, L+S_o, P+S_o, C (control). In 1981, they were L, S_o, S_b, L+S_o, L+S_b, C. Statistical comparisons were made for each species and for the grouped kangaroo rat species and for the other species.

Predation by owls was monitored by regularly collecting all owl pellets from a permanent roost located on the study site. Rodent skeletal remains were removed from the pellets, and counts were made of each rodent species based on recovered skulls. Owl pellets were collected at the time of each census. Selectivity by owls for each rodent species was computed for each census by dividing the relative abundance of rodent species in owl diet to its relative abundance in the census (Cock, 1978).

RESULTS

The rodent community fluctuated from 1980 to 1981 in species compositon, density, and relative abundance (Table 1). In both years, there were six common species, as defined by Brown (1973), although the species that comprised these six differed. In 1981, *P. maniculatus* was the most abundant rodent on the dunes; yet, in 1980 it was completely absent. *D. ordii* was much rarer in 1981 than in 1980. Although it had a modest density on the census area in 1981, it was captured only 41 times in 7000 trap nights on the experimental plots. Although overall rodent densities were similar in both years, heteromyid rodents, especially bipedal taxa, were rarer and had lower relative abundances in 1981.

Now, what can be said about community structure? In both years, there were significant differences among species in microhabitat use—see Table 1 (Kruskal-Wallis test: for 1980, H = 19.74, $P < .005$; for 1981, H = 47.64, $P \ll .001$). In addition, most species that were present in both years had

Table 2.—*Effect of light and shadow on capture rates in 1980. Average captures per night for two levels of moonlight on the control grid during high (1 July to 7 July) and low (8 July to 18 July) amounts of moonlight shows the effects of natural moonlight on foraging activity. Density changes for* D. merriami *and* P. longimembris *prevented comparisons. Average difference,* di *(standard error), of paired observations of capture rates per night between the experimental and control grid for the parachute treatment shows the effects of shadow. Paired t-tests are used for parachute treatment comparison.*

| Species | Moonlight (average captures per night) | | | Shadow (average difference of capture rates) | |
	1-7 July 1980 (high moonlight)	8-18 July 1980 (low moonlight)	t	di	t
Dipodomys merriami	19.0	22.67	—	−.003(.08)	0.11
Dipodomys ordii	0.86	2.00	2.28**	.49(.09)	3.8***
Dipodomys microps	3.14	4.33	4.65***	.08(.24)	0.9
Dipodomys deserti	2.43	3.00	0.96	−.98(1.99)	1.2
Microdipodops pallidus	1.28	2.17	0.77	−.11(.13)	2.3*
Perognathus longimembris	2.71	3.50	—	.02(.17)	0.08

*P < .05, **P < 0.1, ***P < .001

similar microhabitat selection behavior and retained the same relative rank to each other in regard to how heavily they used the open microhabitat. The range in habitat selection behavior from the species with the greatest preference for the open to the least were also similar. However, the presence of *P. maniculatus* in 1981 foraging heavily in bushes and the relative rarity of kangaroo rats coincided with heavier use of the open by *M. pallidus* and *P. longimembris*.

Animals altered foraging behavior in response to changes in illumination in both years. Due to the necessity of running all experimental treatments on a single grid in 1980, only a few unequivocal comparisons could be made. In the other cases, differences between behavior of rodents on the control and the experimental grids may have been due to density dependent affects on habitat selection behavior (M'Closkey, 1981; Rosenzweig and Abramsky, 1985) and differences in rodent abundances on the two grids. Densities for four species on the control grid did remain unchanged over two contiguous sampling periods during a waning moon. Therefore, we can test for the effect of decreasing moonlight for these species (Table 2). As moonlight declined, foraging activity increased for *D. ordii*. Also, adding shadow by using parachutes led to high levels of activity for *D. ordii* on the experimental grid (paired *t*-test, $t = 3.8$, $P < .001$; Table 2) but a decline in activity for *M. pallidus* (paired-*t*, $t = 2.3$, $P < 0.05$; Table 2). In 1981, increased illumination caused a restriction in the use of open (Table 3) in four species, *D. merriami* ($t = 2.30$, $P < .025$), *D. microps* ($t = 5.78$, $P < .001$), *M. pallidus* ($t = 2.82$, $P < .01$), and *P. maniculatus* ($t = 1.77$, $P = 0.055$), as well as decreased foraging activity of other than *Dipodomys* species ($t = 2.02$, $P < .05$). Hence, predatory risk as affected by illumination has largely consistent effects on microhabitat utilization.

TABLE 3.—*Effects of experimental treatments on habitat selection (percentage of captures occurring in the open) for 1981 experiments. L = lantern treatment, S_o = seeds added to open habitat, S_b = seeds added to bush microhabitat.*

Species	Level	Treatment		
		L	S_o	S_b
Dipodomys merriami	experimental	37.0	69.0	44.0
	control	53.0*	56.0	50.0
Dipodomys microps	experimental	41.0	71.0	36.0
	control	58.0***	60.0	55.0***
Dipodomys deserti	experimental	90.0	100.0	88.0
	control	100.0	80.0	100.0
Microdipodops pallidus	experimental	57.0	85.0	45.0
	control	68.0**	64.0***	66.0***
Perognathus longimembris	experimental	56.0	45.0	53.0
	control	28.0	47.0	35.0*
Peromyscus maniculatus	experimental	18.0	20.0	13.0
	control	27.0	28.0	22.0

* $P < .05$, ** $P < .01$, *** $P < .001$; t-test, n = 14

Effects of added resources on foraging activity as measured by live-trapping are difficult to interpret due to the use of seeds as bait in the traps because the resource is enriched (Kotler, 1983). However, the 1981 experiments provide direct tests of the effects of resource distribution on microhabitat use. Enrichment of the open microhabitat caused significant increases in the use of the open by *M. pallidus* ($t = 5.65$, $P < .001$) and the three kangaroo rat species as a group ($t = 2.30$, $P < .01$; Table 3), whereas *P. longimembris* and *P. maniculatus* showed no response to the enrichment. In contrast, such enrichment in the bush microhabitat caused a significant shift into bushes for *P. maniculatus* ($t = 2.08$, $P < .01$) despite its already heavy bush use (Table 3). *M. pallidus* ($t = 4.75$, $P < .001$) and *D. microps* ($t = 6.36$, $P < .001$) also showed significant increase in their use of the enriched bush microhabitat (Table 3).

The morphology of the rodents seems to determine the response to the enrichment of microhabitats. *P. maniculatus*, which lacks antipredator morphology, did not respond to the enrichment in the open, despite having had the opportunity to encounter the seeds (as indicated by the small proportion of captures in the open). The risk was apparently too great. Deer mice, however, responded to the bush enrichment, so they can respond to resources unless overwhelmed by risk. Kangaroo rats and kangaroo mice, with their antipredator morphology, not only could respond to enrichments in the safe bush microhabitat, but could respond to seed enrichments in the open. These results suggest that habitat selection of rodents is affected by resources, but only within bounds set by predatory risk.

Other evidence also suggests that animals combine risk and resources together when making foraging decisions. I assumed that both risk and

resources affect foraging decisions, and ranked the experimental treatments *a priori* according to their expected effect on habitat selection based on this assumption. Treatments that should have led to high use of the bush or avoidance of the open were given high ranks (L, S_b, L + S_b; lanterns should make the open more dangerous, so, in contrast, the bush should be more attractive; seeds added to the bush should cause animals to spend more time foraging there; the two combined should make the bush still more attractive). Those that should lead to heavy use of the open were given low ranks (S_o, adding seeds to the open increases energetic rewards for foraging there; P, adding parachutes and shadows to the open should decrease risk there; P+S_o, the combination of the two should make the open still more attractive). Treatments that should have similar effects were given the same ranks (for example, L and S_b, S_o and P, C and L + S_o). The rank for each treatment for each species was then graphed against mean habitat selection use for that treatment. Distribution-free regression techniques (Maritz, 1981) were used to fit lines to the points, and the trends indicated by the lines were tested for significance by Chaco-Shorak test (a distribution-free isotonic regression technique that uses *a priori* ranking of treatment to increase statistical power—Lehmann, 1975). Significant negative trends should be seen if animals use both assessment of risk and resources to determine how to exploit microhabitats. Because control and experimental treatments were run on separate grids in 1980 and because density changed throughout the time of the experiments, trends in the experimental data (solid line, Fig. 1A) were compared to trends in the control data (dotted line, Fig. 1A) on both experimental and control grids. This comparison controls for density changes. For 1980, the slope of the line for the experimental treatments should be negative relative to the slope of the controls. (Nonzero slopes in the control data may have been due to density effects). In 1981, randomization over time and space allowed the control data to be treated as another treatment level. For that year, the slope of the line must be negative to support the prediction. In 1980 (Fig. 1A), significant trends, which differed from controls, were seen for the kangaroo rats *D. ordii* (K′ = 2.77, P $\ll$ .001), *D. microps* (K′ = 14.87, P = 0.001), and *D. deserti* (K′ = 18.48, P $<$ .001). In 1981 (Fig. 1B), significant trends also were seen for three kangaroo rat species, *D. merriami* (K′ = 6.05, P = .037), *D. microps* (K′ = 6.747 P = .035), and *D. deserti* (K′ = 9.993, P = .009). As before, most kangaroo rat species respond to both resources and predatory risk, but other species are more constrained in their foraging choices.

Microhabitat segregation in both years appeared to be strongly affected by rodent morphology. The auditory bullar volume of a species is positively correlated with the use of the open microhabitat in the absence of experimental manipulations (Fig. 2). Because size of the auditory bullae is correlated with the ability to hear low-frequency sounds (Webster and Strother, 1972) and the ability to detect predators, bullar volume can be regarded as a measure of antipredator specialization. Antipredator specialists
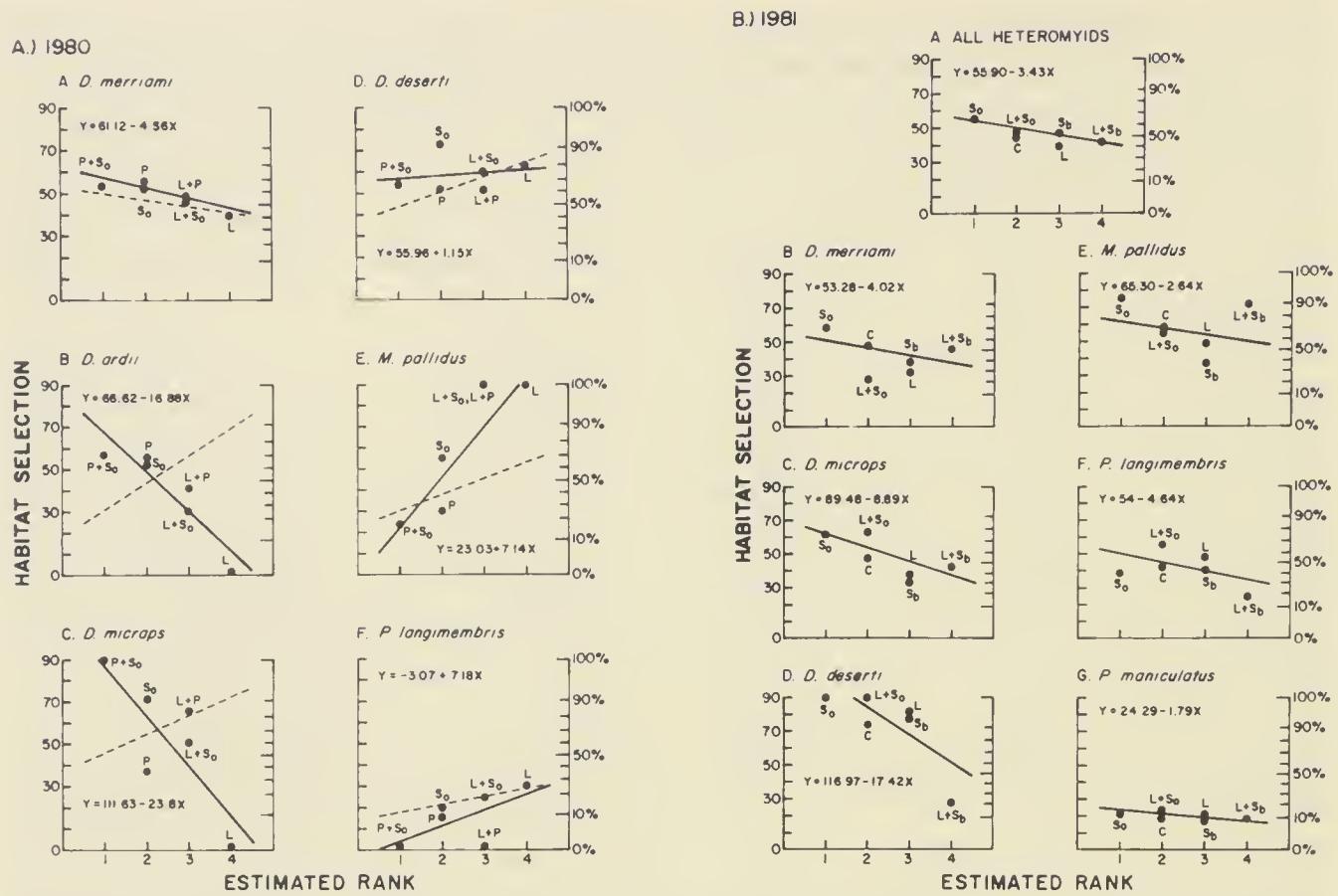
Fig. 1—Resources and risk of predation are combined to affect habitat selection behavior of desert rodents. Experimental treatments (abscissa scale) are ranked according to their expected effect on habitat selection behavior. The habitat selection value axis is scaled both in percentagle of captures occurring in the open (right ordinate) and its angular transformation (= arcsin $\sqrt{p}$, left ordinate). Equations for the lines are derived from distribution-free, regression techniques. Similar patterns are seen in A) 1980 and B) 1981. In A, dotted line represents data from the control grid. Nonzero slopes may be due to density effects. Figure 1B from Kotler (1984a) by permission of the Ecological Society of America.

foraged more in the risky open microhabitat (Fig. 2). The relationship was nearly identical in both years (for 1980, $y = 26.69 + .011$ x, $r = .90$, $P < .05$; for 1981, $y = 29.33 + .015$ x, $r = .957$, $P < .01$). Even with a different species composition, the community was organized similarly in both years.

How does mortality from predators relate to density changes from one year to the next? Mortality from long-eared owls was monitored from June 1979 to July 1981. Overall, owls did not capture rodent species in the proportion in which they occurred in the environment ($G = 62.88$, $P < .005$). Owls captured species lacking inflated bullae and bipedal locomotion (*Peromyscus, Reithrodontomys, Perognathus*) in greater proportion and species with inflated bullae and bipedal locomotion (*Dipodomys, Microdipodops*) in lesser proportions. This last generalization was not true in each census period. Figure 3 shows population changes from 1979 to 1981 for bipedal species (*Dipodomys, Microdipodops*) and quadrupedal species (*Peromyscus, Perognathus, Reithrodontomys*) as well as selectivity by owls for these two groups. The bipedal group is mostly dominated by data from *D. merriami* and the quadrupedal group is dominated by data from *P. maniculatus*. Population declines roughly correspond to selectivities by owls
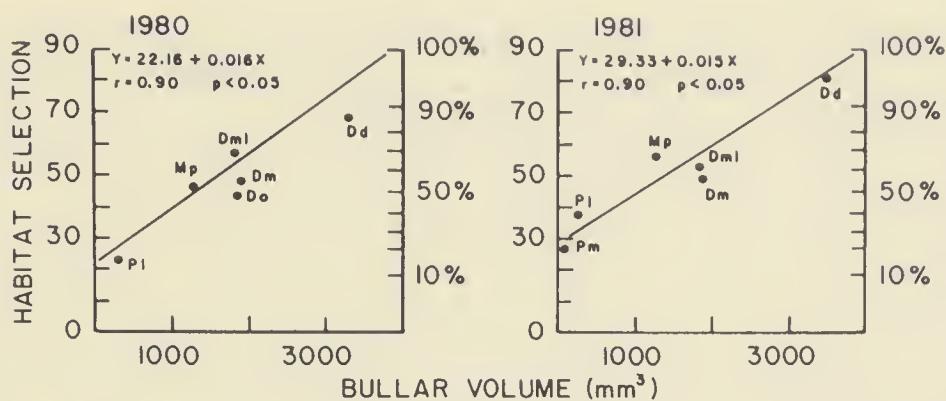
FIG. 2—Relationship between mean habitat selection and mean bullar volume of coexisting species for 1980 and 1981. The dependent axes are scaled in percentage of captures occurring in the open (right) and its angular transformation (left). Abbreviations for species as in Figure 1.

much greater than one (preference), and population increases correspond to selectivities much below one (avoidance). For example, the density of quadrupedal rodents declined in three out of five time periods, and selectivity by owls in these periods were more than two. In the two periods of population increase, owls had selectivity below 1.5. Changes in population densities for the rodents is reflected in the behavior of owls and may suggest a causal relationship.

DISCUSSION

Despite the volatile nature of this community—with species disappearing and later reinvading and the density of others fluctuating greatly—there appear to be certain generalizations that can be made about this community. 1. Coexisting species partition microhabitats. 2. Predatory risk affects how animals exploit microhabitats. 3. Resources affect how animals use microhabitats, within limits set by predatory risk. 4. Animals combine assessments of risk and resources together in determining where to forage. 5. Microhabitat use of a species is affected by morphology.

What does this mean in regards to the role of predation and resource competition in structuring this community and in regards to the mechanism of coexistence? Desert rodents take both predatory risk and resource availability into consideration in making foraging choices, although risk appears to be of greater "importance" because response to seed enrichments only can be understood in the context of predatory risk. It also is of greater importance in affecting community organization by promoting microhabitat segregation among species (Fig. 2). Yet animals that are not adapted to escape predators form an important segment of the community. These points indicate that there may be an important ecological trade off involving foraging efficiency and cost of predation. If so, predation and competition are inextricably linked in structuring this community. Small rodents by virtue of their lower total metabolic costs gain more net energy per seed consumed than do larger rodents for all seed sizes (Rosenzweig and Sterner, 1970). Similarly, small rodents have lower total costs of transport
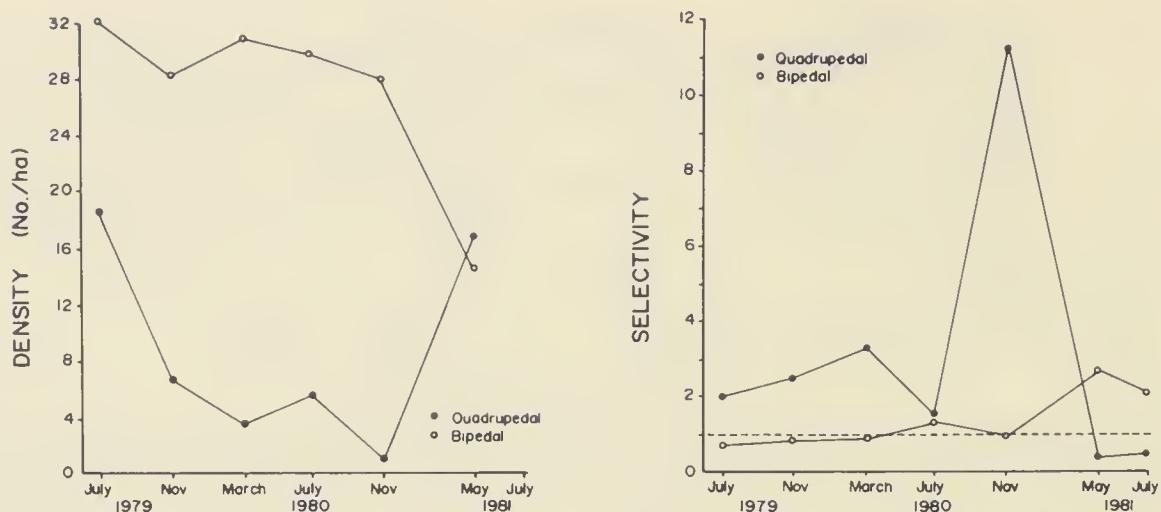
FIG. 3—(Left) Density (number per hectare) for bipedal species (*Dipodomys merriami, D. ordii, D. microps, D. deserti*, and *M. pallidus*) and quadrupedal species (*Perognathus longimembris, Peromyscus maniculatus*, and *Reithrondontomys megalotis*) throughout the study. (Right) Selectivity of rodents by owls (relative abundance of rodent species in own diet/ relative abundance in population) for bipedal species and quadrupedal species throughout the study; from Kotler (1985).

(Taylor *et al.*, 1970). Their gains from foraging should be greater, and their costs while traveling between patches should be smaller. Therefore, across all microhabitats, rodents of small body size should be better competitors for seeds. However, unless they also possess antipredator morphology of inflated bullae and elongated hind legs, they will face high predation costs, at least in the open microhabitat.

In contrast, animals with inflated bullae and elongated hind legs have lower costs of predation, but should have higher energetic costs to exploit the bush microhabitat owing to the inefficiency of using a bipedal gait with long hind legs while maneuvering through branches. Larger body size typical of kangaroo rats would add further to their higher energetic costs. Overall, kangaroo rats should have lower costs of predation, especially in the open. However, their morphology and larger size also lead to higher energetic costs of foraging, especially in the bush microhabitat. The small body size of *Microdipodops* alleviates their energetic costs somewhat, but may make them more susceptible to interference (Frye, 1984). In contrast, deer mice and pocket mice have high costs of predation in the open microhabitat. However, their small body sizes may allow them to out-compete kangaroo rats in the bush microhabitat (Rosenzweig and Sterner, 1970). It seems that coexistence is promoted because one group of species has lower microhabitat specific costs of predation, which make them the most efficient foragers in the risky microhabitat, whereas the other set of species remain the energetically most efficient foragers in the safe microhabitat. Microhabitat use, morphology, and body size are all closely tied together in the scheme of coexistence.

What accounts for the changes in species densities? The major differences between 1980 and 1981 is the entry of *P. maniculatus* into the community in high density and the decline in the density of *D. merriami. Peromyscus*

maniculatus has a high reproductive potential relative to the other species in the community and has a more generalized diet. Yet its increase was not a result of opportunistic exploitation of abundant resources. What little evidence there is on resource availability indicates that density of seeds was lower in 1981 than in 1980. Perennial plants at the site are the primary source of seeds. They produce seeds that ripen in the autumn, but are not dispersed until the following spring. In October 1979, out of 250 shrubs surveyed, 167 bore seed crops. In October 1980, only 66 of these exact same plants had seed crops. Furthermore, there were few if any seeds produced by annuals in 1980. Populations of *P. maniculatus* had increased to high levels prior to production of any seeds by annuals in 1981. Therefore, the increase in *P. mainculatus* was not due to increased food availability. It is possible that the density changes were mediated through predation, as indicated by the relationship between owl selectivity and changes in population size. But predator numbers were low in both 1980 and 1981 (Kotler, 1985). Also, there is no way of knowing at this point whether rodent densities changed as a result of owl selectivity, or owl selectivity changed as a result of changing rodent densities (Getty, 1985). In addition, other factors outside of the community may have been in part responsible for the increase of *P. mainculatus*, because most individuals were immigrants (as indicated by subadult body size of most individuals and few breeding adults on the study site). At this time, it is not possible to draw conclusions on the causes of year-to-year variation in community composition.

In 1981, *P. longimembris* failed to respond to experimental treatments as predicted (Kotler, 1984a; Table 3). In fact, the signs were in the opposite direction. This suggests that they were responding to some other factor, perhaps interference from kangaroo rats (Frye, 1984). In fact, there is a negative correlation between the microhabitat use of *P. longimembris* and the kangaroo rats on a night-to-night basis (Kotler, 1984a). With *P. maniculatus* foraging heavily under bushes and reducing seed densities there and the kangaroo rats interfering with *P. longimembris* wherever they were, *P. longimembris* was the odd man out and foraged wherever kangaroo rats were not. Likewise in 1980, *M. pallidus* may have been the odd man out. *Peromyscus maniculatus* was absent that year and *P. longimembris* foraged in bushes; the kangaroo rats were much more common than in 1981 (Table 1). The kangaroo rats (35-120 grams) could have easily displaced the small (12 grams) *M. pallidus* from highly preferred microhabitats. The significant avoidance of open microhabitats by *M. pallidus* during the parachute treatment (Table 3) may be indicative of this.

There are other general patterns in the community. There are always several kangaroo rat species that exploit open microhabitats, an odd man out that avoids kangaroo rats, and only one species that exploits the bush. Species differ significantly in microhabitat utilization; there is a relationship between microhabitat selection and morphology. All these point to the importance of the trade off between foraging efficiency and cost of predation

based on morphology. But more is needed to completely understand community structure and density changes. Brown (this volume) has suggested the existence of another ecological trade off involving foraging speed and foraging efficiency mediated through body size. Large animals can gather resources in patches quickly, but cannot forage profitably on low seed densities that are still profitable for small animals. Temporal and spatial variability in seed densities create situations where one species or another has the advantage at various times and in various microhabitats. Both trade offs operating together may be responsible for the remarkable species diversity of desert rodents. Detailed investigations of foraging economics and predation costs for desert rodent communities are currently underway and may lead to a better understanding of its structure and volatility.

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THE ROLE OF RESOURCE VARIABILITY IN STRUCTURING DESERT RODENT COMMUNITIES

JOEL S. BROWN

ABSTRACT—Variability is a universal, but poorly understood, property of ecosystems. The common belief that environmental variability has a destabilizing effect is being challenged by a growing body of theoretical research. Environmental variability and variance in resource abundances may actually promote species coexistence and community stability. Two models of coexistence on a single resource are considered: 1) coexistence is possible on a resource in which abundance varies spatially if there is a trade off between foraging efficiency and the cost of travel; 2) coexistence is possible if the species that is the most efficient forager switches seasonally. A community of four desert rodent species—*Perognathus amplus* (11 grams), *Dipodomys merriami* (43 grams), *Ammospermophilus harrisii* (98 grams), and *Spermophilus tereticaudus* (119 grams)—was used to test the models. Artificial seed trays were used to measure relative foraging efficiencies. The second mechanism of coexistence appears to explain the presence of *P. amplus*, *D. merriami*, and *S. tereticaudus* in the community. Each enjoys a season during which it is the most efficient forager. The first mechanism of coexistence explains the presence of *A. harrisii* in the community. This species preferred to forage a large number of widely spaced patches to a high giving-up density rather than foraging a few patches to a low giving-up density.

When coexisting species have similar habits and diets, two familiar mechanisms that promote coexistence are habitat selection and diet separation. However, even when there is complete diet and habitat use overlap, coexistence can occur along a niche axis provided by variance in resource abundance (Levins, 1979) or variance in resource consumption rates (Stewart and Levin, 1973; Abrams, 1984). Although the theoretical feasibility of species coexistence on a single variable resource has been well documented (Gadgil and Gadgil, 1975; Chesson and Warner, 1981; Chesson, 1982; Namba, 1984; Vance, 1984), actual field investigations are few (for exceptions see Johnson and Hubbell, 1975; Hubbell and Johnson, 1978).

This report uses data from field experiments to test for the feasibility of species coexistence on a single resource. I will consider two mechanisms. The first assumes that resource abundance varies spatially and temporally. Coexistence is possible if the more efficient foraging species simultaneously has the greater travel cost (Brown, 1986). The second makes no assumptions about the constancy of resource availability but assumes that the foraging efficiency of a species varies temporally. Species coexistence is possible if each species possesses some time period during which it is the most efficient forager (Stewart and Levin, 1973; Abrams, 1984; Brown, 1986). Both mechanisms operating alone or together can promote species coexistence.

Foraging experiments, using artificial seed trays, were conducted on a community of four desert granivorous rodent species—*Dipodomys merriami* (Merriam's kangaroo rat), *Perognathus amplus* (Arizona pocket mouse),

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Spermophilus tereticaudus (round-tailed ground squirrel), and *Ammosper-mophilus harrisii* (Harris' antelope ground squirrel). Desert rodents live in an environment where the abundance of seed resources exhibits tremendous spatial and temporal variability (Reichman, 1984). Furthermore, sympatric species of desert granivorous rodents exhibit little diet separation (Lemen, 1978; M'Closkey, 1983). Finally, the nature of the resource (sessile seeds) permits easy measurement of relative foraging efficiencies under natural conditions. These characteristics of desert rodents make them testable candidates for species coexistence on a single resource.

Coexistence of a Single Resource

May and MacArthur (1972) and May (1973, 1974) concluded that environmental variability has a destabilizing effect on communities and that environmental variability inhibits the coexistence of competitors. These results, however, are dependent upon the linear growth response of a species to resource density. Several authors (Koch, 1974; Armstrong and McGehee, 1976, 1980) have demonstrated that by relaxing the linearity assumption, limit cycles exist where several consumer species can coexist indefinitely on a single resource. Their models require that either the density of foraging species or the density of resources vary through time. Levins (1979) has shown that variance, covariance, and higher statistical moments in resource abundance can behave as "consumable resources." It appears, therefore, that environmental variability in resource abundances actually may enhance the diversity and stability of ecosystems.

In this section, mechanisms of species coexistence on a single resource are outlined where 1) the more efficient foraging species also has the higher cost of travel, and 2) the species that is the most efficient forager varies through time (Brown, 1986). The models of this section are in the spirit of Tilman's (1980, 1982) resource theory in that interactions between foraging individuals or species occurs only through the harvesting of resources. Foragers, regardless of species, have no direct interference effect on the fitnesses of other foragers.

Foraging efficiency is the ratio between the output (O) and the input (I) of foraging, O/I. Output corresponds to the benefits and input corresponds to the costs of foraging. The benefits of foraging may include energy, nutrients, water, nesting material or some combination thereof. The costs of foraging may include energy, risk of predation, or accidental death or injury. Actual measurement of output and input presents a formidable challenge because all of these factors contribute to fitness in a complex fashion. Fortunately, for the purposes of measuring relative foraging efficiencies, it is not necessary to know the various fitness currencies of these costs and benefits.

The density of resources within the environment at which a forager ceases foraging (giving-up density) provides an indicator of foraging efficiency. A forager, if it has the ability and if it has been molded by natural selection, should cease foraging when the benefits and costs of foraging are balanced,

that is, when O=I. This translates into a foraging efficiency of one at the giving up density, $O/I = 1$. If, at species A's giving-up density, species B has the higher foraging efficiency, then $O_B/I_B > O_A/I_A = 1$, where the subscripts refer to species A and B. It follows that at A's giving-up density B is still experiencing a net profit from foraging, that is, $O_B > I_B$, and B should continue foraging to a lower giving-up density. Thus, 1) giving-up density provides an indicator of foraging efficiency and 2) the species with the lower giving-up density is the more efficient forager (Brown, 1986).

Travel cost, like the input and output from foraging, is a complex function of metabolic costs, predation risk, and other risks of injury or death.

Coexistence on a Resource in Which Abundance Varies Spatially

If a single resource achieves an equilibrium density with no temporal or spatial variability then the most efficient foraging species will competitively exclude all others. This occurs because at equilibrium each foraging species will reduce the resource density to its subsistence level. But, by definition of foraging efficiency, this subsistence level will be lowest for the most efficient forager. Thus, the most efficient forager will reduce the resource density to below subsistence for all other species and exclude them from the community (Tilman, 1982).

When the abundance of a resource varies spatially, two attributes of a forager will contribute to its success—1) travel cost, and 2) foraging efficiency. Travel cost determines to what extent an individual can benefit from periods or places with high resource densities. When resources are abundant, $O \gg I$, foraging costs are less important than the ability to travel inexpensively from one rich patch to another. Foraging efficiency determines to what extent an individual can profitably harvest resources from periods or places with low resource densities. When resources are scarce, $O = I$, travel cost is less important than the ability to achieve an energetic profit from harvesting resources at low densities (Brown, 1986).

The species with low travel cost and low foraging efficiency tailors a distribution of resource densities among patches with low variance and high mean. The species with high travel cost and high foraging efficiency tailors a distribution with high variance and low mean. In summary, periods or places with high resource density favor individuals that have low travel costs. Low resource densities favor individuals that have high foraging efficiencies. If, among foraging species, there is an evolutionary trade off between travel cost and foraging efficiency, then spatially variable resource abundances can promote competitive coexistence on a single resource (Brown, 1986).

Temporal Variation in Foraging Efficiencies

Seasonal changes in the environment may alter the benefits and costs of foraging. For instance, an energy surplus may be more valuable during the

breeding season. Thus, all else being equal, during the breeding season the fitness output from foraging may be greater. Seasonal changes in the climate, such as temperature and precipitation, or seasonal changes in predation risk may alter the costs of foraging. Cold temperatures or higher predation risks should increase the input into foraging. These changes in output and input result in seasonal variation in foraging efficiencies.

Coexistence on a single resource does not require a trade off between travel cost and foraging efficiency if there is seasonal variation in foraging efficiencies. Stewart and Levin (1973) and Abrams (1984) have shown that competitive coexistence is possible if each species possesses a season in which it is the fastest forager. Or, similarly, coexistence is possible if each species possesses a season in which it is the most efficient forager. Coexistence can occur because there is a seasonal rotation in the species that is competitively superior.

Several factors increase the likelihood of coexistence by this mechanism. Coexistence is facilitated if the temporal covariance of the densities of the species is negative. During the season when a given species is the most efficient forager, its increase in density is propelled both by its high foraging efficiency and by the decline in the density of its competitors. Coexistence is facilitated if there is a fixed and variable cost component to foraging. During harsh periods, that is, periods of low foraging efficiency, a species can recoup its variable cost of foraging by remaining inactive or dormant (Brown, 1986).

In summary, coexistence on a single resource is possible if there is a trade off between foraging efficiency during environmental conditions pertaining to different temporal periods. If the conditions of a given season were permanently fixed through time, then the foraging species that is the most efficient forager under these conditions would competitively exclude all other species.

DESERT RODENTS

The desert granivorous rodents of North America have provided an important model ecosystem for studying the effects of competition and predation on community structure (for reviews see Brown, 1975; Rosenzweig, 1977; Price and Brown, 1983). Sympatric species, which usually have similar diets and habits, exhibit two striking patterns: 1) coexisting species usually have dissimilar body sizes (nonrandom pattern of body size) (Brown, 1973, 1975; Bowers and Brown, 1982), and 2) two distinct morphologies represented by the presence or absence of elongated hind limbs and inflated auditory bullae.

The desert environment is characterized by randomly or uniformly distributed islands of perennial shrubs scattered in a sea of open space. This provides at least two distinct microhabitats: 1) space under shrubs, and 2) space in the open. Both diet separation through selection of seed size (Brown and Lieberman, 1973; Reichman, 1975) and habitat selection

(Rosenzweig and Winakur, 1969; Brown and Lieberman, 1973; Rosenzweig, 1973; Price, 1978; Thompson, 1982; Kotler, 1984) have been investigated as possible mechanisms of coexistence. There is little evidence of diet separation (Lemen, 1978), but there is strong evidence that quadrupedal rodents predominate in the shrub microhabitat, whereas bipedal species predominate in the open. Either microhabitat structure (Price, 1983) or predation risk (Kotler, 1984, this volume) provide explanations for why quadrupeds may be more efficient foragers in the bush microhabitat and why bipeds are more efficient in the open microhabitat.

In reference to the two mechanisms of coexistence of present interest, body size may represent a trade off between travel cost and foraging efficiency. This would occur if larger species forage faster but not sufficiently fast to compensate for the proportionately greater foraging costs. A seasonal rotation of the species that is the most efficient forager may result from changes in climate or predation risk. As the temperature becomes cooler, the energetic costs of foraging will rise proportionately more for smaller rodent species (Calder, 1984). Also, many rodent predators, such as snakes and raptors, are migratory or undergo periods of dormancy, causing seasonal changes in the intensity and nature of predation risk.

Measuring Foraging Efficiency

Recall that "giving-up densities" provide an indicator of foraging efficiency. Three criteria must be satisfied before giving up densities in resource patches can be used to measure relative foraging efficiencies in natural rodent communities. First, foraging speed must be an increasing function of patch resource density. This guarantees that as an individual harvests resources the benefits from additional foraging declines. Second, the species that utilize the patch must be identifiable. Third, the initial and remaining density of seeds in the patch must be measurable.

To measure relative foraging efficiencies in a natural community, I conducted experiments with artificial seed trays (see below). The study site was in the Sonoran Desert, located three kilometers east of the boundary of the Tucson International Airport, Tucson, Arizona. The 20 percent shrub cover was provided primarily by creosote bush (*Larrea tridentata*). Four species of rodents regularly foraged in the seed trays: Merriam's kangaroo rat (*Dipodomys merriami*, 43 grams), Arizona pocket mouse (*Perognathus amplus*, 11 grams), round-tailed ground squirrel (*Spermophilus tereticaudus*, 119 grams), and Harris' antelope ground squirrel (*Ammospermophilus harrisii*, 98 grams).

Bimonthly, during 1983-84, I conducted two nights and one day of mark-release trapping for a total of 12 trapping periods. Trapping was conducted on four seven-by-seven grids with station intervals of 25 meters for a total of 196 stations.

From August 1983 through July 1984, a total of 60 seed trays were divided over two of the trapping grids. The 30 seed trays on each grid were divided

into pairs and assigned to 15 stations picked each month at random from the 49 trap stations. At each station with seed trays, one tray was placed directly under the canopy of a creosote bush and the other was placed two to four meters away in the open microhabitat. Although shadowed by the canopy, the surface of trays under shrubs was unobstructed by branches or leaves up to a height of at least 15 centimeters.

Aluminum trays measuring 45 centimeters on a side and 2.5 centimeters deep were used as seed trays. Into each tray, I measured three grams of unhusked millet that had been mixed into three liters of sifted dirt. Each month, data from seed trays were collected for eight mornings and seven afternoons. The morning run was at sunrise and followed the cessation of activity by kangaroo rats and pocket mice and preceeded activity by squirrels. Afternoon checks were at sunset and followed squirrels and preceeded kangaroo rats and pocket mice. Thus, pocket mice and kangaroo rats had the entire night to forage at the trays and squirrels had the entire day.

Running the seed trays consisted of noting any footprints in the sifted dirt, sifting the dirt to recover the remaining seeds, and reseeding the trays. The distinctiveness of footprints permitted identification of the foragers to species and sometimes to the exact individual (based on toe-clips). With regard to identifying squirrel forages, round-tailed squirrels leave a pencil-like tail drag, whereas antelope squirrels leave no tail drag. A forage was attributed to antelope squirrels if there were no tail drags present and a forage was attributed to round-tailed squirrels if there were tail drags. In some cases, the footprints of two rodent species were visible either within a seed tray or at a station. Data from such stations were not used in the following analyses. The seeds recovered from a seed tray were cleared of debris and weighed to measure the giving-up density.

RESULTS

The results of the rodent censuses are given as the total number of different individuals captured during the particular census (Fig. 1). The density of kangaroo rats fluctuates seasonally from a high in March to a low in July and September. Pocket mice and round-tailed squirrels are even more seasonal. Both are dormant for the winter; pocket mice live off of stored seeds and round-tailed squirrels live off body fat with brief periods of activity on warmer winter days. Although antelope squirrels are active throughout the year, their population peaks during the summer and declines over the winter.

The giving-up densities of kangaroo rats, pocket mice, and squirrels are shown together as a monthly graph (Fig. 2). Figure 2 (top) shows giving-up densities in the bush microhabitat and Figure 2 (bottom) shows giving-up densities in the open microhabitat. The giving-up densities of the two squirrel species have been lumped because within a month or within a microhabitat their giving-up densities never differed significantly.
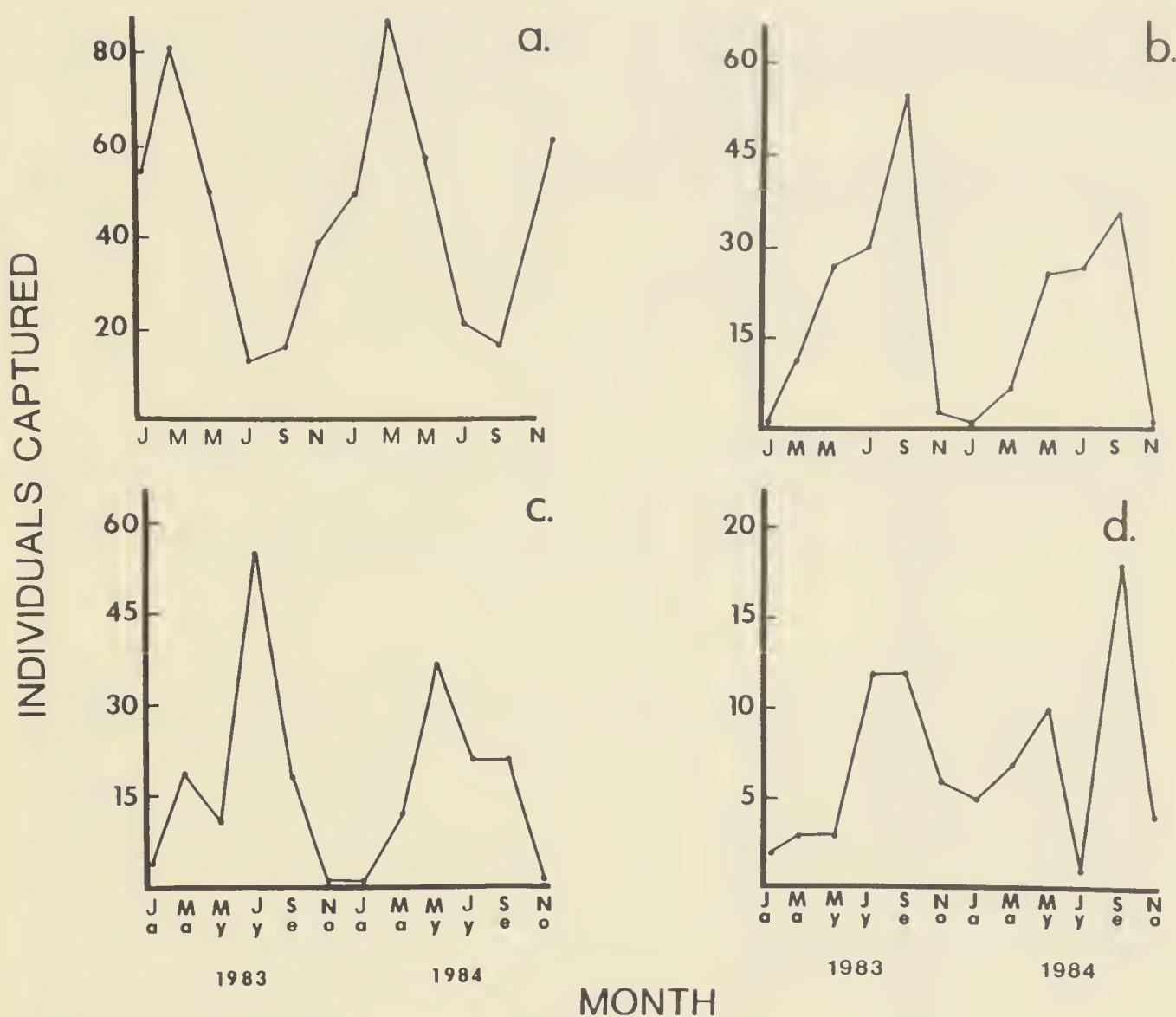
Fig. 1.—Population sizes of (a) *Dipodomys merriami*, (b) *Perognathus amplus*, (c) *Spermophilus tereticaudus*, and (d) *Ammospermophilus harrisii*. Size is given as the total number of individuals captured during a particular bimonthly census (beginning January 1983 and ending November 1984). Note how *D. merriami* peaks in early spring, whereas the other three species reach peak densities in late summer.

Table 1, on a monthly basis and by species, shows which microhabitat had the lower giving-up density. Entries in the table indicate whether bush, open, or neither had the significantly lower giving-up density. The results were determined by a paired sign test comparing trays at a station. Throughout the year squirrels always had lower giving-up densities in the bush microhabitat, pocket mice either had no difference or had a lower bush giving-up density, and kangaroo rats switched their lower giving-up density on a seasonal basis, preferring the open microhabitat in the summer and the bush in the winter.

Figure 3 is a summary that permits comparisons of giving-up densities on a species, microhabitat, and seasonal basis. The axes are giving-up density in the bush as opposed to open microhabitat. Each species is represented by a line the intercepts of which approximate the giving-up densities in the bush and open. A line with a slope negative one indicates no significant
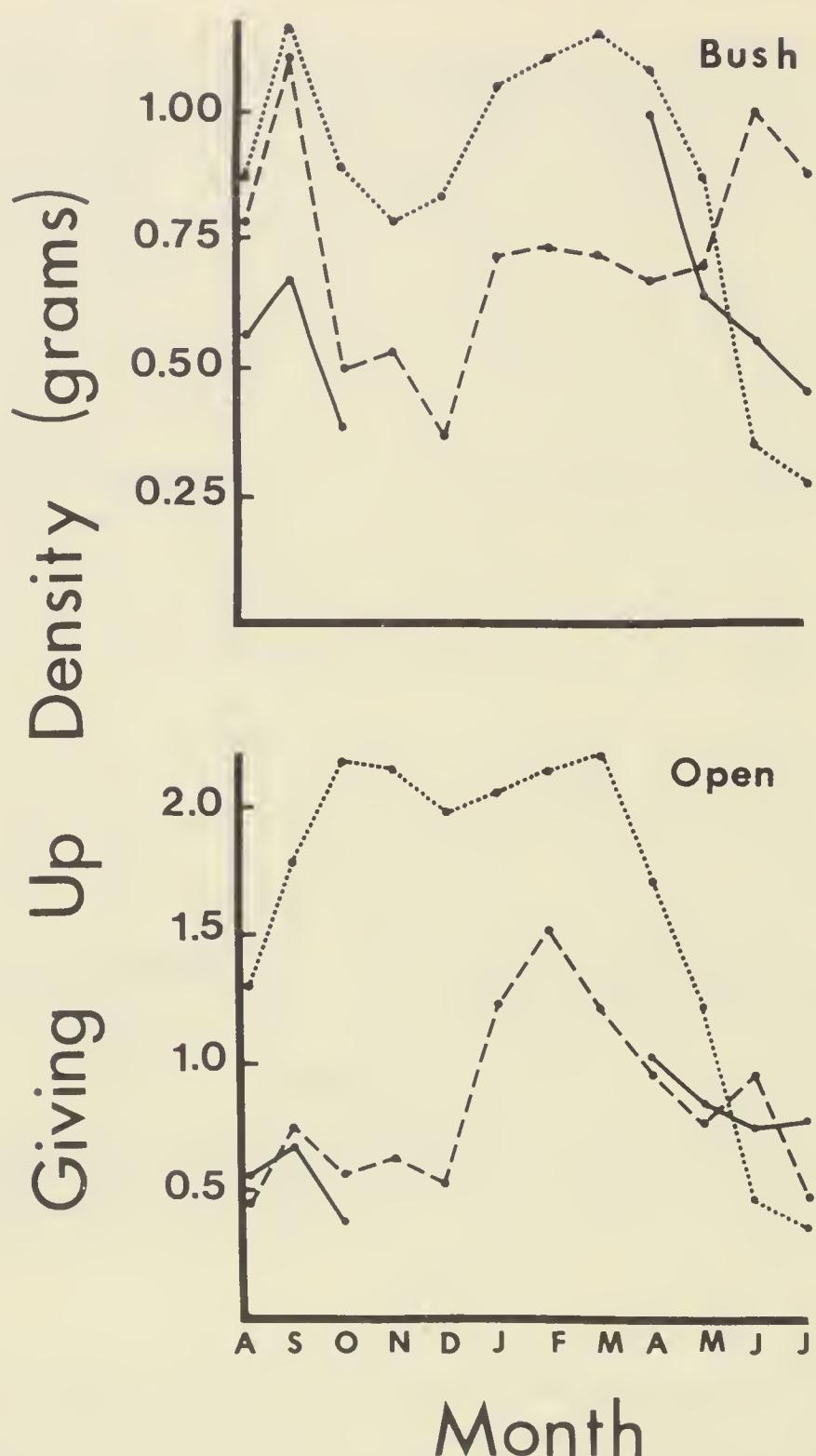
FIG. 2.—The average remaining weight of seeds in seed trays (giving-up density) following foraging by *D. merriami* (dashed line), *P. amplus* (solid line), and *A. harrisii-S. tereticaudus* (dotted line). The upper and lower graphs depict the bush and open microhabitats respectively. The monthly points begin with August 1983 and end with July 1984.

difference in giving-up density between the microhabitats, a steeper line indicates that the bush giving-up density is lower, a shallower line indicates that the open giving-up density is lower. If on an axis the intercepts of two lines coincide, then there is no significant difference between the two species in their giving-up densities in that microhabitat. If the intercept of one species lies below that of another than it has a significantly lower giving-up density in that microhabitat.

TABLE 1.—*The habitat preference of each species by month. The rows are the species and the columns are the months (abbreviations). A "B", "O", or "N" indicates that the bush, open, or neither microhabitat had the significantly lower giving-up density (P < .05). A dash indicates that the species was not present.*

Species	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
P. amplus	N	B	B	—	—	—	—	—	N	B	N	B
D. merriami	O	O	B	B	B	B	B	B	B	B	N	O
Squirrel	B	B	B	B	B	B	B	B	B	B	B	B

DISCUSSION

The results permit us to gain insights into three mechanisms of coexistence: 1) habitat selection, 2) seasonal rotation in the most efficient species, and 3) trade off between travel cost and foraging efficiency.

Habitat Selection

Habitat selection could promote coexistence if each species possesses a microhabitat in which it is the most efficient forager. During the year, there was only one month, July, in which there is a pair of species where one is more efficient in the open and the other is more efficient in the bush (Fig. 3). In this case, kangaroo rats have a lower giving-up density than pocket mice in the open, whereas pocket mice have the lower in the bush microhabitat. During July, however, squirrels are the most efficient foragers in both microhabitats. If the conditions pertaining to July were fixed, squirrels should exclude both kangaroo rats and pocket mice from the community.

Although the data presented here suggest that microhabitat selection is not important in promoting coexistence, it does not preclude its importance under different circumstances or in other communities. J. S. Brown *et al.* (unpublished data) have shown that the foraging efficiency of Merriam's kangaroo rats decreases but that of the Arizona pocket mouse remains unchanged when tangles of branches and leaves create a jungle gym effect on the surface of seed trays. Dense tangles of shrubbery may represent a third important microhabitat that was not considered in this study. Kotler (1984, this volume) has evidence from the Great Basin Desert that suggests that kangaroo rats are more efficient in the open, whereas pocket mice are more efficient in the bush microhabitat.

Data on the giving-up densities in the open and bush microhabitat indicate the habitat preferences of the different rodent species when presented with equal resources and substrate. In the experiments using seed trays, the harvest rates and energetic costs of foraging should be the same regardless of microhabitat. Thus, differences in giving-up densities between microhabitats should reflect differences in predation risk. Predators such as owls, hawks, foxes, and coyotes may exert greater predation risk in the open microhabitat (see Kotler, 1984). Therefore, giving-up densities should be

lower in the bush microhabitat. It is interesting to note that the preference of kangaroo rats switches to the open microhabitat during July to September. Coincident with this shift is an increase in the nocturnal activity of rattlesnakes. It would be of interest to investigate whether rattlesnakes cause this shift in preference by exerting greater predation risk in the bush rather than open microhabitat.

Seasonal Rotation of the Most Efficient Foraging Species

Coexistence, without either diet separation or habitat selection, is possible if each species is the most efficient forager during a particular season. This seems to be the case (see Fig. 3). During the months of August to October (Fig. 3), the Arizona pocket mouse is the most efficient forager in both microhabitats. From November to April, Merriam's kangaroo rat is the most efficient. In May, both the pocket mouse and the kangaroo rat are the most efficient foragers. In June and July, squirrels are the most efficient foragers.

Additional support for this hypothesis comes from the trapping data. The densities of the pocket mouse, the kangaroo rat, and the round-tailed squirrel covary negatively through time. Only the density of the antelope squirrel does not contribute to this negative covariance (Brown, 1986). Furthermore, both the pocket mouse and the round-tailed ground squirrel become inactive during what may be periods of low foraging efficiency (November through April and October through February, respectively).

Both climate and predators may contribute to the seasonal variation in foraging efficiencies. Relative to the Merriam's kangaroo rat both the Arizona pocket mouse and the round-tailed ground squirrel should find cold weather more energetically costly; the pocket mouse because it is smaller (Calder, 1984) and the round-tailed ground squirrel because of its extremely high thermal conductance (Hudson, 1964). Thus, cold weather should decrease the foraging efficiency of kangaroo rats proportionately less and warm weather should increase the foraging efficiency of the pocket mouse and the round-tailed ground squirrel proportionately more.

Seasonal changes in predators may also account for the changes in foraging efficiencies among the different species. During the winter there was an increase in the amount of activity of daytime raptors over the study site and a decrease in the observable activity of nocturnal snakes and owls. Predation risk for squirrels is probably highest in the winter and lowest in the summer, whereas the opposite is true for the nocturnal rodents. This corresponds to the periods during which the diurnal or nocturnal rodents are the most efficient foragers.

Trade off Between Travel Cost and Foraging Efficiency

If there is a trade off between travel cost and foraging efficiency then the species with the lower foraging efficiency should have a higher giving-up density and (in proportion to its body size) should visit more patches. With
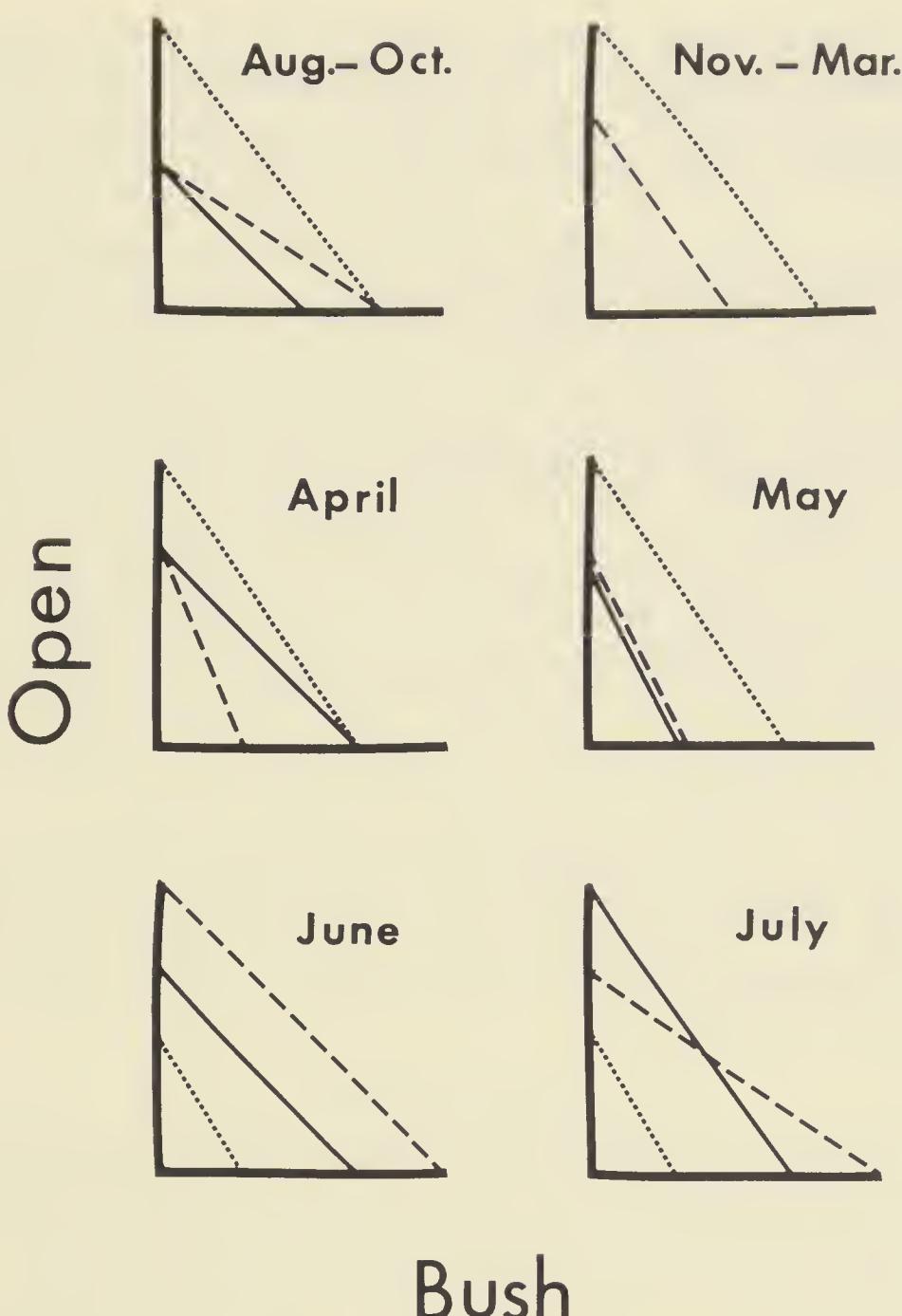
Fig. 3.—A summary of the foraging data that permits comparisons of giving-up densities on a species, microhabitat, and seasonal basis. Species are represented by the lines: *D. merriami* is the dashed line, *P. amplus* is the solid line, and *A. harrisii-S. tereticaudus* is the dotted line. Axes represent bush and open microhabitats. A slope of negative one indicates no significant difference in giving-up densities between microhabitats. A shallower slope indicates that the open had the significantly lower giving-up density and a steeper slope indicates that the bush was foraged significantly lower. If the intercept of one species lies below that of another than it had the significantly lower giving-up density in that microhabitat. When the line of one species lies inside that of another then the former species should competitively exclude the latter if the conditions pertaining to that season were maintained indefinitely.

respect to the data, those species with low giving-up densities should also have low mean distances between recaptures.

The pocket mouse, kangaroo rat, and round-tailed ground squirrel do not differ significantly in their mean distances between recaptures (Brown, 1986). In addition, the data on giving-up densities fit the necessary

conditions for coexistence through a seasonal rotation in the most efficient foraging species (see previous mechanism). Therefore, the mechanism of this section may be unnecessary. However, the persistence of the antelope ground squirrel in the community is not explained by the previous mechanism.

The antelope squirrel is active throughout the year. During winter, it is the least efficient forager and when squirrels are the most efficient foragers it is outnumbered by the round-tailed squirrel. The presence of two squirrel species may be the result of the two mechanisms operating simultaneously. The round-tailed squirrels being promoted by the period when squirrels are the most efficient foragers and the antelope squirrels being promoted by the spatial and temporal variation in resource abundances. Relative to the kangaroo rat, the pocket mouse, and the round-tailed squirrel, the antelope squirrel has a significantly greater mean distance between recaptures. On winter afternoons, the footprints of a single individual antelope squirrel could be found at five or more stations. (Footprints of individuals of other species were never found at more than two stations). During these months the high giving-up density of the antelope squirrel suggests that this species found it more profitable to move 25 to 75 meters to another station rather than to continue foraging at the present station. In contrast, during this period (recall that the pocket mouse and the round-tailed squirrel are inactive), kangaroo rat individuals moved much smaller distances and had much lower giving-up densities.

Conclusions

In the community of desert rodents investigated here, it appears that both temporal variation in foraging efficiencies, and a trade off between travel cost and foraging efficiency promote coexistence on a single resource in which abundance varies temporally and spatially. Habitat selection does not seem to be important in this community. However, many desert rodent communities have much richer diversities and in these communities habitat selection probably joins with these other mechanisms to yield a rich diversity of body sizes and morphologies.

The phenomenon of coexistence on a single variable resource may be widespread. Communities where the sympatric species exhibit little diet separation or habitat selection invite investigation. Such communities include African grazing ungulates, aerial insectivorous bats, granivorous birds, and nectarivorous birds and insects.

Acknowledgments

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MORPHOLOGICAL FACTORS AND THEIR CONSEQUENCES FOR RESOURCE PARTITIONING AMONG AFRICAN SAVANNA UNGULATES: A SIMULATION MODELLING APPROACH

NORMAN OWEN-SMITH

ABSTRACT—Despite evidence that ungulate populations are commonly food-limited, experimental confirmations of competition are lacking. The effects of morphological differences on resource partitioning are evaluated within a simulation modelling context. The animal features incorporated include the grazer-browser category determining modifications of digestive anatomy, body mass controlling size dimensions and bioenergetic requirements, and relative mouth dimensions influencing bite size. The model demonstrates how these factors can lead ungulates of differing morphology to favor different vegetation structures. Resource partitioning is achieved primarily through habitat selection and plant parts favored, despite overlap in the plant species eaten. Overlap in the use of abundant vegetation components does not lead to any significant depression of food availability. The potential for competition exists mainly 1) during the wet season, when uncommon but highly nutritious plant parts can make a significant contribution to dietary quality, thereby influencing reproductive success, and 2) during the early dry season, when ungulates become dependent upon less abundant food sources. However, competition is probably of lesser importance than other ecological interactions, including facilitatory effects on vegetation structure and food quality, induction of plant defenses, and security against predation.

Some 15 to 20 species of ungulates may coexist in African savanna habitats within regions encompassing a few hundred square kilometers or less. There is evidence that many of these populations are food-limited (Sinclair, 1975, 1977). Different ungulates commonly favor the same plant species (Jarman, 1971; Stewart and Stewart, 1971; Owen-Smith and Cooper, 1985). The potential thus exists for interspecific competition to be widespread and chronic. Indeed, wildlife managers may invoke competition as a reason for the active manipulation of the population levels of certain species of ungulates for the supposed benefit of others (Joubert, 1974; Macdonald and Brooks, 1983; Pienaar, 1983). Nevertheless, there are as yet no experimental demonstrations of interspecific competition among such large herbivore species, and the circumstantial evidence presented in support is equivocal and open to other interpretations. Several studies have indicated resource partitioning operating at a finer level, in terms of the microhabitats favored for feeding, and the plant parts that are ingested (Lamprey, 1963; Gwynne and Bell, 1968; Bell, 1970; Ferrar and Walker, 1974; Leuthold, 1975; Page and Walker, 1978).

In this paper, I use a simulation modelling approach to demonstrate the mechanisms leading to resource partitioning among assemblages of ungulate species, and also to indicate the circumstances in which competition is most likely to occur. This background analysis may be useful

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as a starting basis for more critical experimental investigations of competition among large herbivores.

STRUCTURE OF THE SIMULATION MODEL

Owen-Smith and Novellie (1982) formulated an optimal foraging model applicable to large herbivores. Habitat structure is specified in terms of an array of potential food types, defined in terms of their nutrient concentrations and abundances. The model calculates the maximum nutritional profits (gain measured against expenditure) that an ungulate of specified morphological characteristics could achieve while foraging in this habitat, determined by the relation between nutrient ingestion rate, nutrient digestion rate, and daily foraging time. It incorporates rate of movement while searching, path breadth and height scanned, ingestion rate while feeding, gut capacity, digestive passage rate, maximum daily foraging time, and metabolic requirements for protein and energy.

All of these parameters can be scaled in relation to body mass. For example, linear dimensions such as foraging path breadth are scaled according to the cube root of body mass, gut volume is scaled as a direct proportion of body mass, whereas resting metabolic requirements vary in relation to the three-quarters power of body mass. However, the relation between ingestion rate and body mass is controlled not only by mouth dimensions, but also by features of plant structure restricting bite size (for example, thorns, leaf size—see Cooper and Owen-Smith, 1986). Furthermore, as bite size increases relatively more stem is ingested per bite, if bite size exceeds leaf size.

Although allometric trends with body size indicate general patterns of variation, particular kinds of species deviate from the overall trend because of specific adaptations. For example, ruminants (or foregut fermenters) differ from nonruminants (or hindgut fermenters) in features of gut morphology. In ruminants, the forestomach is compartmentalized to restrict rates of passage of the digesta from the main fermentation chamber, the rumino-reticulum, until particles have reached a certain degree of comminution (aided by remastication). Thereby ruminants achieve a high efficiency of digestion, although at the cost of a slow rate of passage. Among nonruminants the main sites of fermentation are the cecum and colon, and digestive passage rate is relatively high and little affected by the fiber content of the food. The result is that on high fiber diets nonruminants may digest less efficiently, but nevertheless extract more nutrients per unit time than ruminants of comparable body mass (Bell, 1971; Janis, 1976).

Among ruminants there are further distinctions in gut anatomy between grazers, feeding primarily on graminoids, and browsers, eating mostly the foliage of woody plants and nongraminaceous herbs. Grazing ruminants have a larger rumen capacity relative to body mass, and a higher rumen fill relative to its capacity, than browsing ruminants. For browsers the

absorptive area of the rumen wall is much greater due to denser papillation, and the size of the openings connecting different foregut compartments (particularly the reticulo-omasal ostium) is relatively larger than is the case for grazers (Hofmann, 1973). These differences are related to the fact that the leaves of dicotyledonous plants ferment more rapidly, although achieving a lower ultimate digestibility, than those of grasses (Short *et al.*, 1974; Mertens, 1977). Certain ungulate species eating a mixture of grass and browse are correspondingly intermediate in their digestive anatomy. Hofmann (1973) classified these into the subcategories of intermediate feeders favoring grass and intermediate feeders favoring browse, with supporting distinctions in digestive anatomy.

Bell (1969, documented in Owen-Smith, 1982) showed furthermore that browsing bovids exhibit consistently narrower muzzles in relation to their body mass than do grazers. There is also variability among grazing bovids in relative mouth width. Mouth dimensions influence the bite size and hence rates of food ingestion, and also the mix of plant parts plucked.

In Figure 1 the spectrum of African savanna ungulates is arrayed in terms of three features: 1) grazer-browser category; 2) body mass; 3) relative oral dimensions. Among browsers, clusters of species of similar body mass are apparent at about 15 , 38, and 70 kilograms. Notably the four species with a body mass of about 70 kilograms (nyala, lesser kudu, sitatunga, Grant's gazelle) are almost completely allopatric in their distributions. Other pairs of species of similar body mass occupy discrete habitat types (for example, bushbuck and gerenuk, klipspringer as opposed to grey duiker or steenbok). Browsers larger than 70 kilograms show a distinct spacing in body size. Intriguingly, the mean body mass ratio between adjacent species or clusters of species of browsers along the body size axis is 2.1 (range 1.8 to 2.6). This happens to equal the cube of the ratio of 1.3 suggested by Hutchinson (1959) to be the limiting similarity for linear dimensions among coexisting species of similar ecology.

Among grazing ungulates there is no apparent patterning in terms of body size ratios. Whereas the five species with a body mass of about 65 kilograms are allopatric, the eight species falling between 120 and 250 kilograms in body mass overlap to varying degrees in their geographic ranges. Neverthelesss differences in relative oral dimensions are evident among the latter. Four broad-mouthed species exhibit muzzle width indices of 0.76 to 0.85 (wildebeest, oryx, sable, Lichtenstein's hartebeest); two narrow-mouthed species show indices of about 0.58 (roan antelope, waterbuck); and two species are intermediate with indices of about 0.67 (hartebeest and topi, which are also smaller in size than the other six) (Fig. 1). Interestingly, recalling the Hutchinsonian ratio referred to above, the two extremes in relative muzzle dimensions differ by a factor of 1.4. Among the four broad-mouthed species, there are differences in geographic distribution between three in terms of tolerance for conditions of varying aridity. However, the four narrower-mouthed grazers in this size range
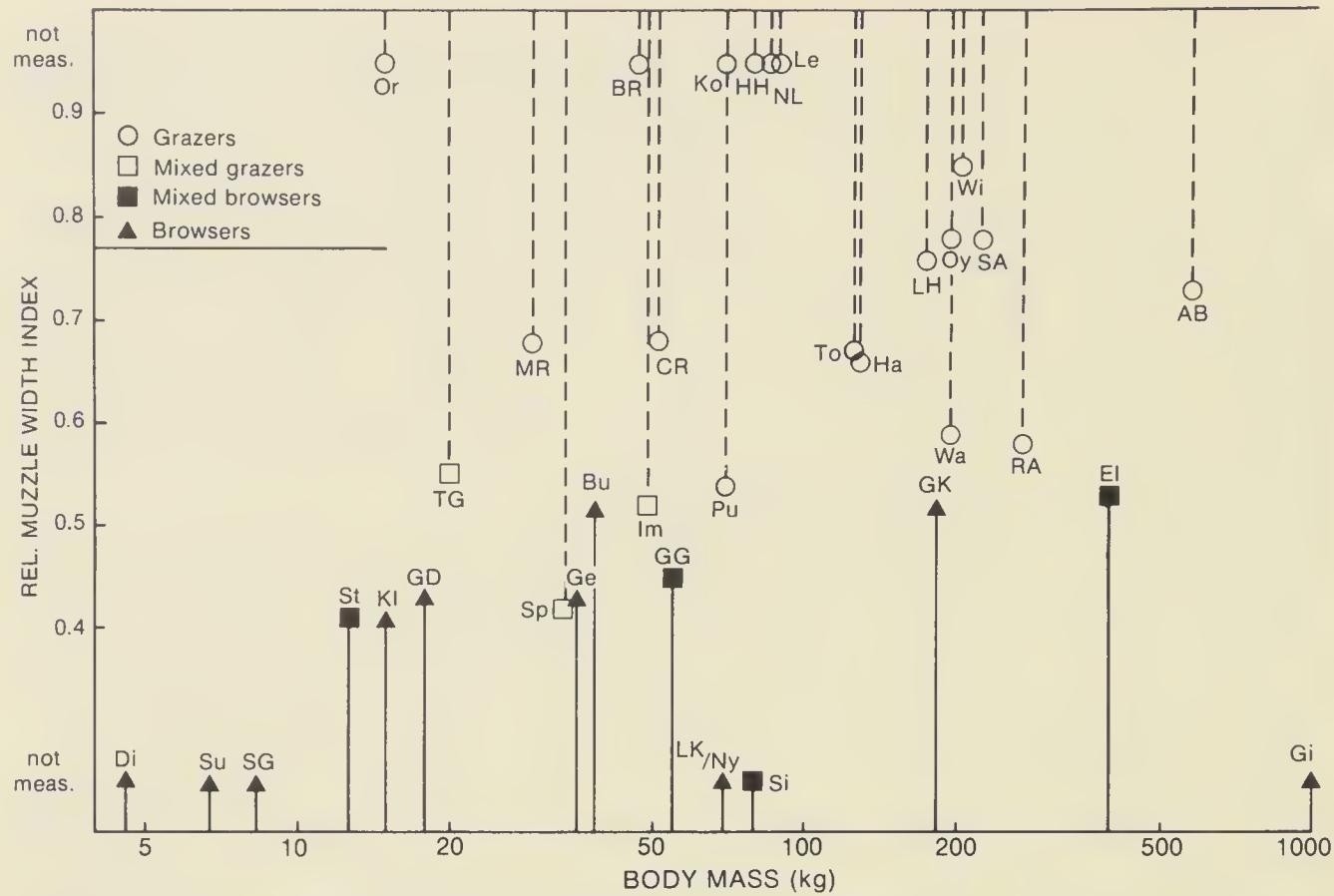
Fig. 1.—The spectrum of African savanna ruminants arrayed in terms of 1) grazer-browser category, 2) body mass, 3) relative oral dimensions. Open circles indicate grazers, open squares mixed feeders favoring grass, solid triangles browsers, and solid squares mixed feeders favoring browse (following Hofmann, 1973). Dashed lines indicate body mass for primarily grazers, solid lines body mass for primarily browsers. Muzzle width index (= ratio between width of incisor row and distance between rear upper molars of mandibles) from Bell (1969) with measurements for additional species supplied by N. Caithness. Key to species labels: AB—African buffalo *Syncerus caffer*; BR—Bohor reedbuck *Redunca redunca*; Bu—bushbuck *Tragelaphus scriptus*; CR—reedbuck *Redunca arundinum*; Di—dikdik *Madoqua kirkii*; El—eland *Taurotragus oryx*; GD—gray duiker *Sylvicapra grimmia*; Ge—gerenuk *Litrocranius walleri*; GG—Grant's gazelle *Gazella granti*; GI—giraffe *Giraffa camelopardalis*; GK—greater kudu *Tragelaphus strepsiceros*; Ha—hartebeest *Alcelaphus buselaphus*; HH—Hunter's hartebeest *Damaliscus hunteri*; Im—impala *Aepyceros melampus*; KI—klipspringer *Oreotragus oreotragus*; Ko—kob *Kobus kob*; Le—lechwe *Kobus leche*; LH—Lichtenstein's hartebeest *Alcelaphus lichtensteini*; LK—lesser kudu *Tragelaphus imberbis*; MR—mountain reedbuck *Redunca fulvorufula*; NL—nile lechwe *Kobus megaceros*; Ny—nyala *Tragelaphus angasi*; Or—oribi *Ourebia ourebi*; Oy—Oryx *Oryx gazella*; Pu—puku *Kobus vardoni*; RA—roan antelope *Hippotragus equinus*; SA—sable antelope *Hippotragus niger*; SG—Sharpe's grysbok *Raphicerus sharpei*; Si—sitatunga *Tragelaphus buxtoni*; Sp—springbok *Antidorcas marsupialis*; St—steenbok *Raphicerus campestris*; Su—suni *Nesotragus moschatus*; TG—Thomson's gazelle *Gazella thomsoni*; To—topi-tsessebe *Damaliscus lunatus*; Wa—waterbuck *Kobus elipsiprimnus*; Wi—wildebeest *Connochaetes taurinus*.

overlap in their geographic ranges and habitat choice, so that niche separation must involve other ecological distinctions.

In order to examine resource partitioning among ungulate species, the original optimal foraging model was modified to take account of the above patterns of variation in functional morphology. Species morphology was characterized in terms of these features: 1) body mass, used as a basis for

scaling body dimensions, movement rates, and bioenergetic requirements; 2) grazer-browser, or ruminant-nonruminant category, determining the relative capacity of the fermentation chamber and the passage rate of material from it; 3) relative oral dimensions, influencing the bite mass obtained and the leaf to stem ratio of the ingested material. If bite size was less than leaf size, only green leaf was ingested. If bite mass exceeded leaf mass, the quality of the ingested material was diluted by the leaf to stem ratio typical of each food type. The order of acceptance of food types (their value ranking) was determined by the mean protein concentration in the ingested material, and thus varied with body size and relative oral dimensions.

Findings from Simulation Modelling

Summarized below are some of the findings from the model that have a bearing on patterns of resource partitioning. Graphical examples of output are presented in Owen-Smith (1985).

1. Larger ungulates achieve their optimal foraging performance including a wider range of food types in their diets than smaller ungulates (Fig. 2). This is due not to bioenergetic relations, as might be suspected, but rather to the relation between food ingestion rate and food digestion rate. In consequence, larger ungulates are dependent upon lower quality, but more abundant, food types not eaten by smaller ungulates. This leads ungulates of different body size to favor different habitat types. For example, a small browser like a bushbuck can occupy a thicket patch where there is a local abundance of nutritious forbs, whereas a large browser like a kudu needs to range more widely through areas where its staple deciduous trees are more abundantly available.

2. A nonruminant attains its optimal foraging performance eating a wider quality range of food types than does a ruminant of similar body mass. This is due to the higher passage rate of indigestible material from the fermentation chamber of the nonruminant compared with an equivalent ruminant. Nonruminants have a lower digestive efficiency, but in compensation can exploit profitably a wider range of habitats. For example, zebras are distributed through a wider range of grassland types than wildebeest, even though the two species commonly overlap in their occurrence (Bell, 1969; personal observations).

3. Differences in oral dimensions lead ungulates of differing body size (or relative mouth width) to favor plant species of differing leaf size or, in the case of grasses, height above ground level. For example, among mixed-feeding ruminants, eland favor broad-leaf savannas or forb-rich grasslands (Hillman, 1979), whereas impala are prevalent in fine-leaved *Acacia* woodlands (Jarman and Sinclair, 1979). Differences in oral dimensions can be overridden, however, by differences in feeding technique. For example, giraffe, with a tongue-stripping method and tolerance of thorns, successfully exploit *Acacia* trees (Pellew, 1984). Among grazers, wildebeest with their broad muzzles favor short-grass grasslands, whereas topi with their

NUTRIENT PROFITABILITY SPECTRUM
LATE DRY SEASON
MAINT. ENERGY RQM ~ 1.6 x BMR
MAINT. PROTEIN RQM ~ 2 x EUN + MFN
MAX. FORAGING TIME = 60% of 24 h. day

| FOOD	F1	F2	F3	F4	W1	W2	W3	W4	G1	G2	G3	G4
PROTEIN %	15	14	13	12	11	10	9	8	7	6	5	4
BIO MASS	0.33	0.5	0.75	1.0	1.5	2.2	3.3	5	7.5	10	15	22
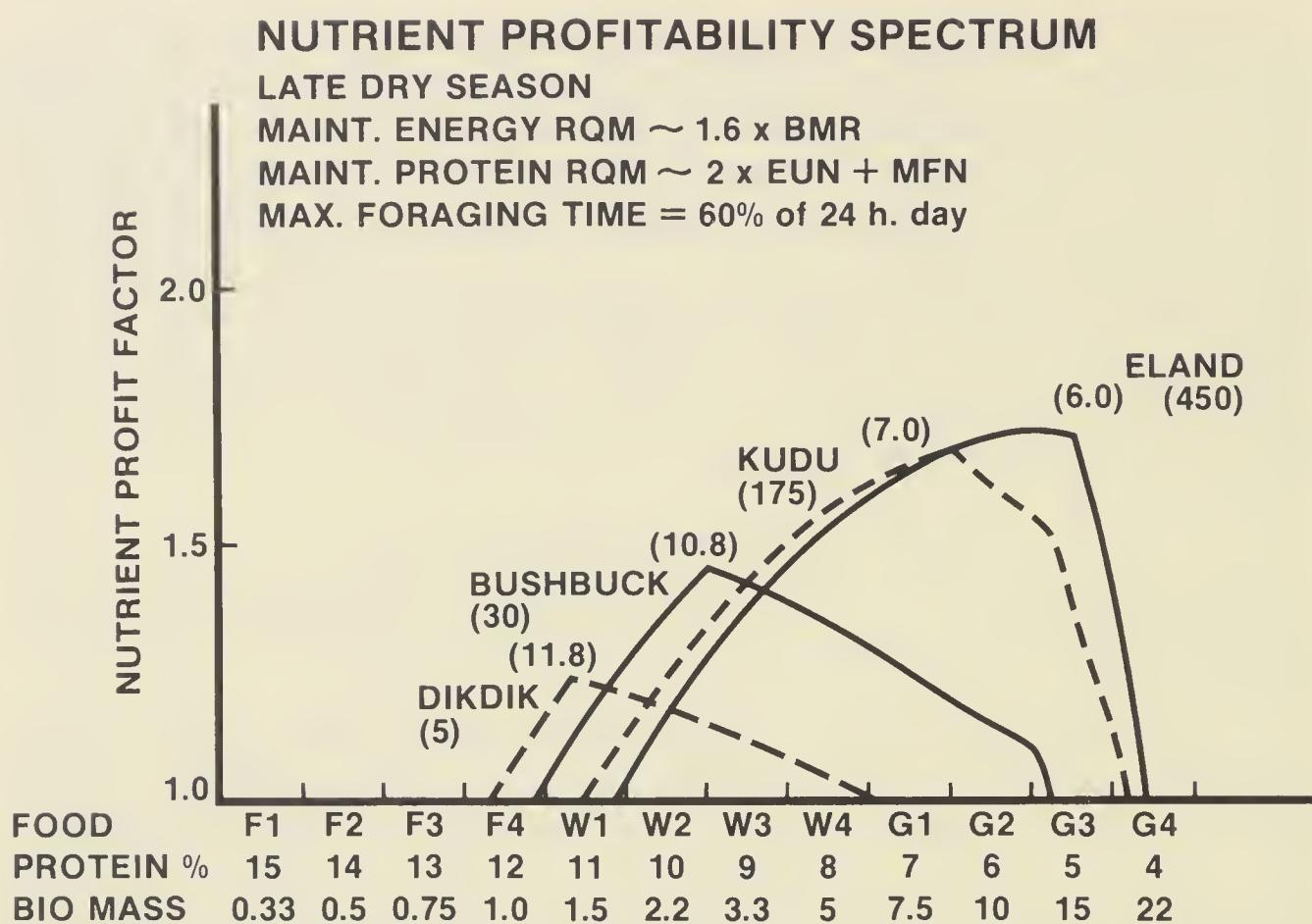
Fig. 2.—Model output showing differences in optimal dietary ranges for four species of browsing ruminant of differing body mass. Lower axis represents 12 food types arranged in order of descending crude protein concentration (expressed as percent of dry mass) and ascending biomass (in grams per square meter); leaf:stem ratio variation not incorporated. Food types designated suggestively as forbs (F), woody plant leaves (W), and grasses (G). Nutrient profit factor is the ratio between rate of nutrient gain and maintenance nutrient requirements. For each species, the ascending portion of the plot is determined by the increase in nutrient ingestion rate as the dietary range is widened to include more food types, whereas the descending portion reflects the decline in rate of digestive processing due to lowered dietary quality. Indicated in brackets for each species are its body mass in kilograms and the mean protein concentration in the optimal diet predicted by the model. BMR = basal metabolic rate, EUN = endogenous urinary nitrogen, MFN = metabolic fecal nitrogen.

narrow muzzles occupy areas of intermediate-height grassland (Bell, 1970; Duncan, 1975). African buffalo, with their larger size and tongue-plucking technique, are dependent upon taller grasslands than are topi (Jarman and Sinclair, 1979).

Consequences for Resource Partitioning

The model demonstrates how morphological differences lead different species of ungulates to achieve optimal foraging performance in different vegetation structures. The differences in foraging profits (nutrient gains weighed against nutrient expenditures) indicated by the model appear small, of the order of a few percentage points; but they are cumulative. A five percent profit margin integrated over the plant growing season amounts to a large surplus to be invested in reproduction; a five percent deficit

integrated over the plant dormancy period could soon drain body reserves to lethal levels. Thus, ungulate species should selectively forage in those habitat types that yield the best foraging returns. A food-rich patch for a small ungulate need not be attractive to a large ungulate, because available food items may be too small in size to be ingested at a sufficient rate by the larger animals. For example, fallen leaf litter from deciduous trees is an important food source for small browsers, from suni to impala, during the dry season, but forms a relatively minor component of the diet of kudus (Owen-Smith and Cooper, 1985).

Spatial variability in vegetation structure may occur on a small enough scale for ungulate species to appear superficially to be occupying the same habitat type. For example, grazing species favor different grass tiller lengths, and thus may feed only a few meters apart in the same broad grassland type (R. H. Emslie, personal communication). Under these conditions the potential for facilitation rather than competition exists, because larger species may modify grass height or tiller length to make it more favorable for smaller species (Vesey-Fitzgerald, 1960; Bell, 1970; McNaughton, 1976).

Potential Circumstances for Competition

Mere overlap in resource use cannot be equated with competition. For a competitive relation to exist, the effects of feeding by one species must be such as to reduce the foraging efficiency of another to the detriment of the population density or recruitment of the latter (MacNally, 1983).

For most ungulates, the abundance of the staple plants providing the bulk of their dietary intake during the wet season is such that depletion is insignificant, at least on a regional scale. These food sources are attenuated in supply mainly by the reduction in soil moisture for plant growth during the dry season. Grass leaves turn dry and brown, with reduced nutrient and elevated fiber concentrations, and the leaves of deciduous woody plants are shed and dispersed.

Ungulate population densities are controlled mostly by the food reserves persisting through the late dry season. Depletion of vegetation components utilized during this period readily may become significant. Jarman (1971) described how ungulate species overlapped extensively in their dietary constituents during the wet season in the Zambezi Valley, but became dependent upon distinct food "refuges" during the early dry season. During the late dry season when food resources were most restricted, food overlap increased. Dietary overlap between kudu and impala kept in the same 200 hectare enclosure in the Nylsvley Nature Reserve in the northern Transvaal declined over the seasonal progression from the early wet season to the late dry season (Fig. 3).

In the late dry season, ungulates commonly turn to vegetation components with nutritional quality or digestibility so low that their quantitative abundance is irrelevant. Examples of such material include standing dry grass for grazers, and the foliage of chemically defended
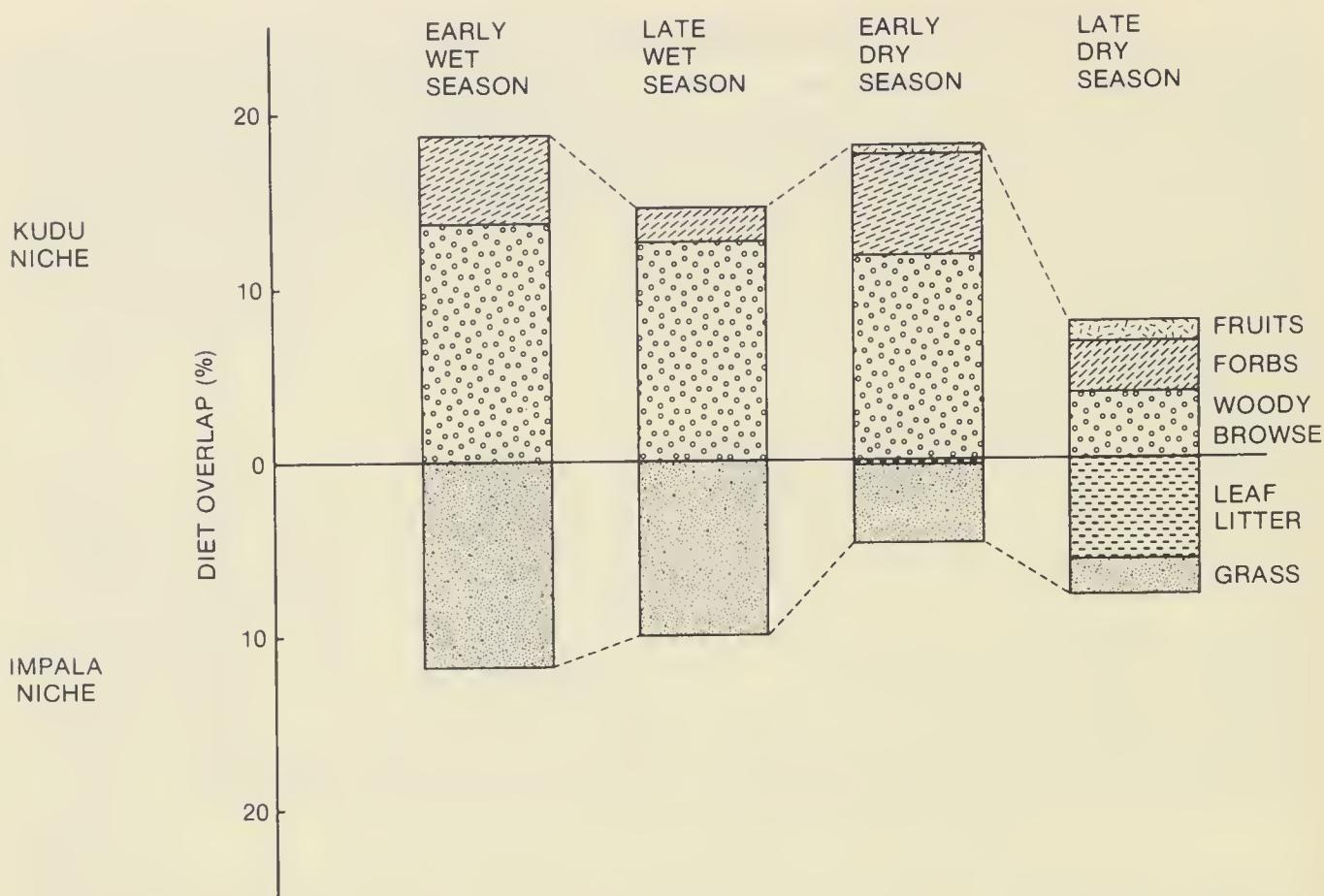
Fig. 3.—Seasonal fluctuations in dietary overlap between kudu and impala in the Nylsvley Nature Reserve in the northern Transvaal, determined from observations on hand-reared animals ranging together in a 210-hectare paddock (N. Owen-Smith and S. M. Cooper, unpublished data). Dietary overlap is calculated as the sum of the proportions of each plant species or form shared in common, after Jarman (1971); that is, if species A forms 25 percent of the diet of kudu and 5 percent of the diet of impala, the proportion shared in common is five percent. The grass category was not subdivided into species. The "impala niche" includes those vegetation components more abundant in the diet of impalas than of kudus, and vice versa for the "kudu niche."

evergreen species for browsers. Inasmuch as these components are hardly depleted, there is little potential for competition. The strategy for many species seems to be to limit the drain on body reserves through the late dry season until the new vegetational growing season is initiated. It is the abundance of the alternative food sources favored during the early dry season that is of critical importance in determining the length of the period over which animals must subsist on submaintenance food resources. For grazers, these include particular zones of grassland retaining green leaves for an extended period into the dry season, for example, drainage sumps or shaded sites. For browsers, they consist of the more palatable species of evergreen trees or shrubs, and dry season fruits such as the pods of certain acacias and other leguminous species. An abundant ungulate species moving into a habitat favored by a rarer species during the early dry season, and consuming such vegetation components, could depress the population level of the latter species.

However, it is not only during the dry season that potential for competition exists. Simulation modelling shows that differences in the

abundance of rare but high quality food types can make a notable difference to herbivore foraging performance during the wet season. Although foraging profits may be well above maintenance levels, differences in resource gains still can influence reproductive success. Owen-Smith (unpublished data) found that calf survival of kudus was directly correlated with the ratio between current seasonal rainfall and mean annual rainfall; and that most calf mortality occurred during the perinatal period before the dry season commenced. What these rare but high quality vegetational components are for kudus remains to be established; potentially they include soft-stemmed creepers, wet season fruits, and nutrient-rich new shoots on staple woody plant species. Any depletion of such food resources by another species could lower calf survival, and hence depress population levels.

The model also demonstrates that, for staple food sources, differences in quality have a much greater effect on foraging efficiency than changes in abundance. Foraging by one ungulate species may improve food quality for another both by removing interfering dry material and stems, and by stimulating regrowth of green leaves (Bell, 1970; McNaughton, 1985). However, grazing or browsing also can have a negative effect on food quality by inducing higher contents of chemical defenses in leaves. These include silica for grasses, and tannins and other digestion-inhibiting compounds in woody plants (McNaughton *et al.*, 1984; Rhoades, 1985).

Feeding interactions may be overridden in importance by predation risks. Rather than avoiding feeding areas occupied by migratory wildebeest in the Serengeti, other ungulate species tend to join the wildebeest concentrations. Advantages probably arise from lowered vulnerability to predators as a consequence of increased group size (Sinclair, 1985).

Conclusions

Ungulate species that are sympatric in their geographic distributions usually differ in phenotypic attributes influencing their foraging efficiency from different vegetation components. This leads these species to favor different habitat types for foraging. Where varying grassland structures are arranged in a tight mosaic, several ungulate species may forage side by side although selecting distinct habitat patches for feeding. Feeding by one species may modify grassland structure such as to make it more suitable for another species, leading to a time sequence in utilization of particular habitat patches or zones.

Ungulates commonly overlap in their dependence on the same plant species as staple food sources during the wet season. Competitive effects do not result unless significant food depletion occurs. Interspecific competition is most likely to occur where ungulate species overlap in their use of 1) uncommon plant forms or parts that offer a high quality supplement to the diet during the wet season, especially over the perinatal period and 2) plant species or parts, or habitat zones, of restricted availability that are sought

out during the early part of the dry season. However, ungulate species seem to be most distinctive in their patterns of habitat or dietary choice at such times of the year.

Direct competition through food depletion seems of relatively minor significance in structuring ungulate communities in African savannas. Other ecological interactions seem of far greater importance. These include facilitatory effects on vegetation structure or quality, induction of plant defenses, and mutual security from predation.

ACKNOWLEDGMENTS

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STRUCTURE OF BAT GUILDS IN MANGROVES: ENVIRONMENTAL DISTURBANCES AND DETERMINISM

N. L. McKenzie and A. N. Start

Abstract.—We examined the species structure of assemblages of obligate insectivorous bats that forage in stands of mangrove. The potential foraging niche of each bat species was represented in terms of its flight morphology, and its realized foraging niche estimated from field observations of foraging microhabitats. Differences in flight morphologies of species could be related to their foraging microhabitats in the mangal.

Compared with random subsets drawn from the pool of potential colonizers, the bat assemblages observed in relatively stable mangrove stands had a deterministic structure; a single axis related to locomotor morphology accounted for the separation of all guild members. In contrast, bat assemblages in mangrove stands that are more subject to environmental disturbances had a less deterministic structure.

Environmental disturbance is thought to modify the importance of biotic interactions, such as competition and predation, in structuring communities (Sale, 1977; Wiens, 1977; Grossman, *et al.*, 1982; Ross *et al.*, 1985).

This study concerns assemblages of obligate insectivorous bats that forage in the stands of mangrove found along the tropical coastline of Western Australia. An earlier paper confirmed the deterministic nature of the species structure of the bat assemblages from relatively stable stands in the Kimberley region (McKenzie and Rolfe, 1986). This paper focuses on the adjacent Pilbara district, where mangrove stands have experienced greater disturbance. We examine the hypothesis that bat assemblages in the less stable Pilbara stands have a more stochastic structure than Kimberley assemblages.

Mangrove stands more than four kilometers square in extent are frequent along the tropical coastline of Western Australia. They have clearly definable boundaries because they are forests and have almost no plant species in common with the adjacent grassland and savanna woodland communities. These mangrove stands also show little sign of frequent disturbance; species similarity levels between stands are high (more than 90 percent) and stand architecture is persistent, being controlled by long-lived perennial plants that are not subjected to the frequent bushfires that disturb adjacent terrestrial communities. Because such stands occur in bays and estuaries, they also are sheltered from storm damage. In addition, marine influences maximize predictability (see Sale, 1977) by minimizing year-to-year variation, as well as annual, seasonal, and daily fluctuations in humidity and temperature. For nocturnal species (bats, nocturnal insects, and so forth) these fluctuations are even further reduced.

In contrast to mangrove stands in the Kimberley (tropical mesic), those of the adjacent Pilbara district are subject to greater disturbances.

(1) They occur in a region with an arid climate characterized by much lower and (locally) less reliable annual rainfall.

(2) The mangrove vegetation is poorer in species, lower and less dense, and the stands are smaller in area and generally more linear in shape. Thus, Pilbara mangrove microhabitats are more exposed to climatic variation, and are more perturbed by storms and cyclones. Cyclones in 1982 caused virtual defoliation of the eastern half of the Cape Keraudren stand.

(3) People have disturbed many of the stands in the Pilbara. Areas of the Samson (Cossack) and Sherlock (Balla Balla) stands were cleared for port facilities *ca.* 1900 and have subsequently regenerated. Many people have settled in coastal parts of the Pilbara since 1960, so other areas of the Samson stand have been cleared for roads, town facilities, and the massive port facilities associated with the region's iron ore and salt mining industries. The intertidal evaporation ponds of the latter also have resulted in the destruction of substantial areas of these stands. All stands are now regularly visited by fishermen and sightseers.

The Kimberley bat fauna of Western Australia comprises one predatory species, two fruit-blossom eating species, one nectarivore, and 22 obligate insectivores. The Pilbara bat fauna comprises one predatory species, two fruit-blossom eating species, and 15 obligate insectivores. The pool of bat species available to insectivorous guilds in these regions includes no omnivores, seasonal or otherwise; omnivores were suggested as a source of structural complexity in the Panama bat guilds studied by Humphrey *et al.* (1983).

In terms of the size range (mean adult body weight four to 50 grams) and flight speeds (< 30 kilometers per hour) of the insectivorous bat fauna of the Kimberley, the mangrove stands described above may be considered: 1) nonpatchy, even allowing for the apparent zonation in the vegetation (see Buckley, 1982), and homogeneously diverse (Hutchinson, 1957) in that "the elements of the environmental mosaic (trees, bushes, etc.) are small compared with the mean free paths of the organisms of concern;" 2) sufficiently large in area to support populations of any insectivorous bat species from the available pool of potential colonizers; 3) to have sufficient vertical height to provide a typical array of the flight microhabitats found in terrestrial communities of the Kimberley. Small, damaged, or species-poor stands were avoided during sampling.

Only the largest of the Pilbara stands were sampled for bats. Although these stands were considered to have sufficient area and height to support all potential colonizers, the stands are patchy; they include extensive monocultures (*Avicennia marina*) of low, open-canopied woodland as well as relatively species-rich patches of low closed-forests dominated by *Rhizophora stylosa*.

METHODS

Six Kimberley and three Pilbara mangrove stands were sampled for bats belonging to the insect foraging guild. A location map for the stands

sampled in the Kimberley was presented in McKenzie and Rolfe (1986) although it should be noted that the Mount Connection stand was referred to as "East Cambridge Gulf" in that paper. The Pilbara stands sampled were at 20° 00'S 119° 45'E (Keraudren), 20° 40'S 117° 40'E (Sherlock), and 20° 40'S 117° 10'E (Samson).

The methods of sampling and analysis were detailed in McKenzie and Rolfe (1986). Mist nets and a bat detector with a spotlight and shotgun were used. To ensure that the species recorded as assemblage members were actually foraging, their mouth contents were examined at the time of capture. To ensure that syntopic species were not assigned to different assemblages, species recorded from the same mangrove stand were considered to belong to the same assemblage; only stands that were separated by at least 15 kilometers of nonmangrove habitat were treated as separate stands.

Studies of resource partitioning among small, insectivorous mammal and bird communities usually have found that the primary separation occurs along microhabitat-locomotor morphology dimensions rather than food-feeding morphology dimensions (Hespenheide, 1975; Karr and James, 1975; Meserve, 1981). Therefore, the structure of the bat assemblages was analyzed in the following terms.

Potential foraging niche.—An ecomorphological approximation based upon calculations of the locomotory indices, wing loading, and aspect ratio (Farney and Fleharty, 1969), that characterize the flight capabilities of each species. Calculations were made at the point of minimum wing loading in the wing-beat cycle, a standardization that allowed interspecies comparisons. The flight morphology of each species was represented graphically by plotting wing loading against aspect ratio for a series of adult individuals. To circumscribe each species' cluster of points, extreme points were connected by straight lines.

The flight morphologies of Kimberley and Pilbara populations of one species were found to be different; Pilbara populations of *Chaerephon jobensis* included individuals with relatively high aspect ratios, so specimens from the appropriate population were used to generate the clusters for the analysis. Seven specimens belonging to the Pilbara population of *C. jobensis* were measured.

Species pools of potential colonizers for the mangrove stands in the Southwest Kimberley and the East Kimberley were provided in McKenzie and Rolfe (1986). The Pilbara fauna has three species not found in these Kimberley districts: *Tadarida australis* (Gray, 1839) (17 measured), *Taphozous hilli* (Kitchener, 1980) (eight measured), and *Chalinolobus morio* (Gray, 1841) (five measured). The complete pool of insectivorous bats in the Pilbara comprises 15 species and can be derived from Figure 2.

Realized foraging niche.—Field observations were accumulated on the spatial use of the mangrove stands by each bat species during foraging. Four microhabitats were distinguished, based on differences in the obstruction to
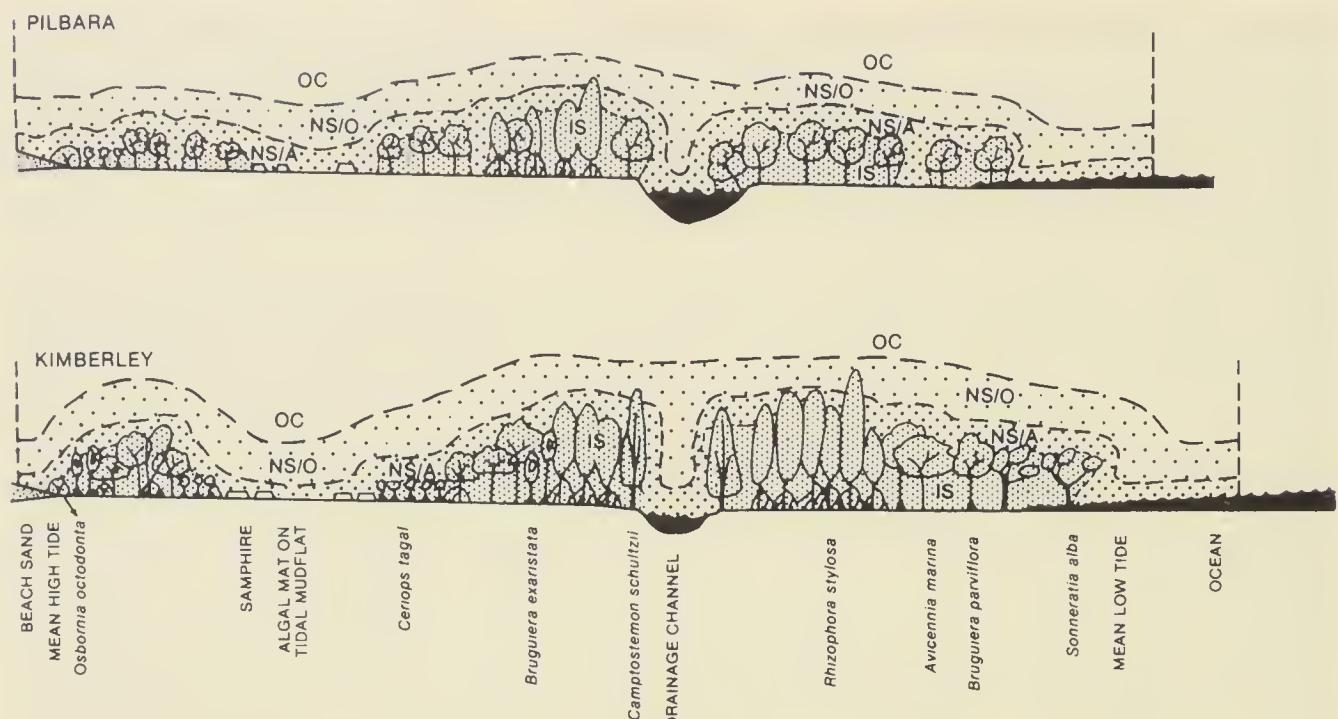
FIG. 1.—Profile of typical mangrove stands showing the foraging microhabitats: OC—unobstructed flight paths well above (> 4m) the general canopy of the vegetation; NS/O—emergent trees require occasional changes in direction, well clear of obstructions when flying through clearings or over adjacent flats; NS/A—within two meters of tree canopies, the sides of the stand, mud flats or water surfaces; IS—between trunks, prop roots, branches, and among foliage.

straight-ahead flight (Fig. 1). Different observations of possibly the same individual were treated as separate observations.

In testing the structures of the observed bat assemblages for stochasm, a criterion was needed to distinguish marginal overlaps in species potential foraging niches from those overlaps likely to produce an ecological effect. Only if the area of a species' flight morphology cluster overlapped that of another by at least five percent was it considered to be significant. The advantages of using overlap, rather than restricting attention only to the mean values of the utilization spectra, are discussed by Sugihara (1986).

RESULTS

The insectivorous bat species recorded in the assemblages are listed in Table 1. That these species actually were foraging in the mangal was checked by an examination of mouth contents as reported in McKenzie and Rolfe (1986). The gut contents of all specimens taken were examined microscopically; although some specimens appeared not to have eaten at the time of capture (mainly specimens captured at dusk), more than 80 percent of specimens, including representatives of all species, had insect material in their stomachs or intestines, or both.

Figures 2 and 3 diagram the array of flight morphologies represented in: 1) the bat fauna of the entire Pilbara district (Fig. 2), and 2) the assemblage of bats in each Pilbara mangrove stand sampled (Fig. 3). In each assemblage, there are two substantial overlaps in flight morphology and, in

TABLE 1.—*Numbers captured in each mangrove stand and recorded* in each foraging microhabitat. Stand abbreviations: Cape Bossut (CB), Broome (Br), Barred Creek (BC), Point Torment (PT), Mount Connection (MC), Wyndham (Wy), Keraudren (Ke), Sherlock (Sh), and Samson (Sa). Usual foraging microhabitats are shown in Fig. 1.*

KIMBERLEY	Stand name code						Foraging microhabitats				
	CB	Br	BC	PT	MC	Wy	OC	NS/O	NS/A	IS	
Taphozous flaviventris (Tf)	3+	D+	4+	7+	2+	1	37	5			OC
Chaerephon jobensis (Cj)	6	5+	6	4+	2	3	36	8			OC
Taphozous georgianus (Tg)				7+	2	4	18	2			
Mormopterus loriae (Ml)	7	4	3	1+			3	19			NS/O
Miniopterus schreibersii (Ms)					3			8	2		
Chalinolobus gouldii (Cg)	1	2		3+		5		10	2	1	
C. nigrogriseus (Cn)			7		1			3			
Nycticeius greyi (Ng)	12	1	3	9+	D+	19		12	24	10	NS/A
Pipistrellus tenuis (Pt)	2	1		10+	9	1		8	24	4	
Nyctophilus arnhemensis (Na)	8	3	7	6	1				7	44	
N. geoffroyi pallescens (Ngp)						1				1	IS
Hipposideros ater (Ha)						2				2	

PILBARA	Ke	Sh	Sa	OC	NS/O	NS/A	IS	
Tadarida australis (Ta)	5+	1+	D+	25				OC
Chaerephon jobensis (Cj)	12+	24	1+	43	3			OC
Taphozous georgianus (Tg)	6+	7	29	33	2			
Mormopterus loriae (Ml)	32+	56	15	9	48	16	6	NS/O
Chalinolobus gouldii (Cg)	1	2	1	1	4			
Nycticeius balstoni caprenus (Nbc)		2				1	1	NS/A
Eptesicus pumulis (Ep)			12			1	7	
Nyctophilus arnhemensis (Na)	11	9	10			6	15	IS
N. geoffroyi pallescens (Ngp)	16	5	12			5	17	

D Species heard using bat detector as well as seen with spotlight but not captured.
+Additional specimens heard with bat detector and seen with spotlight.
*Includes records from preliminary work at other stands.

the Samson and Sherlock stands, a third (marginal) overlap is present. In all Pilbara assemblages, substantial overlap involves the same two pairs of species—*Chaerephon jobensis* overlaps with *Tadarida australis* and *Nyctophilus arnhemensis* with *N. geoffroyi*.

Levels of overlap observed in bat assemblages of Pilbara mangrove stands were not significantly different from those observed in random subsets drawn from the Pilbara fauna (the pool of potential colonizers available to the Pilbara stands—Table 2); the observed assemblage structures may include species that are independently arrayed.

Figure 4 diagrams the array of flight morphologies represented in the assemblage of bats in each Kimberley mangrove stand sampled. The flight morphologies of species belonging to the same assemblage seldom overlap. In the three instances where overlap was detected, its extent was marginal. The array of flight morphologies comprising the combined bat fauna of the Southwest and East Kimberley Biophysical districts is included in McKenzie and Rolfe (1986:fig. 3).
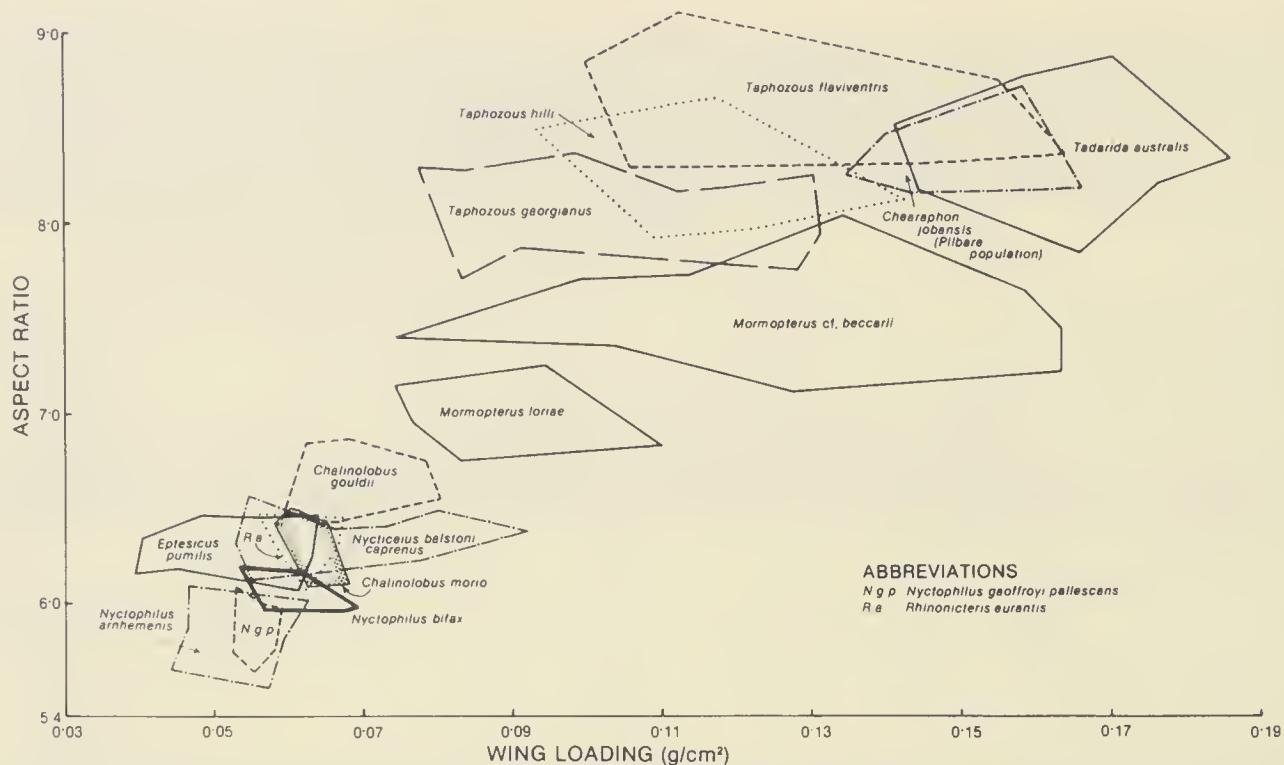
FIG. 2.—Flight morphologies of species comprising the insectivorous bat fauna of the Pilbara; this is the pool of potential colonizers for the mangrove stands sampled in the Pilbara.

When random subsets of equal species richness to the observed assemblages were drawn from the pool of potential colonizers available to each Kimberley stand (see McKenzie and Rolfe, 1986:table 2), significantly higher ($P < 0.05$) levels of overlap were found in all cases (Table 2). It is unlikely that any of six naturally occurring assemblage structures was the result of a stochastic process in which species were independently arrayed.

Table 1 shows how species involved in the assemblages actually partition the foraging space in the stands. It also shows that all the foraging microhabitats distinguished in each Kimberley stand during the field study were occupied by at least one species of bat although, in two of the three Pilbara stands sampled, the NS/A microhabitat was barely exploited. Comparison of the position of each species in Figures 3 and 4 with its foraging microhabitat in the mangal shows the close relationship between flight morphology and foraging microhabitat.

DISCUSSION

Field studies of guilds seldom have provided the clear-cut patterns of resource partitioning predicted from theoretical models; debate on the relative importance of deterministic versus stochastic processes in structuring communities has endured.

For this study we have tried to select a field situation theoretically likely to yield a strongly deterministic guild (Grossman *et al.*, 1982), noting the reservations of Herbold (1984), Rahel *et al.*, (1984), as well as Yant *et al.*, (1984). We selected for study a guild of species with strong connectance that
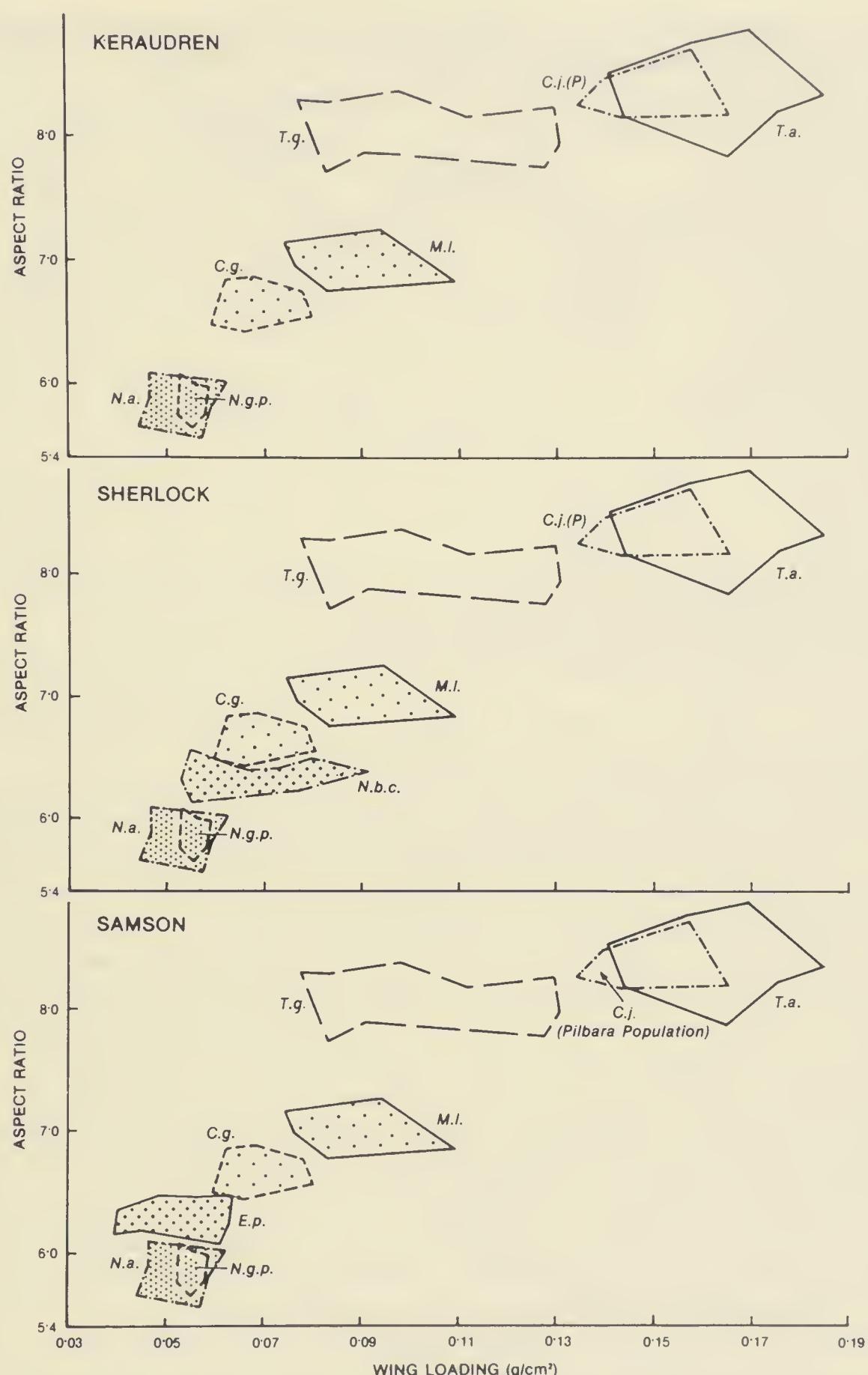
FIG. 3.—Flight morphologies of species comprising the bat assemblages of the Pilbara stands. Species abbreviations are defined in Table 1. Usual foraging microhabitats (see Fig. 1 and Table 1) are indicated by the shading.

TABLE 2.—*Number of interspecies overlaps—observed assemblages compared with random subsets drawn from the pool of potential colonizers available to each stand.*

| Biophysical District | Assemblage | Number of overlaps[1] | |
Mangrove Stand	Species Richness	Observed Assemblage	Random Subsets[2]
Southwest Kimberley			
1. Cape Bossut	7	0*	3.8(1.6)33
2. Broome	7	0*	
3. Barred Creek	6	0*	2.5(1.2)33
4. Point Torment	8	0*	5.1(2.0)33
East Kimberley			
5. Mount Connection	8	0**	4.6(1.6)33
6. Wyndham	8	0**	
Pilbara			
7. Keraudren	7	2[NS]	3.7(1.9)33
8. Sherlock	8	2[NS]	4.8(1.8)33
9. Samson	8	2[NS]	

Significance (confidence intervals about the mean): **$P < 0.01$; *$P < 0.05$; [NS]$P > 0.05$.

[1]Marginal overlaps (of less than 5 percent) are ignored.

[2]Mean (standard deviation) number of random subsets drawn.

forages for insects, a resource likely to be limiting, using flight (a locomotory strategy sensitive to microhabitat differences).

In the Kimberley study areas, the organisms under study are appropriately scaled to the available patches of a stable and easily delimited community that has an architecture that includes a variety of suitable foraging mircohabitats. Though otherwise similar, the Pilbara study areas experience a harsher climate, are patchy, and have been disturbed.

Care was taken to ensure that the species recorded in each assemblage was actually foraging syntopically. Although no formal attempt was made to examine persistence in the species composition of the mangrove bat assemblages through time, the results presented in Table 1 were accumulated over a number of dry season visits to each mangrove stand spanning the years 1977 through 1986. The effect of predation and other interguild interactions on assemblage structure was not known.

Pervasive determinism is apparent from the lack of overlap between species within the Kimberley mangrove bat assemblages. However, at least marginal overlap in resource usage along niche axes characteristically has been found in studies of vertebrate community structure.

The flight morphology cluster for each species probably underestimates the size of both its potential and realized foraging niche: 1) the clusters are only an indirect measure of the food resource the bats actually hunt; 2) a bat does not necessarily have to forage within the efficiency band indicated by flight indices that were calculated at an extreme position in the wing-beat cycle; 3) subadults and visibly pregnant females were not taken into account.
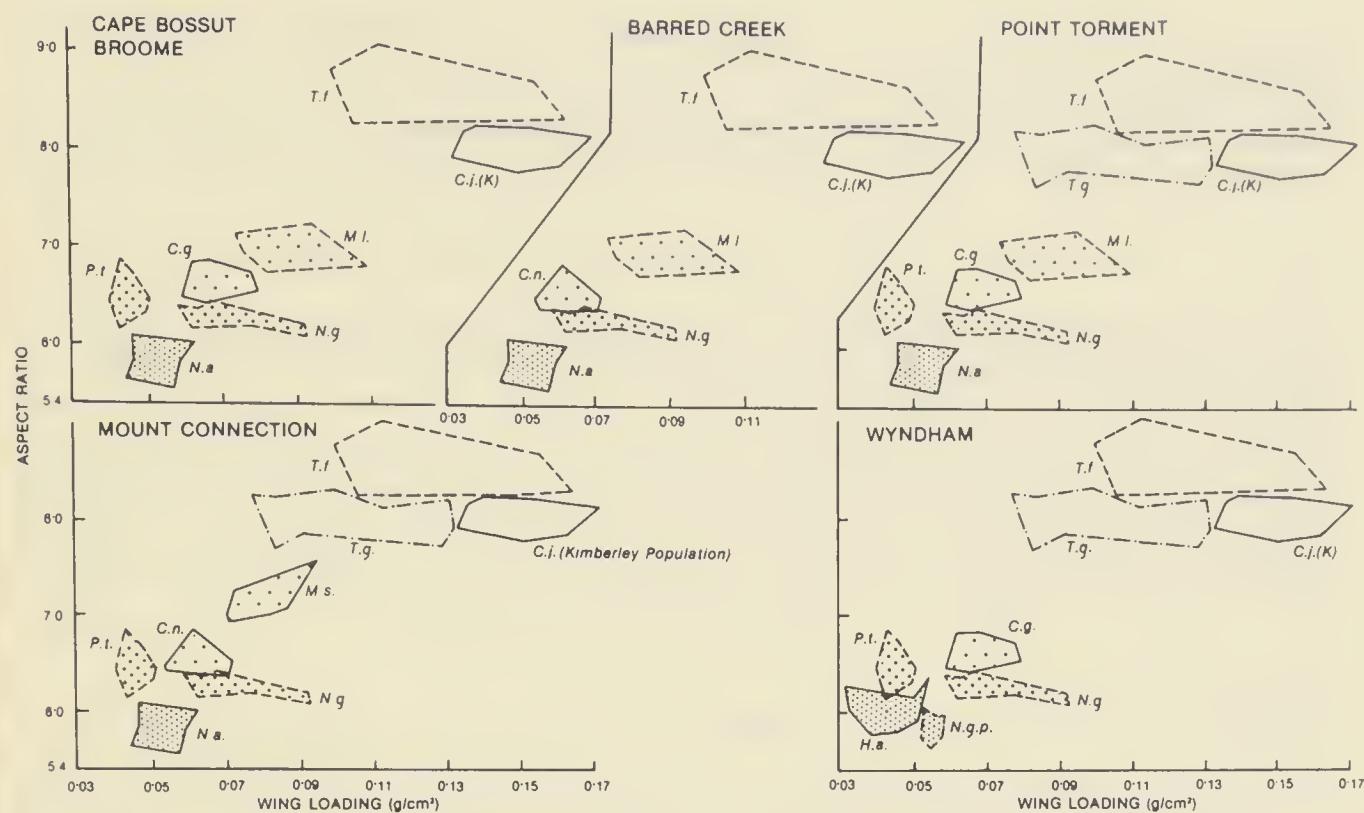
FIG. 4.—Flight morphologies of species comprising the bat assemblages of the Kimberley stands (modified from Mckenzie and Rolfe 1986). The species abbreviations are defined in Table 1. Shading code explained in Figure 1.

Thus, the rather close packing of the bat species in each assemblage (Fig. 4) suggests that "real" foraging niches overlap to some extent. This view is supported by the realized foraging niche data (Table 1—Kimberley).

Differences in the flight morphologies of these obligate insectivore can be related to their foraging microhabitats in the mangal. However, the morphological data suggest that a finer partitioning of foraging zones actually occurs. A single axis related to locomotor morphology accounts for the separation of all guild members.

Table 2 shows that Pilbara assemblages were not distinguishable from stochastic structures. A more sensitive analysis to distinguish true patterns in community organization, from those generated by random processes, would involve measuring the actual extent of interspecies overlaps; Sugihara (1986) has pointed out that the "less sensitive" measures result in a null hypothesis (of randomness) that is difficult to falsify. Furthermore, the overlaps found in the three Pilbara assemblages are so consistent that stochasticity, on its own, does not provide a satisfactory explanation.

The overlapping flight morphologies of *Nyctophilus arnhemensis* and *N. geoffroyi* found in each Pilbara assemblage (Fig. 3) can be explained by the patchiness, peculiar to the Pilbara mangrove stands, which was described earlier. Preliminary field data suggest that *N. arnhemensis* favors closed canopy, species-rich patches in the mangrove stands, whereas *N. geoffroyi* favors the more open patches of monoculture. In this context, it is worth noting that *N. arnhemensis* never has been found away from humid tropical

environments, whereas *N. geoffroyi* also occurs throughout semiarid and desert regions of Australia.

The overlap between *Tadarida australis* and *Chaerephon jobensis* in the Pilbara assemblages (Fig. 3) implies that these species are independently arrayed. The reason may relate to the ephemeral and patchy nature of the over-canopy insects for which these two species forage. The insect resources of the over-canopy microhabitat are even more exposed to the relatively harsh and unpredictable climatic fluctuations of the Pilbara district than are insects in the other microhabitats. If this is the case, over-canopy foragers in the Pilbara need to have a higher cruising speed (a higher aspect ratio for a given wing loading) than their Kimberley counterparts, because successful foraging in the locally unpredictable, less productive, and lower biomass ecosystems demand that they fly much greater distances. The higher aspect ratio noted for Pilbara populations of *Chaerephon jobensis* provides support for this view.

However, it is also worth noting that the presence of these two high-aspect ratio competitors for the over-canopy foraging microhabitat appears to have resulted in the exclusion of *Taphozous flaviventris* from all three Pilbara mangrove stands sampled. Even in the over-canopy microhabitat, some structure remains in the bat assemblages.

Whereas the flight morphologies of mangrove bats in the Pilbara can be related to their foraging microhabitats (compare Fig. 3 and Table 1—Pilbara), the relative rarity of bats specializing in the NS/A foraging microhabitat can be explained by the lower and more open structure of Pilbara mangrove stands compared with those of the Kimberley; the NS/O and NS/A microhabitats are not as different in their degree of obstruction to straight-ahead flight as they are in Kimberley stands. Thus, the proportionally greater usage of NS/A found for Pilbara populations of *Mormopterus loriae* (compare Table 1—Kimberley with 1—Pilbara) is understandable; Kimberley populations of *M. loriae* forage almost exclusively in the NS/O microhabitat. However, it is also worth noting that Matthews and Hill (1980) and others have found that specific habitat use in fish communities is less structured in physically harsh systems than in benign systems.

Studies of the effect of environmental disturbances on the structure of species assemblages are relevant to understanding the importance of biotic interactions such as competition and predation. We have shown the species composition of bat assemblages in a relatively stable, benign environment to be more structured than assemblages in more disturbed versions of the same environment under a harsher climatic regime. This conclusion is consistent with the findings of a number of previous studies involving other sorts of organisms (see Rapport *et al.*, 1985; Ross *et al.*, 1985).

Further observations will need to be sought in suboptimum and damaged Kimberley stands and in Pilbara stands less subject to human interference. Diamond (1983) has discussed the weakness of natural experiments (observations) in identifying causation. Before any causal relationship

between the dynamic or the disturbed nature of the Pilbara community and the presence in assemblages of apparently independently arrayed species can be confirmed, experimental manipulation of the assemblages will be required.

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THE SIGNIFICANCE OF
DISTRIBUTION, ABUNDANCE,
AND DIVERSITY

THE FOURTH DIMENSION IN NORTH AMERICAN TERRESTRIAL MAMMAL COMMUNITIES

S. David Webb

Abstract.—Regularities in the rich record of land mammals from the Cenozoic Era of North America shed light on the structure and dynamics of ancient communities. The secular trend toward less equable climates produced the following succession of predominant biomes: broad-leafed evergreen forest; deciduous woodland savanna; herb and grassland savanna; and finally, during glacial stages, steppe and tundra. Within this major succession, communities are assembled and disassembled in a punctuated manner. Chronofaunal intervals of stable faunal composition and high diversity endure at least 10 million years; they are then terminated by relatively brief intervals of rapid change and lower diversity. Each chronofauna can be compared with roughly replicate communities in similar environments today; for example, the late Miocene savanna fauna of North America bears many structural resemblances to the living fauna of subsaharan Africa. Peaks of land mammal immigration into North America tend to coincide with intervals of low diversity and with the early phases of new chronofaunas. Evolutionary replacements of one higher taxon by another, for example multituberculates by rodents in the Eocene, also coincide with times of rapid turnover and low diversity. The history of land mammal diversity suggests the existence of an equilibrium between new taxa and extinctions. The low diversity intervals, when chronofaunas are interrupted, are the foci for rapid community reorganization.

Scaling problems are often the most difficult to resolve in mammalian community studies. It is not trivial to decide how large an area to sample in a particular habitat or how intensely to sample it. In the Canadian Rockies, for example, the scale may differ from that used in the Mosquitia of Honduras, and it will differ in each according to whether one is looking at sciurids or cervids. In forested settings, the third dimension becomes an important consideration; indeed, in tropical rainforest the canopy may open a whole new world of mammalian diversity.

Even greater questions of perspective arise when one considers communities in the fourth dimension or time perspective. Temporal scaling introduces an additional set of practical and conceptual problems for students of mammalian communities. Lewontin (1969:13) observed that ". . . an exact theory of the evolution of communities of organisms . . . must explain in some sense the present state of the biosphere, but must also contain statements about the past history of living communities and about their future as well." Several recent contributions to community ecology have attempted to exorcise the Ghost of Competition Past, but have not succeeded simply because in a community every organism is partly a product of its evolutionary history. In their studies of living Central American ecosystems, Janzen and Martin (1982) have assigned a crucial role in seed dispersal to the proboscidean genus *Cuvieronius*; since the Pleistocene its apparition has haunted the reproductive success of Ceiba

trees. Evidence from the fourth dimension must be reconciled with that from the other three dimensions, and in the process may shed light on studies of extant communities.

Paleontology offers the most direct approach to sampling communities in the fourth dimension. The fossil record of mammals is remarkably extensive; it comprises more than 4000 extinct genera (and the number is still increasing at a rapid pace). The purpose of this chapter is to review our knowledge of ancient terrestrial mammalian communities in North America and to explore the perspectives that such knowledge may bring to bear on the study of extant communities.

I have selected the fossil mammals of North America because this continent offers the most extensively documented record of faunal history compared to other continents. On the other hand, I strongly suspect that the patterns discussed here would emerge along broadly similar lines from consideration of other reasonably rich continental records of Cenozoic mammalian history. Europe and South America have yielded excellent records of land mammal history. Asia occupies third place and is rapidly advancing. Africa and Austrialia have substantial records of the middle and late Cenozoic, but have as yet produced no early Cenozoic land mammal faunas. As its token Cenozoic land mammal, Antarctica has the new genus *Antarctodolops*. Useful recent reviews of the mammalian faunal record include Savage and Russell (1983) for every continent and Woodburne (1987) for North America.

In the next section, I briefly review the Cenozoic history of North American land mammal faunas. In the last section, I suggest a few of the patterns and perspectives that paleontology offers. First, there was a long-term succession of biomes from broadleafed evergreen forest through deciduous woodland savanna to grassland savanna to predominantly steppe and tundra during glacial stages of the Pleistocene. There were long stable periods of high diversity and limited change; these were punctuated by intervals of rapid change, increased immigration, and fundamental reorganization. The fact that terrestrial mammalian communities have been structured in roughly replicate fashion in different times and places reveals something about the coevolutionary fabric that forms community structure. These patterns are briefly discussed and their relevance to community structure is considered.

Cenozoic History

Cretaceous-Tertiary Transition

The first abundant teeth of Mesozoic mammals were discovered a century ago in anthills in the late Cretaceous Lance Formation of Wyoming. Broadly similar samples also are known from the Scollard Formation of Alberta and the Hell Creek Formation of eastern Montana and adjacent states and provinces. In the last two decades, the latter formation has yielded a distinctive new mammal fauna known as the Bug Creek Fauna, which

Clemens *et al.* (1979:47) described as ". . . incomparably the richest known deposit of Mesozoic mammals of any age, anywhere in the world."

Although the Bug Creek Fauna is also of late Cretaceous age, it has significant resemblances to the subsequent Paleocene faunas not found in the typical Hell Creek Fauna. In both faunas, the three major groups of mammals were Allotheria (multituberculates), Metatheria (marsupials), and Eutheria (placentals). The Lance-Hell Creek Fauna comprises seven genera of multituberculates, four genera of marsupials, four genera of placentals, and one deltatheridian, which may or may not be included with the placentals. In the Bug Creek Fauna, there were additionally two taeniolabidid multituberculates and three placental genera, namely *Procerberus, Protungulatum,* and *Purgatorius.* These mammals evidently were immigrants from Asia, and in the case of the three placental genera, evidently gave rise to many of the important Paleocene orders.

The ecological setting of the Bug Creek Fauna differed from that of the Lance. Estes and Berberian (1970:1), after analyzing the 73 nonmammalian vertebrate genera associated with these faunas, found that whereas the Lance Fauna ". . . was probably deposited within the general environment of a swamp forest with relatively small watercourses, the Bug Creek fauna seems to have been laid down in the relatively deeper waters of major rivers issuing from those lowland swamps." Thus, the additional placentals and multituberculates of the Bug Creek facies probably were associated with better-drained habitats set back from the swamps of the Lance-Hell Creek facies. Van Valen and Sloan (1977) further distinguished these two vertebrate faunas and deposital facies, restoring from the Bug Creek Fauna the "*Protungulatum* Community" and from the Lance-Hell Creek Fauna the "*Triceratops* Community." The former was thought to be associated with a cooler temperature forest that had spread from the north, and eventually displaced the swamp community along with its dinosaurian inhabitants.

Paleocene and early Eocene Forest Fauna

The Paleocene mammal fauna of North America consisted of a richly varied group of arboreal and scansorial species. Nearly all were small to medium-sized. Four orders, Multituberculata, Condylarthra, Insectivora, and Primates, comprised almost the entire fauna of the epoch. They all are carried over from the Cretaceous (see Fig. 1). The rodent-like multituberculates were longer-lived than any other order (late Jurassic to early Oligocene). Jenkins and Krause (1983) have shown in some detail that *Ptilodus* had elaborate arboreal adaptations resembling those of a tree squirrel. After limited diversity in the early Paleocene, the primates soon branched into several successful omnivorous and frugivorous groups. By far the most abundant and diverse order was Condylarthra. The number of their genera doubled every few million years, so that even within the Puercan, there were several dozen genera (Van Valen, 1978). This horizontally defined order consists of several distinct families, including the
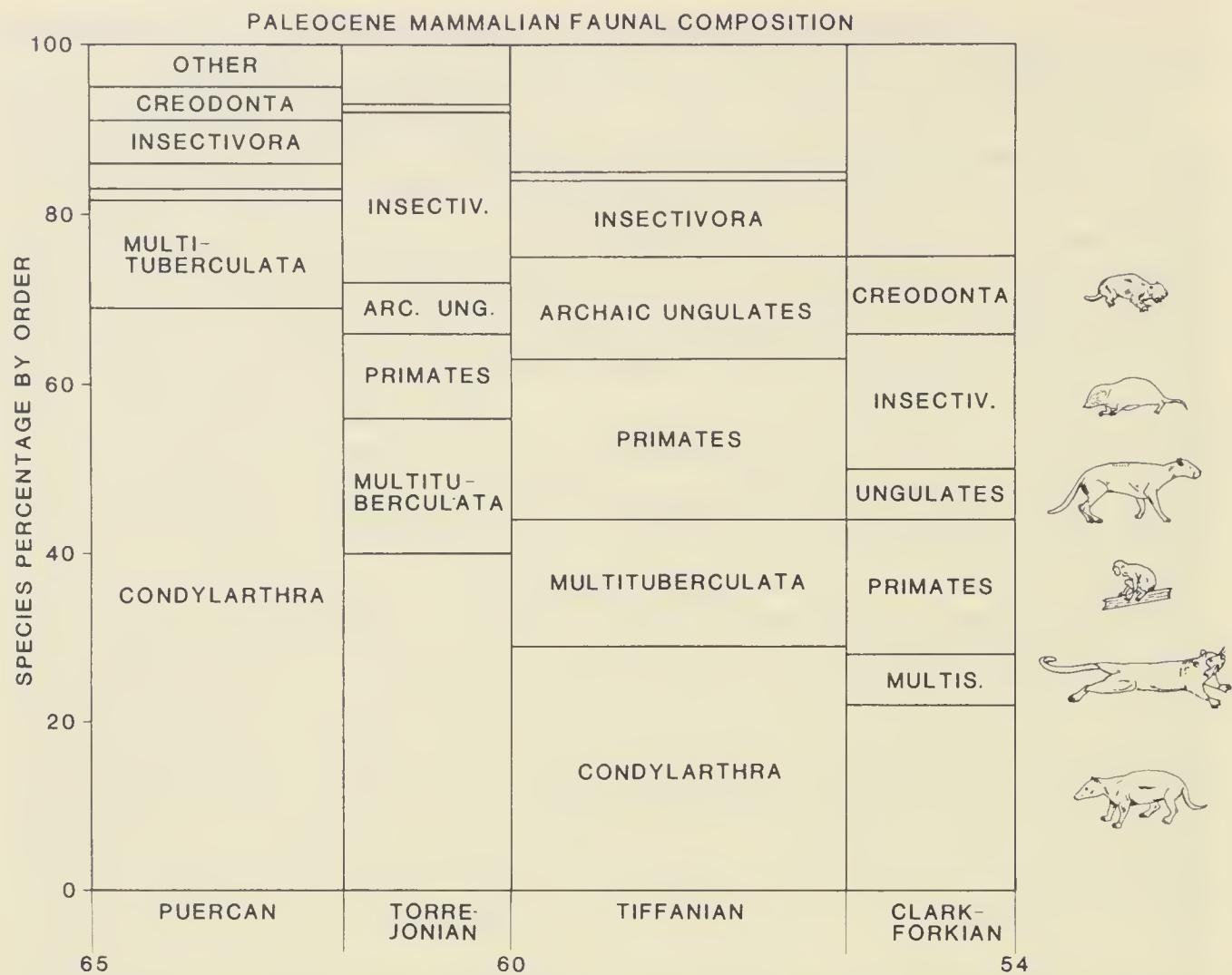
FIG. 1.—Paleocene mammalian species percentages by order. Each land mammal age calculated separately from data in Savage and Russell (1983). Durations in millions of years.

probable ancestors of all subsequent ungulate orders. Most Paleocene condylarths were small and generalized, comparable in several instances to modern hyracoids. Most were evidently arboreal, and their diets ranged from omnivory to herbivory. The Mesonychidae, now often placed in their own order, Acreodi, were carnivorous. Another truly carnivorous order of archaic mammals, the Creodonta, appeared in the mid-Paleocene. The only large herbivores of the Paleocene belonged to the three relatively rare orders, Taeniodonta, Pantodonta, and Dinocerata; each appeared in North America during the middle and late Paleocene. The pantodonts were partly amphibious molluscivores; the other two orders consisted of browsing herbivores; all three orders probably inhabited open woodland.

Productive Paleocene sites span the North American Cordillera from the Paskapoo Formation in Alberta to the Blacks Peaks Formation in Texas. In view of the relatively low topographic relief, extensive marine seaways, and broadly equable climatic zonation then prevailing, these fossil sites may be taken as reasonably representative of the whole continent. The predominant settings were evidently cypress swamps and multistoried subtropical forests; the mammalian fauna tends to corroborate this picture. For a few million years in the late Paleocene (specifically the Tiffanian), the climate cooled as

evidenced by an increasing percentage of deciduous trees and a decrease in floral diversity in the Bighorn Basin. Likewise Rose (1981:386) found in Tiffanian mammal faunas of the Bighorn Basin "dramatically lower species richness and evenness." Similar results extended into the Clarkforkian (earliest Eocene) but by the Wasatchian (early Eocene) the mammalian ". . . assemblages are slightly richer in species and much higher in species evenness, signaling a return to high diversity."

In the Eocene, which Kurtén (1971:81-82) termed the Epoch of Consolidation, he observed: "The mammals had definitely emerged as the dominant group of land animals and were now crowning their victory by conquests of the air (bats) and seas (whales, seacows)." New families continued to appear almost as rapidly as they had in the Paleocene. Several modern orders made their appearance in the early Eocene, most importantly Rodentia, Perissodactyla, and Artiodactyla (see Fig. 2).

In the early Eocene, North America continued to support lush, well-watered, subtropical woodlands. The mammalian fauna was dominated by arboreal rodents and primates, whereas the new orders of progressive ungulates produced diverse terrestrial browsers. Selected groups of Condylar-thra continued to contribute importantly to the herbivore contingent; for example, the squirrel-sized genus *Hyopsodus* was an extremely common, clawed herbivore. Edentate species reached a maximum in the Eocene, possibly indicating reliance on densely distributed termitaria. Winkler (1983) showed that in the Willwood Formation of the Clarks Fork Basin, Wyoming, small, probably arboreal mammals are far more numerous than surface sampling would detect, although some subsamples represent a coherent assemblage of larger terrestrial herbivores.

The Eocene record of mammals, as in the Paleocene, was most fully developed in the Rocky Mountain region. Corroborative records occur in Texas, Oregon, New Jersey, and most recently within the Arctic Circle on Ellesmere Island (West and Dawson, 1978). This last sample strikingly exemplifies the generally equable climatic circumstances that prevailed during the Eocene; for arboreal prosimian primates abounded, the most common species was an extinct dermopteran related broadly to living flying foxes of the Old World tropics, and these mammals were found with warm-adapted groups of Reptilia, as well as with a subtropical flora. The early Eocene biota of North America shows remarkable continuity with the early Eocene biota of Europe, suggesting the absence of climatic and physical barriers between western Europe and western North America.

Late Eocene-Oligocene Woodland Savanna

The Eocene was the longest epoch of the Tertiary Period, lasting some 20 million years; it is not surprising, therefore, that it encompasses many changes. In the middle Eocene, the first indications of seasonal aridity appeared, and by the late Eocene, there is convincing evidence that woodland savanna had become the predominant biome in North America,
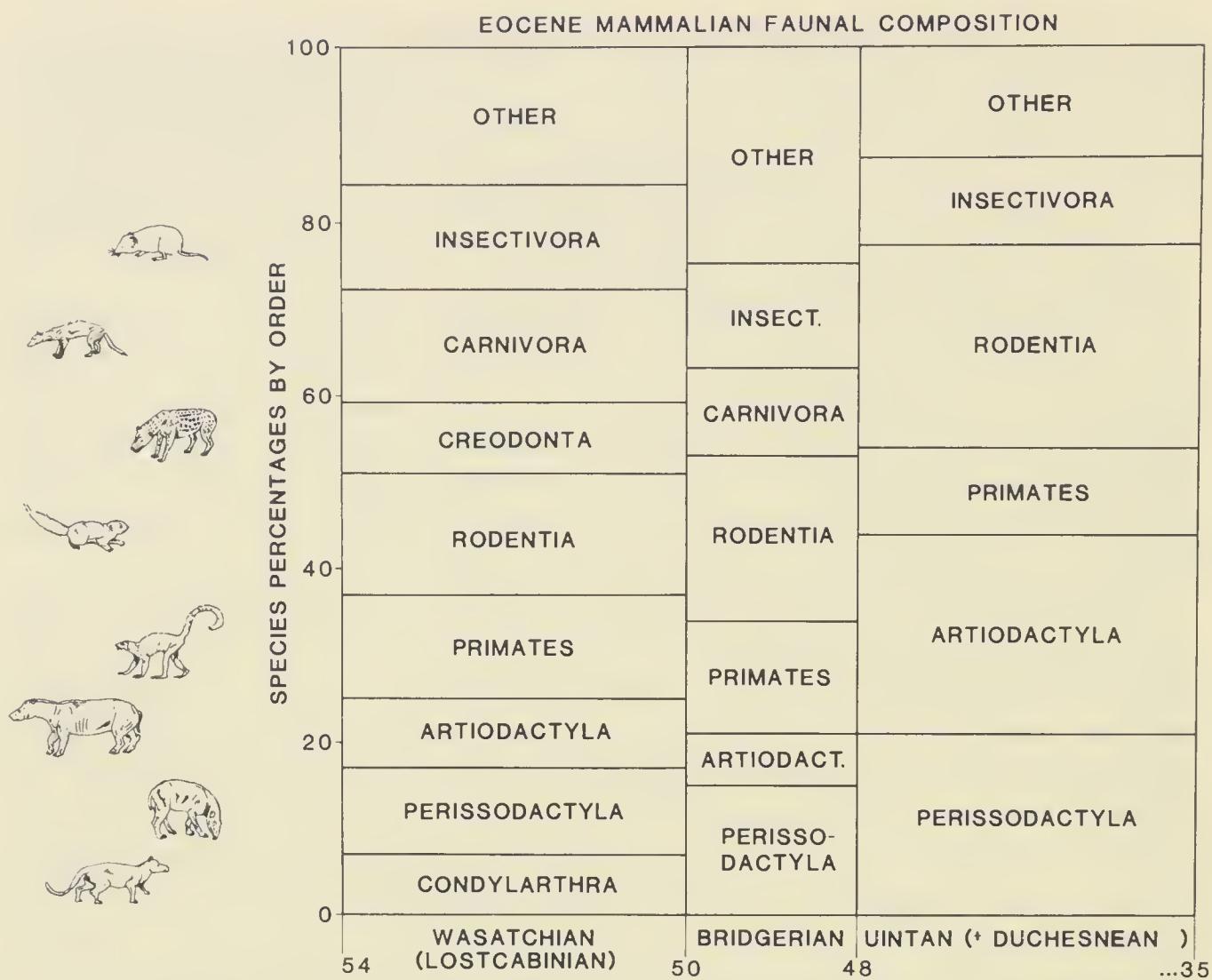
FIG. 2.—Eocene mammalian species percentages by order. Each land mammal age calculated separately from data in Savage and Russell (1983). Durations in millions of years.

displacing the subtropical forests that had prevailed for the first 17 million years of Tertiary history. As the vast Lake Gosiute and other Green River lakes retreated during the middle Eocene, they formed seasonal evaporites and were encroached upon by deeply oxidized redbed deposits. About half of the rich Green River Flora consisted of species with small compound leaves; the families Leguminosae, Sapindaceae, and Anacardiaceae predominated, and the first grass pollen appeared. MacGinite (1969) termed the flora Orizaban-Subtropical by analogy with the seasonally arid woodland savanna now living on the slopes of Mt. Orizaba near the Tropic of Cancer in México.

By the late Eocene, the mammalian fauna reflected still further trends toward seasonal aridity and scrubby habitats. The same three orders that appeared in the early Eocene now played a leading role in producing new families of precocious savanna-adapted herbivores. New rodents included eomyids and zapodids with five-crested lophodont dentitions. The diversity of large herbivores increased markedly: new groups of perissodactyls included helaletid tapiroids, amynodont rhinocerotids, and chalicotheriids; to the bunodont artiodactyls were added piglike entelodonts, and for the

first time a great diversity of selenodont artiodactyl families including camelids, hypertragulids, leptomerycids, and oreodonts. As Cifelli (1981) showed, Perissodactyla diversified earlier in the Eocene, whereas Artiodactyla caught up with them and began to surpass them by the late Eocene when the selenodont radiation took place. Another significant member of the North American fauna is *Mytonolagus*, a rabbit (order Lagomorpha) derived from earlier Asiatic stock. Webb and Taylor (1980) showed that leptomerycids can be traced to the earlier Mongolian genus *Archaeomeryx*. Indeed, a majority of late Eocene open-county herbivores can be traced to Asia, and there is a close resemblance in the late Eocene between the North American fauna and that represented by such Mongolian sites as Irdin Manha and Shara Murun.

These faunal changes coincided with increased epeirogenic uplift and vulcanism in western North America. On the Mexican Plateau and in the Great Basin, seasonal aridity fostered the so-called Madro-Tertiary Geoflora, which was to play an increasingly important role in the development of the North America biota. The last 10 million years of the Eocene in North America are poorly represented by fossil samples and yet there was evidently little change during that interval. Savage and Russell (1983:121) comment: "It is indeed mysterious to us why there is so little taxonomic-evolutionary change among land mammals during the 10 Myr here labeled Uintan and Duchesnean, for this was an interval of notable climatic and vegetative change in various provinces of Nearctica. . . ." This weak late Eocene record seems to show that the important changes in the land mammal fauna were deferred until the Oligocene.

In 1909, H. G. Stehlin, the great Swiss mammalian paleontologist, referred to the early Oligocene as the Grande Coupure in the history of the European fauna. Subsequent work shows that this term is broadly applicable on all continents in which the record has been adequately documented. In North America, a major faunal turnover took place, although detailed biostratigraphic and magnetostratigraphic work by Prothero (1985) suggested that it may have been concentrated more in the mid-Oligocene than in the early Oligocene. Among the many archaic groups that then vanished were the Condylarthra, Taeniodonta, Tillodontia, Dinocerata, and the northern Notoungulata. Prosimian primates declined severely, although minor records persist into the earliest Miocene. Even more impressive are the many modern families first recorded in the early Oligocene of North America. Among the Rodentia alone one can include the Heteromyidae, Cricetidae, Geomyidae, Castoridae, Sciuridae, and Cylindrodontidae. Similarly, first American occurrences of large mammals included the families Canidae, Felidae, Mustelidae, Tapiridae, Rhinocerotidae, Anthracotheriidae, and Tayassuidae (see Fig. 3). Altogether about 60 percent of early Oligocene genera were new, and according to Savage and Russell's count (1983:184) "all orders and 50 percent of the families have living representatives."
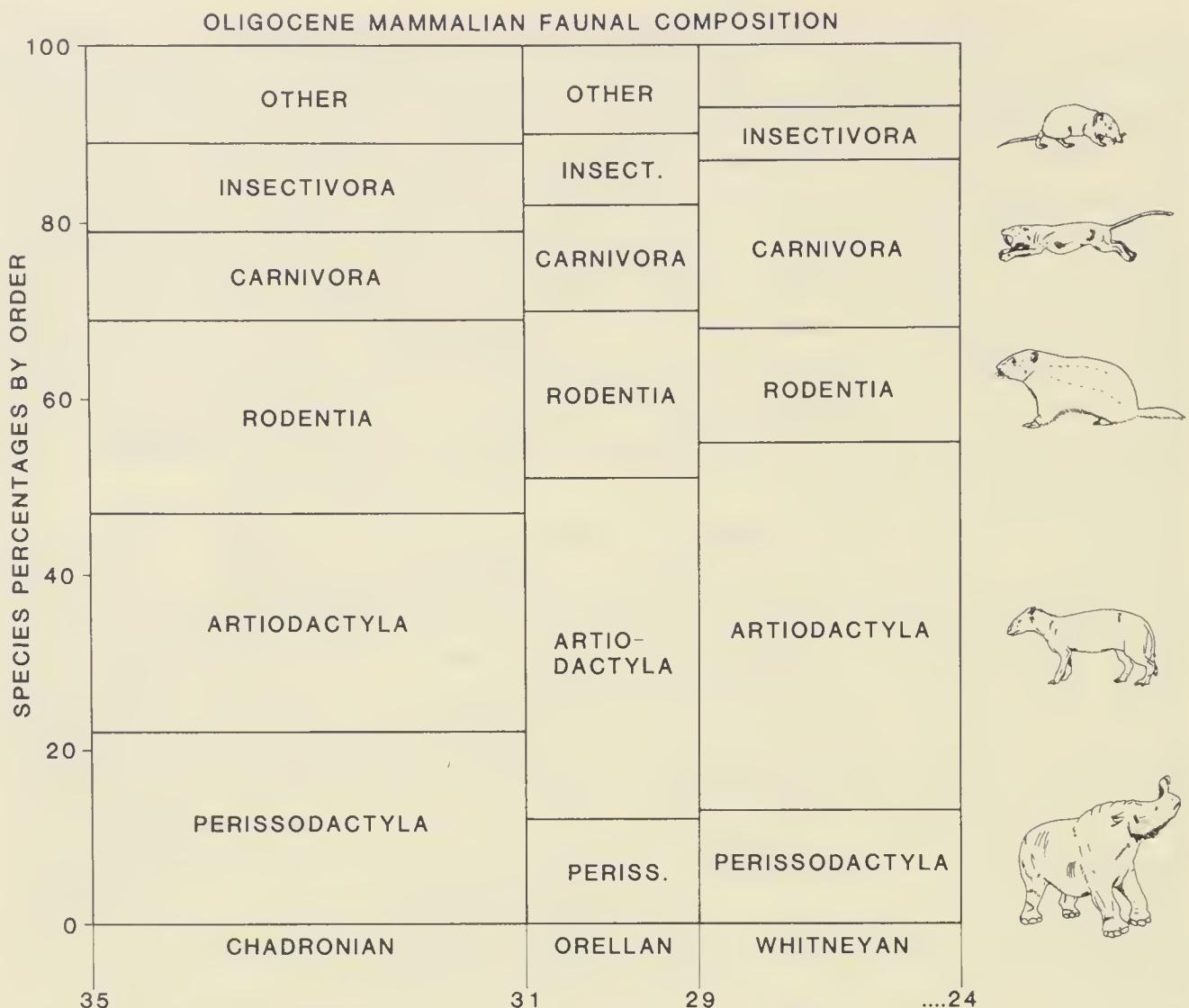
Fig. 3.—Oligocene mammalian species percentages by order. Each land mammal age calculated separately from data in Savage and Russell (1983). Durations in millions of years.

The Oligocene record of the North American mammal fauna is extraordinarily rich. It is particularly well sampled in the Big Badlands of South Dakota and adjacent states and provinces, which together make the world's richest fossil vertebrate terrain. Significant deposits are known also from Southern California, the Big Bend of Texas, and adjacent parts of México. Climatic trends toward cooler mean annual temperature, greater seasonal temperature range, and lower precipitation level, marked especially by more severe arid seasons, continued from the late Eocene into the Oligocene. Hutchison (1982) recognized the effects of such trends, particularly increasing aridity, in the steeply declining diversity curve for aquatic reptiles in the Rocky Mountain region during the Eocene and first half of the Oligocene. Likewise, the percentage of entire-margined leaves in such rich floras as the Florissant in Colorado dropped dramatically, indicating by Wolfe's (1978) formula a drop of some 10 degrees in mean annual temperature. This same interval is recognized as a worldwide time of climatic rigor, when marine biotas were decimated, sea surface temperatures plunged, and eustatic sea levels dropped as much as 200 meters. Thus, the trend toward more open savanna vegetation and more extensive grazing resources extended from the late Eocene into the Oligocene.

By middle Oligocene, a considerable number of families had attained truly hypsodont dentitions (Webb, 1977). Facies analysis of sediments and contained fossils has partly distinguished different terrestrial communities within the White River Group. The open-country community clearly included *Palaeolagus*, a rabbit, and *Leptomeryx, Hypertragulus,* and *Poebrotherium*, all ruminants. The stream-border community included *Protoceras*, a distant relative of camelids, *Elomeryx*, an anthracothere, *Agnotocastor*, a beaver, and *Subhyracodon*, a rhino. Other genera, such as *Mesohippus*, a horse, and *Merycoidodon*, an oreodont, appear to have ranged through both communities. The first clear evidence of fossorial specializations appeared in the insectivores, *Proterix* and *Cryptoryctes*. The abundant samples in the White River Badlands represent probable open-country herd animals such as *Leptomeryx, Merycoidodon,* and *Mesohippus*.

Miocene Grassland Savanna

Beginning about 20 million years ago, another reorganization took place in the major mammal communities of midcontinental North America. This Miocene shift was from woodland savanna to grassland savanna. Undoubtedly, there was a complex mosaic of different local habitats with corridors of gallery forest persisting along fluvial systems. The richest midcontinental Miocene flora is the Kilgore Flora from Nebraska; from it MacGinitie (1962:83) deduced that the plains between streams supported a grassland savanna composed of " . . . small live oaks, pines, blackberry and persimmon, with shrubs of *Mahonia*, currant, hawthorne, sagebrush and relatively abundant species of composites."

The Miocene mammal fauna of North America has been widely sampled, from coast to coast, and from Canada to Central America. More diverse settings are recognized than at any previous time; they include coastal plains and mountains, open savanna and chaparral or desert-border habitats, as well as various aquatic environments from estuaries to marshes. Savage and Russell (1983:300) noted that despite this diversity of local environments "the mammalian fauna of any interval during Miocene time appears to be singularly homogeneous throughout its geographic range."

The most striking feature of the Miocene savanna fauna in North America was its diversity of grazing and browsing herbivores. By the late Miocene, when ungulate diversity reached its peak, there were a dozen genera of horses, including three browsers and nine grazers, and nearly as many camel genera, which also included browsers and grazers. The ancestries of these native ungulates can be traced back into the Eocene, but their Miocene diversification begins in the Hemingfordian. From then until the end of the Clarendonian age, the number of native ungulate genera doubled every three to five million years (see Fig. 4).

A nearly equal contribution to the Miocene herbivore fauna of North America comes from immigrant Asian groups. Early stocks of three ruminant families, Antilocapridae, Dromomerycidae, and Moschidae, as well as the two proboscidean families, Mammutidae and Gomphotheriidae
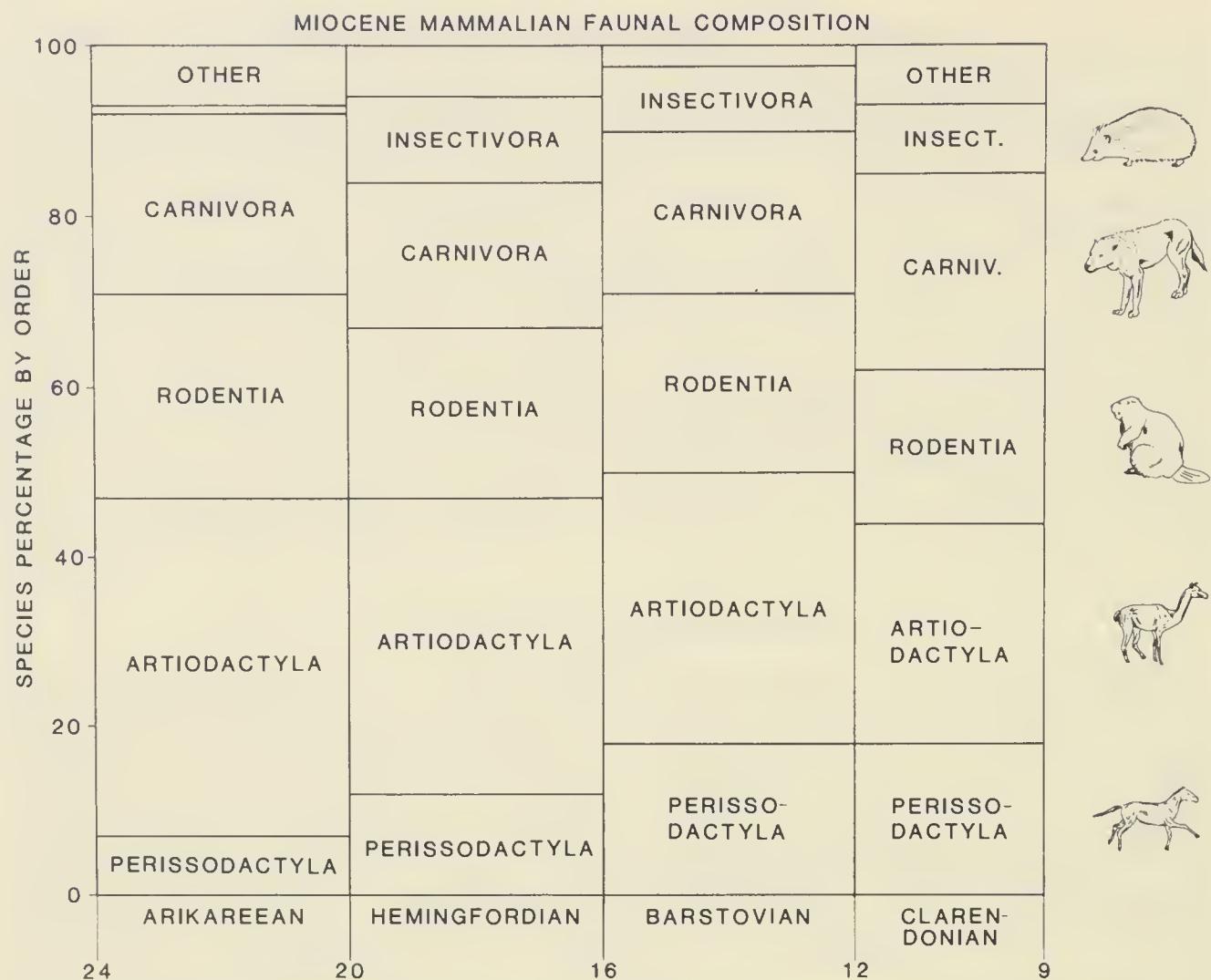
FIG. 4.—Miocene mammalian species percentages by order. Each land mammal age calculated separately from data in Savage and Russell (1983). Durations in millions of years.

burst upon the scene. The rhinocerotid *Brachypotherium* immigrated in the early Miocene, and soon gave rise to the amphibious North America genus *Teleoceras*. A most important immigrant group is the cricetid rodent taxon that gave rise to *Copemys*, and thence to the vast Neogene radiation of New World cricetids, many of which soon spread into South America (Webb, 1984). There also were new beavers, eomyids, and flying squirrels. The most diverse group of immigrants were the carnivores, including felids, ursids, and such genera as *Cynelos*, *Leptarctus*, and *Potamotherium*.

The late Miocene (Clarendonian) of North America records the largest number of fossil mammal genera in any stage (146) and the largest standing crop (80 genera when prorated to the duration of the Clarendonian) known in the fossil mammal record (Savage and Russell, 1983). This high diversity may be attributed to the persistance of an optimum savanna mosaic through an interval of at least 15 million years. The large number of ungulates in the late Miocene invites comparison with the similar ungulate-rich extant fauna of Africa.

Kurtén (1971) termed the Miocene the Epoch of Revolutions and emphasized the worldwide trend toward glacial conditions with their radical fluctuations and generally cooler and drier climates. The now familiar

glacio-eustatic events associated with the Messinian (latest Miocene) stage in Europe, when the Mediterranean dried-up, represented an important phase in such climate deterioration. The sudden decline of the rich savanna ungulate fauna in North America at about the same time suggests that the same cooling and drying trends that produced that savanna fauna, when carried to extremes, led to its demise. Webb (1983) discussed this decline and indicated that coadapted sets of ungulates might be recognized as sets of coextinctions.

Plio-Pleistocene Steppe Fauna

The final step in the secular trend toward deterioration of Cenozoic climates came during the last few million years when glaciers began to form in the northern hemisphere. Midcontinental North America saw the final transition from savanna to steppe as the predominant biome. Deserts were established over a considerable expanse of México and the southwestern United States, while in the north, a unique steppe-tundra biota spread across all of Beringia. During the Pliocene and Pleistocene, provincial differences from one part of the continent to another became far more profound than in any previous epoch. Unlike the Miocene, there were considerable differences between regional faunas. The ratio of allochthonous to autochthonous new taxa vastly increased during successive land mammal ages, beginning with the late Hemphillian and increasing through Blancan, Irvingtonian, and Rancholabrean. Because of the complexity of faunal provinces and the high rate of faunal turnover during the Pliocene and Pleistocene, it is extremely difficult to present a broad view of the land mammal faunas of the last five million years in North America. One of the principal trends was for smaller herbivores to replace larger herbivores, as extinction episodes decimated the latter (see Fig. 5).

PATTERNS IN ANCIENT MAMMAL COMMUNITIES

In this section I discuss some of the patterns that emerge from consideration of the mammalian history previously outlined. It is generally assumed that such broad paleontological patterns reflect large-scale, long-term ecological processes. It may be stated as a corollary of Lewontin's Theorem (see opening comments), that if the underlying principles of community structure may be extended through time as well as space, then the fourth dimension is an effective avenue to understanding that subject.

The Succession of Environments

Throughout this 60 million year history of land mammal faunas, the succession of physical conditions played a governing role. Radiant energy from the sun and the quantity and seasonal distribution of rainfall were surely as important then as they are now. Such physical environmental
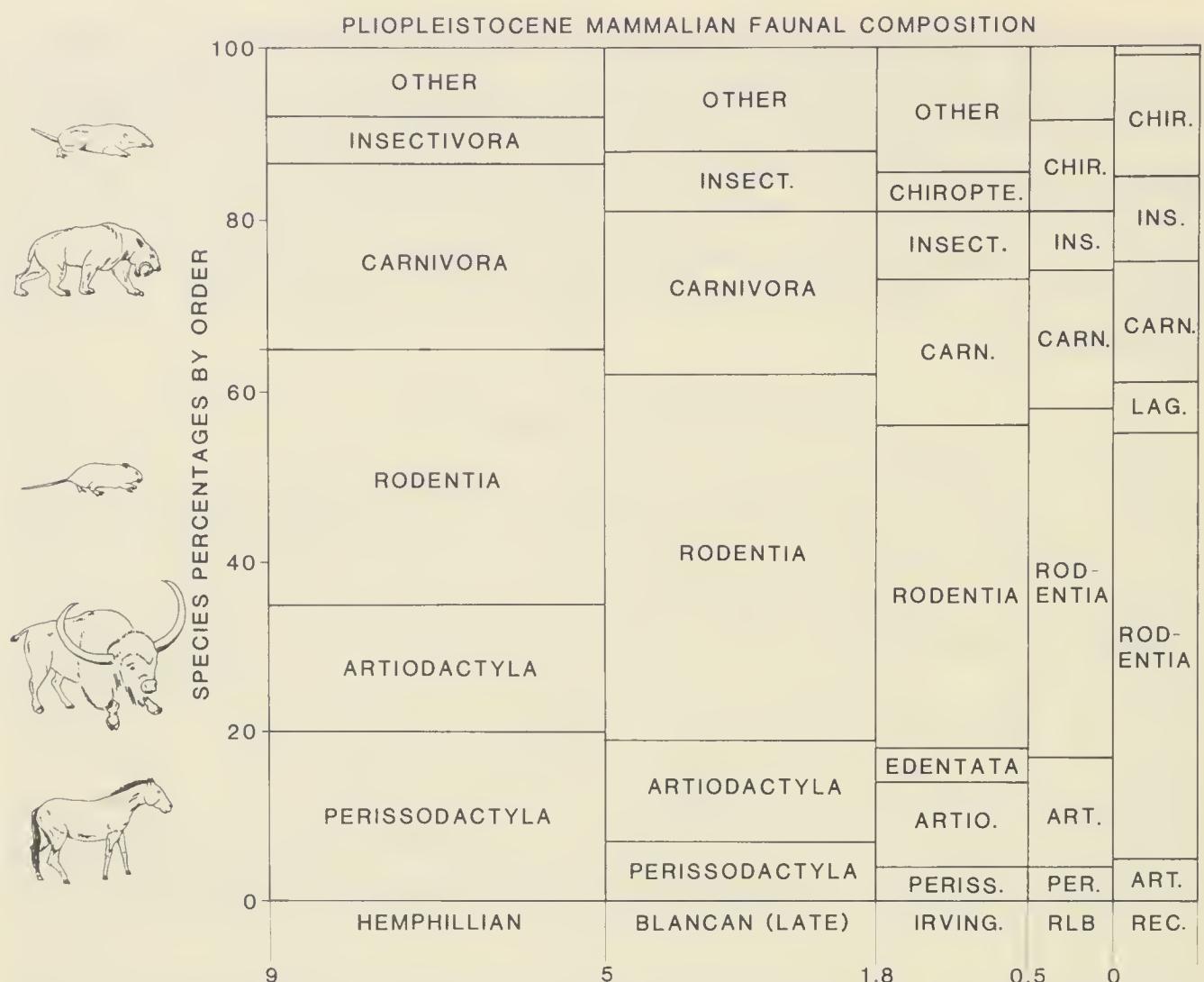
FIG. 5.—Plio-Pleistocene mammalian species percentages by order. Each land mammal age calculated separately from data in Savage and Russell (1983). Durations in millions of years.

factors determined the progression of terrestrial vegetation. The biomes predominating over temperate latitudes in North America progressed from broadleafed evergreen forests, through more deciduous woodland savannas, to grassland savannas, and finally to predominantly steppe and tundra settings during glacial stages of the Pleistocene. The overall trend of environmental change in midcontinental North America moved from more equable to less equable conditions (Axelrod and Bailey, 1969; Wolfe, 1985). Without doubt, this environmental trend had a profound influence, not only on evolutionary trends in most groups of mammals but also on their very survival.

The Pulse of Mammalian Communities

The succession of mammalian assemblages that accumulated in diverse sedimentary basins during the Cenozoic Era represents an immense amount of faunal change. Throughout this history, taxonomic turnover rates were high. If one were hoping to trace living species far back into the past, mammals would be the last group with which to work. Only a few of the modern genera extend beyond the Pleistocene, and most modern families lose their identity in the Miocene or Oligocene (Savage and Russell, 1983).

The contrasting rates of faunal turnover between land mammals and other vertebrates can be illustrated by the rich sample of vertebrate species taken from the Love Bone Bed in the late Miocene of Florida (Webb *et al.* 1981). None of the 41 genera of land mammals is extant and only about half of the families survive on the continent; by contrast 14 of the 17 genera of reptiles are extant and still live in the same area, and 28 of 32 avian genera are still extant, although six no longer live in the same region.

Not only do mammalian faunas turn over rapidly, but their history proceeds in a distinctly uneven cadence. There are long intervals of slow turnover punctuated by brief interludes of major extinction (Fig. 6). The diversity of primary consumer genera remains essentially level for periods spanning two or three sampling intervals (land mammal ages that approach the power of resolution using current biostratigraphic methods). These plateaus are separated by valleys in which diversity drops substantially. These are thought to represent intervals of relatively rapid and severe climatic deterioration (Vrba, 1983; Webb, 1983). The three major points of low diversity occur around 55 million years ago, 30 million years ago, and 10 million years ago, and each coincides with a broad reorganization of the predominant biome. The first decline in diversity coincides with the shift from subtropical forest to woodland savanna in the early Eocene; the second signals the decline of woodland savanna and the opening of more extensive grassland savannas in about mid-Oligocene time; and the last major diversity valley is associated with a shift to cool steppe conditions in the late Miocene.

A remarkable feature of the record of herbivorous mammals in North America is the persistance of recurrent diversity plateaus. These broad patterns are based on accumulated evidence of more than a century of paleontological effort, as summarized by Savage and Russell (1983). It would appear that the number of herbivore genera rose rapidly from the diversity valleys. In the early Eocene, the number rose from about 40 to over 90 in about five million years. But growth in herbivore genera then ceased at about 90 genera. The same apparent growth ceiling at about 90 genera reoccurred in the Miocene, and never again reached that level. Each of these plateaus persisted through two or three census intervals (that is, land mammal ages), and thus is not likely to be an artifact. The implication seems clear that diversity increase is asymptotic, and that the carrying capacity of North American environments limits further diversification of mammals.

There is another more community-oriented way to view this pattern. In certain favorable parts of the fossil record, coherent assemblages of taxa persisted with relatively little change through long sedimentary sequences. Such persistant assemblages have been termed chronofaunas by Olson (1985) and this concept has been widely used by vertebrate paleontologists. The explanation for the chronofauna phenomenon is presumably that an integrated network of organisms persists in a stable environment. In effect is is a well-integrated community with a long fourth dimension.
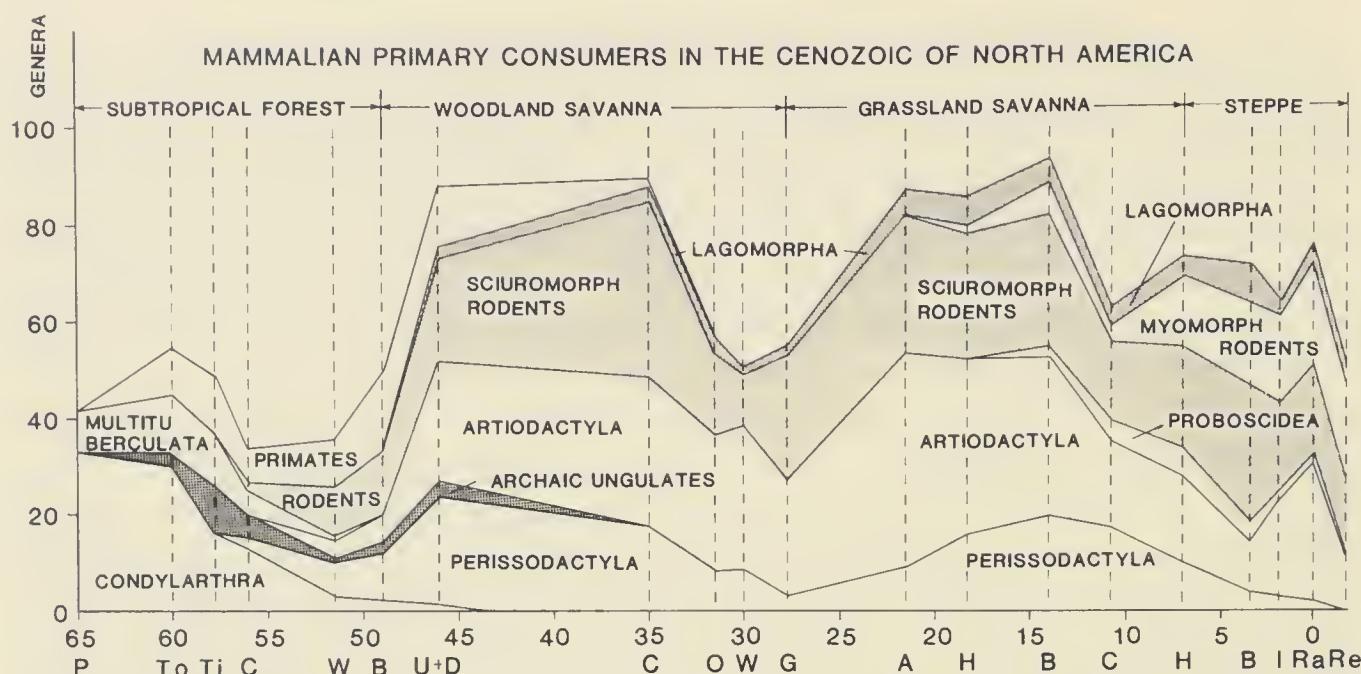
FIG. 6.—Numbers of primary consumer (herbivore) genera in North America during successive Cenozoic land mammal ages (abbreviated P = Puercan, To = Torrejonian, and so on). Mammal ages placed at midpoint of their durations. Data from Savage and Russell (1983).

In the North American record of land mammals, two major chronofaunas have been recognized. These are the Oligocene chronofauna of probable woodland savanna habitats and the Miocene chronofauna of grassland savanna habitats. In fact, these chronofaunas have been subdivided by some into shorter segments, but even in such cases, broader continuity has been acknowledged (Webb, 1977). The important point is that the high plateaus in Figure 6 represent the stable integrated communities during which herbivorous land mammals attained their greatest diversity. The disintegration of these communities coincides with the diversity valleys.

The valleys of lower diversity evidently represent intervals of rapid faunal reorganization. Rates of extinction and origination increase by an order of magnitude or more. Careful study of these intervals may be expected to reveal the disassembly and reassembly rules which define the nature of community structure. The most evident rule is that large herbivores are most vulnerable to extinction. Large carnivores are also among the taxa that are most susceptible to extinction waves, an obvious trophic consequence of decimating large herbivores. Omnivores and small herbivores tend to increase, evidently in response to opportunities made available by extinctions among the larga taxa.

The reassembly rules by which a new community develops are not a mirror image of the disassembly rules. The new herbivores are much smaller at the outset and they undergo rapid diversification within the range of newly available habitats. For example, the principal radiations of herbivores in the Miocene grassland savanna setting were small Antilocapridae and moderate-sized Equidae; both groups rapidly evolved more hypsodont dentitions and tended to add phylogenetic offshoots of larger body size.

Similarly in the most recent (late Pleistocene) episode of disassembly, large herbivores were drastically eliminated, as were large carnivores. The new wave of small herbivores that diversified in adaptations to the new set of environments were the cricetid and microtine rodents (Webb, 1969).

The Timing of Immigration Episodes

When a mammalian species enters a new region, it has potentially disruptive effects on the distribution of resources among pre-existing species in that region. Rabbits in Australia illustrate the manner in which an immigrant species can spread rapidly and brutally affect the rest of the food web. The fossil record can shed light on the long-term frequency of such immigration events and the magnitude of their effects on community structure.

Mammalian paleontologists have known for many years that intercontinental immigrations do not appear uniformly throughout the Cenozoic. Figure 7 summarizes the record of immigrant land mammal genera that evidently reached North America from Eurasia or from South America during the Cenozoic. Four major immigration peaks were separated by intervals of about 20 millions years. The highest immigration rate for land mammal genera in the early Cenozoic occurred during the Tiffanian at the same time that diversity dropped and the fauna underwent major reorganization. The Uintan or late Eocene event was less marked; presumably this reflects the relatively poor stratigraphic record of that and the next mammal age. Had the Uintan age been more completely represented by fossiliferous strata, one may presume that there would have been a more definite peak.

The two immigration peaks of the late Cenozoic fall clearly between chronofaunal diversity peaks (Figs. 6 and 7). The early Miocene valley of low diversity was followed, during the Hemingfordian, by the arrival of a large cohort of immigrant genera from the Old World. As noted above, these included three families of ruminants, two families of proboscideans, the cricetid rodents related to *Copemys*, certain flying squirrels, and numerous carnivores, notably the felids, which had previously vanished from North America. During the next two mammal ages, the Barstovian and Clarendonian, generic diversity reached its acme for the entire Cenozoic while the immigration rate dropped to a low level. Finally, during the Pliocene and Pleistocene, as total diversity slumped, the immigration rate reached its highest levels, as new taxa entered the continent from both Asia and South America.

The record in North America shows a crude but suggestive inverse relationship between numbers of mammalian genera and immigration rates (Figs. 6 and 7). Established chronofaunas of the Oligocene and again of the Miocene evidently resisted major inroads by immigrant taxa. It seems unlikely that physical barriers prevented the possibility of immigrations across the Bering land bridge for such long intervals, and indeed the
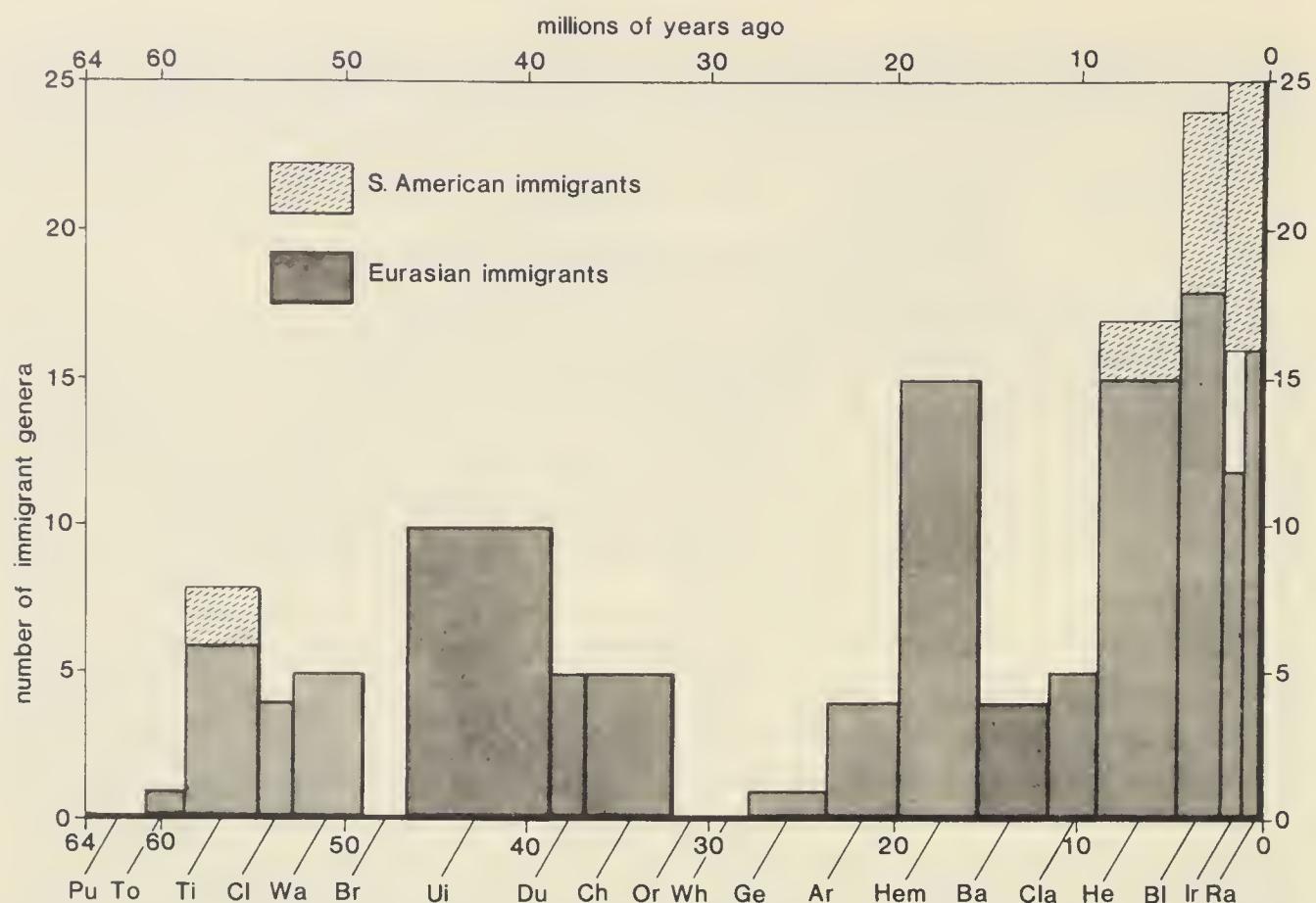
Fig. 7.—Numbers of immigrant genera appearing in North America during successive land mammal ages. Most are from Eurasia, but a few in the Tiffanian and a large number in the last five million years are from South America. Data from Stehli and Webb (1985).

occasional immigrants argue against such complete barriers. It seems more likely that during the Oligocene and Miocene the prevailing resistance to large-scale immigration episodes was an ecological one. In effect, the chronofaunal communities were "full."

The Meaning of Evolutionary Replacements

An important pattern often cited by paleontologists involves the apparent replacement of one higher taxon (family, order, or class) by another. This subject exemplifies the paleontologist's dilemma: patterns in the fossil record are interpreted as evidence of processes, even though the processes themselves cannot be observed directly in organisms and ecosystems long dead. In order to deal with this inherent dilemma, paleontologists have established certain standards of evidence and logic by which purported instances of evolutionary replacements can be judged to be more or less probable.

Replacement phenomena can be divided into two generally distinct categories. One is active displacement of an old group by the radiation of a new group, the other is the opportunistic relay of an old group, after its extinction, by a new group (Simpson, 1964). In practice, to make this distinction between relays and displacements requires detailed evidence. Benton (1983) and Krause (1986) have each explored such problems. The

two minimum requirements for proposing a case of competitive displacement are first, some substantial record of overlapping occurrence of the postulated competing taxa both in time and space; and second, some suggestive body of evidence that the two taxa required the same resources. If these standards are not met, one may suspect the relationship between similar taxa is a relay, a noninteractive replacement in which, as Simpson (1964:160) stated, "new radiation occurs because of prior extinction. . . ."

The best documented instance of displacement among North American land mammals is that of the multituberculates by the rodents during the early Eocene (Van Valen and Sloan, 1966; Krause, 1986). Rodents appeared in the latest Paleocene (Tiffanian) but are known only from one species, *Acritoparamays atavus*, at one site, the Bear Creek Coal Mine in southern Montana. At that time, there were a dozen genera of multituberculates, and the group was diverse and abundant in virtually all sites. The major displacement took place in the Clarkforkian, when both groups consisted of four or five genera, and in the Wasatchian, by which time there were 17 genera of rodents but only three of multituberculates. One multituberculate, genus *Ectypodus*, lasted several more million years, into the Oligocene, when its extinction may have resulted from environmental changes (Ostrander, 1984).

At about the same time, another displacement took place in the ungulates, with the Condylarthra giving way to the Perissodactyla. These two orders maintain between 18 and 24 genera during the Tiffanian and the Chadronian, but the condylarths' proportion declined sharply during the Clarkforkian and Wasatchian (Fig. 6). Cifelli (1981) has shown that the Artiodactyla arose later and, therefore, probably did not compete in any important way with Condylarthra. He has also demonstrated, insofar as possible using patterns of diversity, that the artiodactyls did not displace the perissodactyls, but rather that the two orders diversified independently despite their general ecological similarities.

Another possible replacement pattern in the North American record is the late Miocene decline in ungulate genera, which appears to be complemented by a gain in the number of myomorph rodent genera (see Fig. 6). More detailed analysis (Webb, 1969) shows that this complementary relationship is sustained through a series of finer-scaled declines, and that each decrease in ungulates was followed by an increase in myomorph rodents. Thus, the replacement of ungulates by myomorph rodents probably was a relay, in which a series of extinction episodes affecting large herbivores offered new opportunities to small herbivores.

Each of these suggested replacements of an important group of herbivores by its ecological vicar began during an interval of overall low diversity (Fig. 6). The late Paleocene and early Eocene, and similarly the late Miocene, represented valleys between plateaus of higher diversity. As shown above, new groups were more likely to immigrate during such intervals. Those are the times when some taxa, such as rodents, displaced their ecological vicars,

such as multituberculates, through direct competition, whereas other taxa arrived in time to relay their extinct predecessors, as perissodactyls may have done with respect to condylarths.

The Significance of Replicate Communities

The correspondence of vegetational formations in different parts of the world under similar physical conditions is accepted as commonplace by botanists. In contrast, zoologists generally regard it as more remarkable when avifaunas in widely separated Mediterranean climates or herpetofaunas in the deserts of different continents display some degree of convergent community evolution (Cody, 1975; Pianka, 1975). Convincing examples of structural replication between modern mammalian communities generally are even more difficult to discover. Mares (1976) has compared desert rodent guilds between the Sonoran Desert of North American and the Monte of South America and has demonstrated considerable convergence, although there were fewer fully desert-adapted species in the Monte. In general, mammalogists are far more comfortable discussing convergence of particular mammalian taxa occupying particular adaptive zones, for example "anteaters," than discussing convergences between whole mammalian communities.

Several recent efforts to develop comparisons between land mammal communities feature extinct faunas and operate at the guild level. Van Valkenburg (1988) showed that the Oligocene carnivore guild in North American woodland savanna could be compared closely in species numbers and niche definition with the present east African carnivore guild. The carnivore niches were defined on the basis of three axes—body weight, habitat preference, and diet. Similarly Webb (1983) and Janis (1984) independently compared the ungulate guild of grassland savannas in the Miocene of North America with that living in east Africa.

Although such analyses of replicate mammalian communities are still in their infancy, they promise to shed new light on the nature of land mammal communities and the principles of community structure. Much of the success of this work will depend on further development of paleontological sampling techniques and in particular on the increasing competence of taphonomists to reconstruct paleopopulations (Behrensmeyer and Hill, 1980). Such work is essential if extinct communities are to be compared in meaningful detail with living communities.

The scarcity of "replicates" for mammalian communities makes it all the more desireable to study any available examples, even when they are patently imperfect. I have become progressively more impressed with the magnitude of the structural analogies that can be discerned between successive mammalian chronofaunas of the North American Cenozoic record and various modern mammalian communities. Early Tertiary forest faunas correspond with present forest faunas in the Oriental and the Neotropical realms; comparisons between Oligocene and Miocene savanna faunas of

North America with present savanna faunas in east Africa yield heuristic results; and even the Pleistocene mammal fauna of the Beringian steppe has strong structural resemblances to that surviving in semiarid parts of Africa (Vereschagin and Baryshnikov, 1982).

Punctuated Faunal Equilibria

The existence of mammalian chronofaunas (apparently coadapted sets of taxa that persist for 10 or more million years) demonstrates that certain communities can attain great stability and longevity. On the other hand, the fossil record also documents intervals of reduced diversity when such chronofaunas break up. During such times, as shown above, immigrant taxa more readily establish themselves, new taxa (both allochthons and autochthons) radiate more rapidly than during chronofaunal intervals, and faunal relays take place.

These patterns suggest the possibility that faunal diversity is governed by an equilibrium between extinction and origination rates as suggested by MacArthur and Wilson (1967). In the paleontological corollary of the MacArthur-Wilson Equilibrium Theory, the long chronofaunal intervals represent stable equilibrium points. The low diversity interludes, which are sometimes accompanied by higher turnover rates, represent transitions between stable points. Such interludes are expected in a dynamic equilibrial system.

Several studies of Cenozoic mammal diversity have attributed the patterns observed to a faunal equilibrium (Webb, 1969; Lillegraven, 1972; Gingerich, 1984; and Van Valen, 1985). Mark and Flessa (1977) found more equivocal results among late Cenozoic carnivores, omnivores, small herbivores, and large herbivores of North and South America; however, if their data for large and small herbivores are combined, the results are far more convincingly balanced as noted previously by Simpson (1969) and Webb (1969).

Padian and Clemens (1985) acknowledged correspondence between rates of origination and extinction, but regarded this as purely artifactual. Their position is untenable, however, because sampling errors would not tend to produce apparent equilibria. Indeed, if there were a net loss or a net gain in faunal diversity, it would be reliably reflected in all but the most impoverished faunal samples. Therefore, the prevailing pattern of balance observed by many authors is quite remarkable and can hardly be attributed to chance.

A particularly favorable test of faunal dynamics is provided by the late Cenozoic colonization of South America by North American land mammals. The running mean of land mammal genera in South America was about 45 during the Pliocene, but it increased rapidly during the peak of the faunal interchange in the early Pleistocene until it had nearly doubled in the middle and late Pleistocene. The extinction rate of South American genera trebled at the peak of the interchange and then relaxed somewhat, but still

considerably exceeded the extinction rate for immigrant genera from North America. All of these features are predicted by equilibrium theory, and are difficult to explain otherwise (Webb, 1985; Marshall *et al.*, 1982).

Conclusions

The foregoing discussion of community patterns in the fossil record of North American mammals leads to a general concept of a long-term community cycle. The cycle begins with a diverse chronofauna, evidently representing a complex coadapted network of taxa in a relatively stable ecosystem. The major types of primary and secondary consumers in such chronofaunas bear a strong resemblance to those in similarly structured environments in the world today. Especially striking is the convergence between the Miocene savanna fauna of North America and that living in Africa today (Webb, 1983).

It should be stressed that chronofaunas are not static. Ordinary (horotelic) rates of evolution are maintained. In the Clarendonian Chronofauna, for example, hipparionine horses increased their cheektooth crown heights at rates of about 0.08 darwins when species pairs were sampled at intervals of roughly one million years (MacFadden, 1985). Moreover, intercontinental immigrants establish themselves now and then; the Clarendonian Chrono-fauna, for example, received *Neotragoceras*, the first New World bovid, and *Pliometanastes*, a sloth, heralding the later northward flux of South American taxa. Nevertheless, the chronofaunal intervals last 10 to 20 million years and foster relatively slow evolution and limited immigration compared to the nonchronofaunal intervals.

Stenseth and Maynard Smith (1984:877) proposed that the "choice between the Red Queen and Stationary models will have to depend primarily on paleontological evidence." In effect, the Red Queen hypothesis seems more readily applicable to chronofaunal intervals when coevolution-ary systems are most fully developed. Periodically, however, these chronofaunas crash. The crashes are plausibly attributed to major changes in the physical environments. In North America, the major biome shifted from subtropical forest to woodland savanna to grassland savanna to steppe and steppe-tundra in the course of the Cenozoic. This secular trend toward cooler and more continental (less equable) climates culminated in the ice ages. Each of the major crashes was associated with markedly increased numbers of immigrant taxa, some of which rapidly radiated and displaced older established gorups. These diversity valleys also tended to foster new directions on the part of native groups. For example, the resurgence of perissodactyls following their Oligocene decay results primarily from the exuberant adaptation of the hypsodont Equidae to grassland savanna settings.

The record of North American land mammals provides strong evidence for the operation of a dynamic faunal equilibrium. The plateaus (Fig. 6) clearly deny the hypothesis of continual faunal accumulation. Instead, they

indicate that the number of primary consumers among land mammal genera in North America recurrently reached an asymptote at about 90 genera. The carrying capacity of successive environments evidently imposed definite limits on the number of land mammal taxa that could inhabit the continent. In theory, such faunal equilibria could be sustained by a balance between random immigrations and extinctions, without such biotic interactions as competition and coevolution. In the Cenozoic record from North America, however, the long intervals of high stable diversity (Fig. 6) show a crude inverse relationship with the peak intervals of immigration (Fig. 7) and thus imply highly interactive faunal equilibria.

Acknowledgments

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COMMUNITIES OF GERBILLINE RODENTS IN SAND DUNES OF ISRAEL

Z. Abramsky

ABSTRACT—In the present study, the relative importance of several factors that may determine the geographical and local distribution of a group of gerbilline granivorous desert rodent species in sandy habitats of Israel are reviewed and evaluated. The results indicate that both productivity and area are important factors in determining rodent diversity. However, other factors such as history, geographical barriers, and the structure of the habitat also may be important. Coexistence of the species in any given location is probably possible as a result of habitat selection. Each species seems to specialize on a somewhat different kind of microhabitat. Ongoing competition seems to determine the distribution and abundance of some species. In other species ongoing competition no longer may be detectable.

One of the basic questions in modern ecology is what are the factors that determine the distribution and abundance of animal species. A study of these factors will contribute to our understanding of community structure and organization.

Several factors have been suggested as influencing the distribution and abundance of species. These include interspecific competition (for example, MacArthur, 1972), predation (for example, Paine, 1966; Kotler, 1984), productivity (for example, Brown and Liberman, 1973; Abramsky, 1978; Tilman, 1982; Abramsky and Rosenzweig, 1984), habitat heterogeneity (for example, Rosenzweig, 1981), and physical conditions of the environment (for example, Andrewartha and Birch, 1954; Connell, 1975). The area of the habitat is also an important factor determining the number of co-occuring species (MacArthur and Wilson, 1967) and their abundances (MacArthur *et al.*, 1973).

The relative importance of some of the above factors in determining the geographical and local distribution of a group of gerbilline granivorous desert rodent species that occur in sandy habitats of Israel are reviewed and evaluated in the present study.

STUDY AREA

Sand habitats are found in several locations in Israel (Fig. 1). The sand dunes vary in size, in their degree of isolation, in their origin, and some in the plant community that they support. The dunes occur on a gradient of precipitation ranging from 30 to 650 millimeters (Table 1).

The coastal sand dunes and the dunes of the northwestern Negev are aeolian deposits brought by the Nile, whereas those of the interior Negev are derived from weathering of local sandstone. The dominant plant species are similar on all the coastal dunes and the dunes of the northwestern Negev (*Retama raetam* and *Artemisia monosperma*). In the interior dunes,
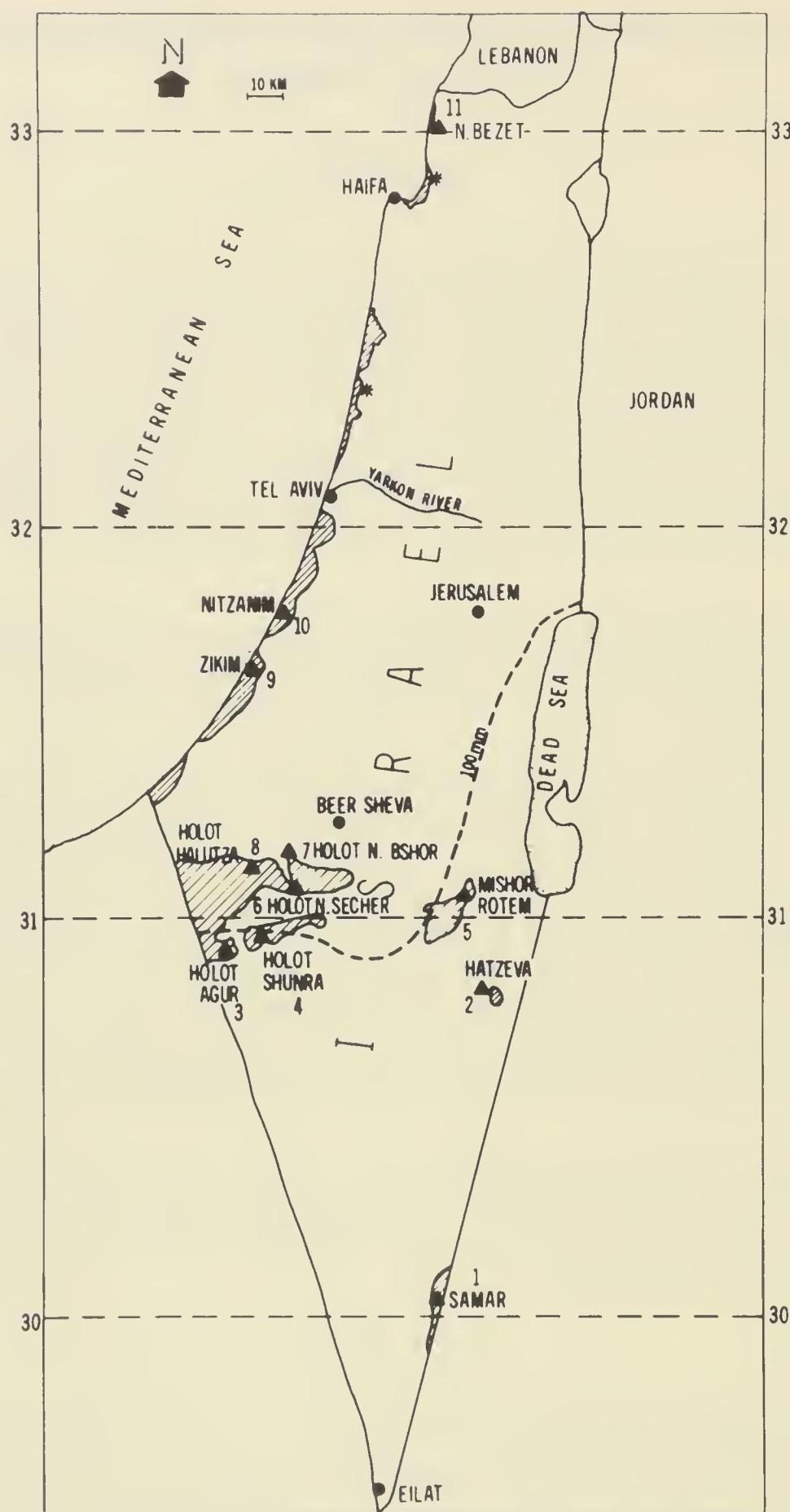
FIG. 1.—Map of Israel. The hatched areas represent sand dune habitats. The numbers represent the study sites.

TABLE 1.—*Mean annual rainfall, annual and perennial cover, number of gerbilline species and their biomass equivalent in each of the studied sites (the numbers in the left column correspond to the study area given in Fig. 1).*

Location	Mean annual rainfall (mm)	Perennial cover (%)	Annual cover (%)	Number of species	Biomass equivalents (kcal/h)
1. Samar	29	6.0	6.2	2	2.8
2. Hatzeva	42	20.7	8.1	2	6.7
3. Holot Agur	71	2.8	10.5	5	8.8
4. H. Shunra	94	10.9	41.8	5	14.1
5. M. Rotem	101	9.9	8.4	4	8.8
6. H. N. Secher	101	9.2	30.3	5	11.1
7. H. N. B'shor	154	9.7	36.6	4	12.2
8. H. Halutza (Gvulot)	168	36.9	25.8	4	11.0
9. Zikim	397	21.6	12.5	2	6.5
10. H. Nitzanim	434	30.8	8.3	2	4.8
* H. Hadera	566	—	—	2	—
* H. Akko	600	—	—	1	—
11. H. N. Bezet	650	—	6.3	1	2.4

different species of plants occur (such as *Haloxylon persicum*). However, despite these differences, the structure of the vegetation on all the dunes is similar in its general appearance and comparison between the rodent communities among the dunes is valid.

Most of the sampled dunes (locations 1 through 10—Fig. 1 and Table 1) were studied for one year between May 1980 and May 1982. Two additional sites were studied between January 1979 and April 1980. These locations are marked by asterisks in Table 1 (after Abramsky and Sellah, 1982). The dune in location 11 was studied by M. Elhad and D. Baharav. The 13 locations cover all the large sand dunes that occur in Israel.

In each of the first 10 locations, four grids, each approximately 1.7 hectares in size, were studied for three consecutive nights during the main four seasons using 160 Sherman traps. In these locations, two grids were selected in sand dunes (unstable sand), whereas the other two were in (stabilized) sand fields. Each grid was as homogeneous as possible. In this way the two pairs of grids were set on the two distinct habitat types of each location. At the locations marked by asterisk (Fig. 1) two grids, each 2160 square meters in size, were sampled on a monthly basis for one year using 80 Sherman traps.

At each grid of the first 10 locations, the following habitat variables were measured: vegetation cover, foliage height density, vegetation height, and the distribution of soil particles. The methods of sampling are reported elsewhere (Abramsky *et al.*, 1985a).

Some 220 Museum Special snap traps were placed in locations 3 and 4 to study the diet of the rodents. Rodents were snap-trapped during winter,

spring, and summer of 1981. For further information regarding the detailed description of the diet analysis see Bar *et al.* (1984).

RESULTS AND DISCUSSION

All eight species of gerbilline rodents that are known to occur in the sandy habitats of Israel (Zahavi and Wahrman, 1957) appeared in the census. Abramsky and Rosenzweig (1984) listed the species captured (and their average mass in grams). These were *Gerbillus pyramidum* (39.9), *G. gerbillus* (21.7), *G. allenbyi* (26.2), *G. nanus* (23.1), *G. henlyi* (9.3), *Meriones crassus* (53.3), *M. tristrami* (78.8) and *M. sacramenti* (116.9). An additional granivorous rodent species, *Jaculus jaculus* (66.0), also was present at all locations south of Tel Aviv but rarely entered our traps. For this reason, this species was excluded from the analysis.

The diet of the common gerbilline species was studied by stomach content analysis (Bar *et al.*, 1984). All the species had a similar diet consisting mostly of seeds and other plant material although the diet changed in different seasons (Table 2). The diet of *M. sacramenti* differed from the diet of the other species in that it contained more greenery.

Once the results of the census of population densities and habitat variables were obtained, a search for possible general patterns of variation in species diversity was initiated. The mechanisms that might produce these patterns also were investigated.

Relationship Between Mean Annual Rainfall and the Diversity and Abundance of Gerbilline Rodents

The number of coexisting rodents species in the sampled locations were highly and significantly correlated with mean annual rainfall (Fig. 2A). The number of gerbilline species rises steeply as a function of rainfall, reaches a peak at relatively poor locations, and then descends at a relatively moderate rate. This pattern follows the prediction of Tilman (1982) for plant species competing on a gradient of limited resources. A humped curve also is obtained in habitats with different levels of disturbance (Grime, 1973). Because the coefficient of variation of rainfall is inversely related to its mean, a gradient of disturbance parallels the rainfall gradient of this study (Abramsky and Rosenzweig, 1984). A similar humped curve also was found when the consuming biomass of the rodents was plotted against mean annual rainfall (Fig. 2B).

Mean annual rainfall is not directly related to the number of gerbilline species and their consuming biomass, but is most likely correlated with seed germination and production of desert annuals on which the rodents feed (Went, 1948, 1955). Annual seed production of each of the sampled locations is impractical to measure directly. However, annual cover, which was sampled in this study, is probably highly correlated with annual seed production. The relationship between annual cover and rainfall is similar to

TABLE 2.—*Percent composition by dry weight of seeds, vegetation, and insects (± S.E.) in the diets of gerbilline rodents. N1 = Number of individuals captured. N2 = Number of stomach contents analyzed. Semicolon = Sample size was not sufficient to meet the determined criterion (details see text).*

Species	N1	N2	Seeds	Greenery	Insects
Gerbillus pyramidum					
Winter	36	35	40.0 ± 6.1	55.0 ± 5.8	4.9 ± 2.1
Spring	83	44	85.3 ± 2.7	8.7 ± 1.7	6.0 ± 1.8
Summer	50	41	59.3 ± 4.8	30.6 ± 4.5	10.0 ± 1.8
Total mean	169	120	63.2 ± 3.1	29.7 ± 2.9	7.1 ± 1.3
Gerbillus allenbyi					
Winter	83	48	11.3 ± 3.4	81.8 ± 3.6	6.9 ± 2.2
Spring	60	38	89.6 ± 1.9	7.4 ± 1.3	2.9 ± 1.5
Summer	75	50	48.7 ± 5.0	39.7 ± 4.9	11.6 ± 2.9
Total mean	218	136	46.3 ± 3.5	45.5 ± 3.4	7.5 ± 1.4
Gerbillus gerbillus					
Winter	10	9	63.3 ± 12.7	35.4 ± 12.7	1.2 ± 0.7
Spring	5	3;	82.1 ± 11.5	1.7 ± 0.5	16.2 ± 12.3
Summer	6	3;	73.5 ± 26.4	21.2 ± 22.0	5.2 ± 5.3
Total/mean	21	15	69.1 ± 9.0	25.6 ± 8.9	5.0 ± 2.7
Meriones sacramenti					
Winter	12	12	1.5 ± 0.5	97.1 ± 1.8	1.4 ± 0.9
Spring	14	14	56.9 ± 1.0	41.5 ± 7.3	1.6 ± 1.2
Summer	19	18	25.5 ± 7.5	69.7 ± 7.9	4.8 ± 4.3
Total/mean	45	44	29.0 ± 5.0	68.2 ± 5.1	2.8 ± 1.8
All species, all seasons	453	315	51.7 ± 1.9	41.7 ± 2.1	6.6 ± .08

that obtained between number of rodent species or their consuming biomass and rainfall (Fig. 2). Although the overall correlation between annual cover and rainfall (Fig. 2C) is not significant ($P = 0.07$), each of the two regression coefficients are ($P < 0.05$). The relationships between both species number and their consuming biomass and percent of annual cover (Fig. 3) suggest that annual cover is limiting only under an extremely low threshold (10 percent). Additional increase in annual cover beyond 10 percent is not followed by an increase in species number or their consuming biomass or both.

The number of rodent species that were captured in the sampled locations is probably constant but their abundances varied between years. Percent annual cover, however, varied considerably from year to year. Annual cover was estimated during two "good" years (in terms of amount of rainfall and its distribution in time). For this reason, the 10 percent threshold value is probably above the mean value of annual cover for these locations and the mean threshold is somewhat lower.

Relationship Between Area and Number of Gerbilline Rodent Species

A close inspection of Figure 1 reveals that the largest sand dune occurs in the northwestern Negev (this dune is also a part of the large sand dunes of
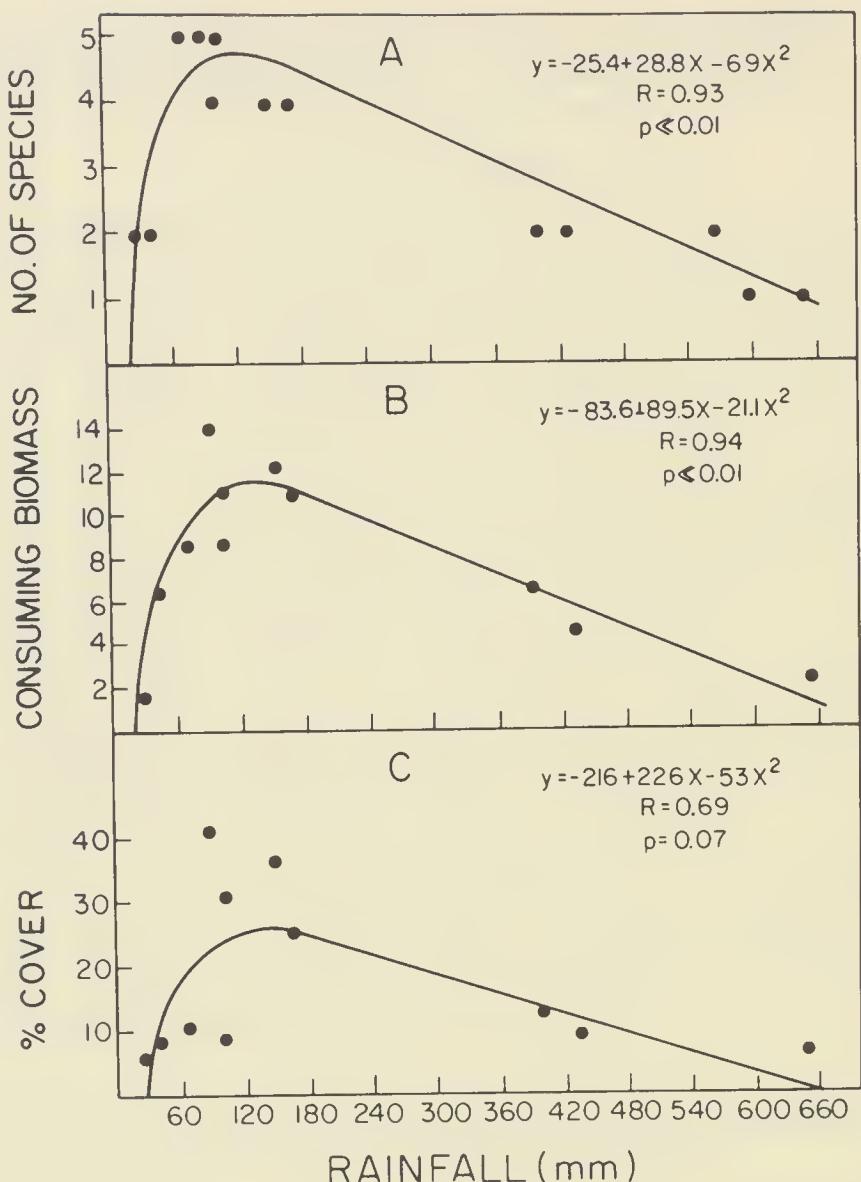
Fig. 2.—The relationship between (A) number of rodent species, (B) consuming biomass, (C) percent annual cover, and mean annual rainfall.

the northern Sinai). In this area, the highest number of coexisting rodent species occurs. The size of the sand dunes decreases gradually toward both southern and northern Israel (Fig. 1). In these latter sand dunes, the number of rodent species decreases as well. Indeed, a significant correlation was found between number of gerbilline species and the area of the sand dune habitats ($S = 1.35A^{0.14}$, $r = 0.78$, $P < 0.05$). This relationship suggests that the number of gerbilline species might be dependent on the size of the sandy area (Abramsky et al., 1985b presented a detailed description of the criteria defining the isolated dunes).

Whereas some of the sand dunes are isolated from the others, they might be depauperate of gerbilline species. Density compensation might be expected (MacArthur et al., 1973) in such cases. However, no significant difference in consuming biomass ($t = 0.19$, $P > 0.50$) was found when mean consuming biomass per species of species in noninsular dunes (locations 3, 4, 6, 7, and 8) was compared to isolated sandy areas (locations 1, 2, 5, 9, 10, and 11). Also, the relationship between area and number of species with $z = 0.14$ indicates a noninsular area effect (MacArthur, 1972). Thus, geographi-
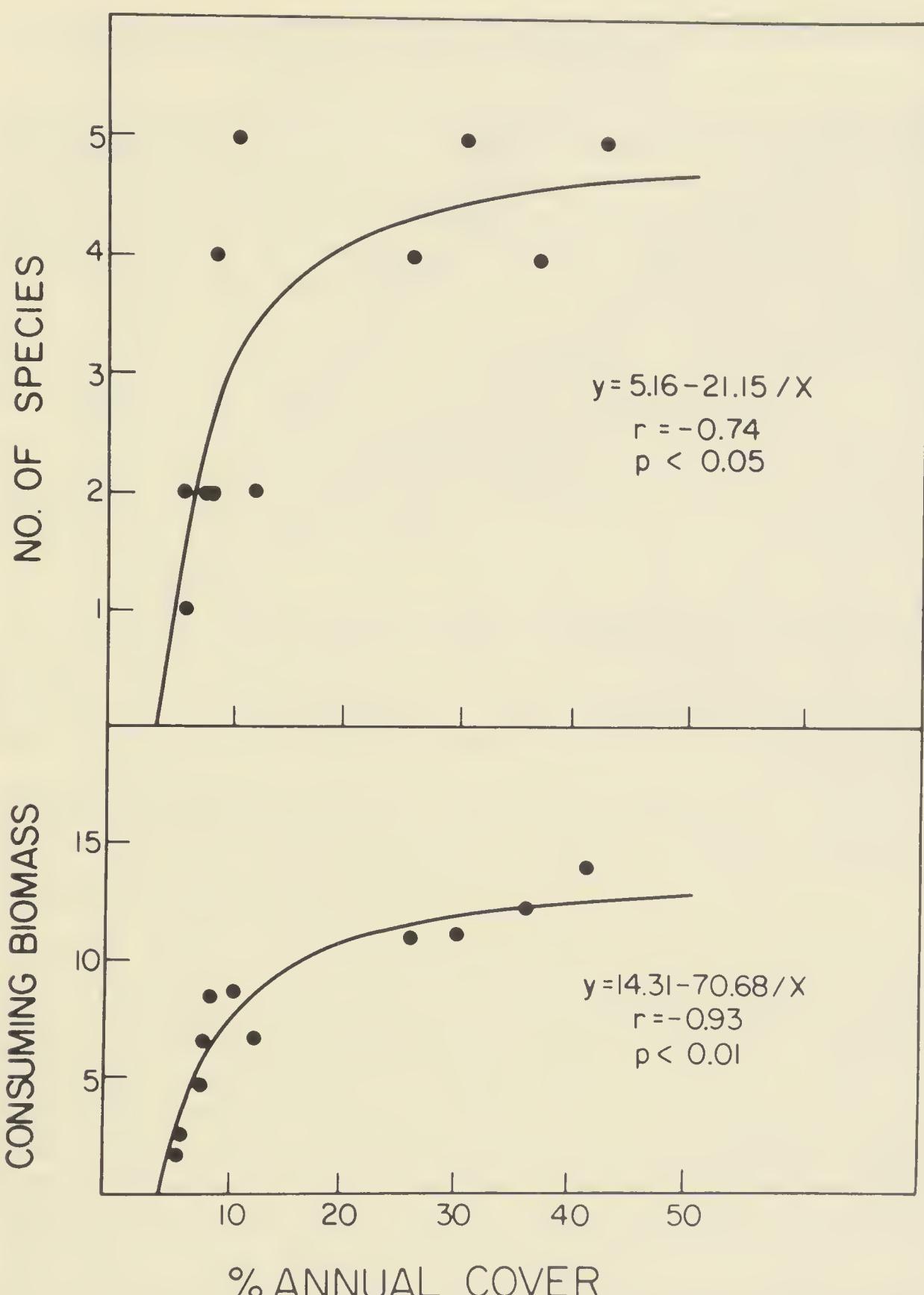
Fig. 3.—The relationship between percent annual cover and number of rodent species and their consuming biomass.

cal barriers and isolation probably have not influenced equilibrium number of co-occuring species. Three of the studied gerbilline species were common so that further analysis regarding their habitat preferences could be carried out.

Relationship Between Habitat Variables and the Distribution and Abundance of Gerbilline Species

The distribution method was developed to establish if a given species was a habitat selector (Abramsky *et al.*, 1985*a*). The method uses censuses from plots encompassing as much variation of the environment as possible with respect to a variable that is hypothesized to be important in determining habitat quality. The habitat within a plot should be as uniform as possible. In this study, the plots were selected in uniform habitats of sand dunes and sand fields. Habitat selection was measured using Simpson's index. Simpson's indices were calculated for a given species for each set of four plots at all sites and sampling dates. This procedure generated values of habitat selection that corresponded to different population densities.

The relationship between the Simpson's indices and the densities can be described by the linear transformation of the function $y = (c + x)/ax$ where x is the density, y is the inverse of Simpson's index, a is the number of habitat types (plots) and c is the slope to be fit by regression. To determine if a species shows habitat selection the slope of the line (c) has to be compared with c obtained from a random distribution generated using a Monte Carlo simulation. Slopes that are significantly smaller than the random slope indicate habitat selectivity. Slopes that are significantly larger than the random slope indicate a tendency to use the habitats more equally than random.

The three common gerbilline species exhibited significant selectivity for habitat types (Fig. 4). To identify the potential habitat variables selected by the species regression analysis was used. Multiple regression analysis between population densities and habitat variables can show not only if the species density is related to certain habitat types but also may point at the potential habitat variable selected by the species. The results of the regression analysis for the three common species were similar to those of the distribution method: the three species exhibited a significant correlation with at least one habitat variable (Table 3). It is interesting to note that the habitat variables selected by the regression procedure agree with the existing knowledge on the natural history of the three species. In general *G. allenbyi* is associated with sandy areas of relatively rich vegetative cover, *G. gerbillus* is found in the poorest environments with shifting sand and little vegetative cover, whereas *G. pyramidum* is found in intermediate environments in terms of vegetative cover. Rosenzweig and Abramsky (1985) have shown that the habitat selectivity of these three species is negatively density dependent.

Role of Ongoing Interspecific Competition

Interspecific competition is widely regarded as a principle mechanism determining the distribution and abundance of species (for example, MacArthur, 1972; Schoener, 1974, 1983; Hutchinson, 1975). For this reason an experiment was conducted to test the existence of competition between
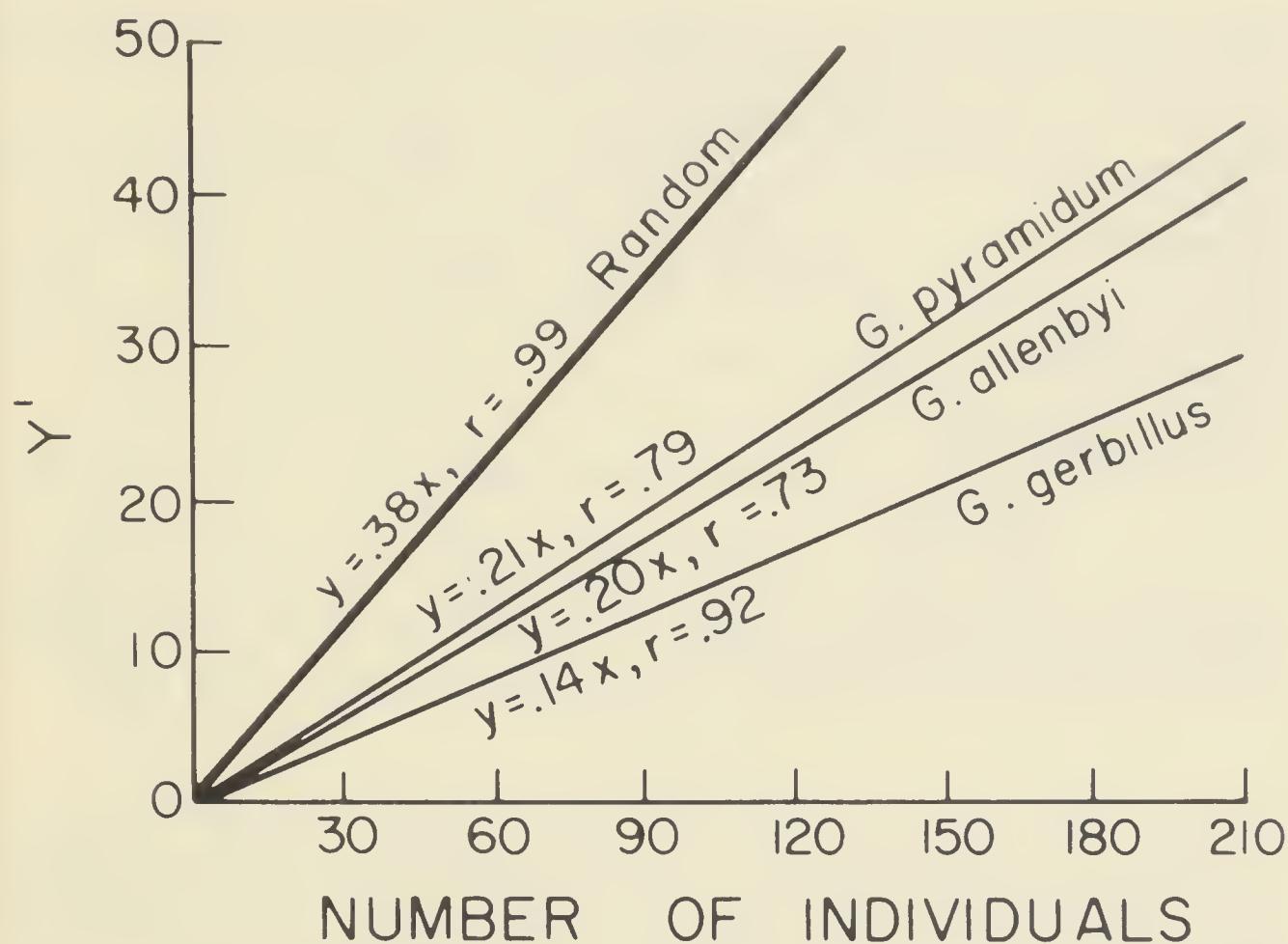
FIG. 4.—Habitat selection was measured using Simpson Index. To determine whether a species is a habitat selector, its slope has to be compared to a random slope. The random slope was generated by fitting a linearized transformation of a hyperbolic curve to the results of Monte Carlo simulation. The slopes for species were estimated using the same transformation of actual selectivity (Y') data. All the species have significantly smaller slope than the random slope indicating habitat selection.

G. allenbyi and *M. tristrami*. The experiment was conducted for a case where all indirect evidence suggested that competition is the most obvious factor in determining the distribution of the rodent species (Abramsky and Sellah, 1982).

M. tristrami and *G. allenbyi* co-occur in the area between Tel Aviv and Haifa. In this area, *G. allenbyi* is found on the sand dunes, whereas *M. tristrami* is found in nonsandy habitats. North of Haifa (Fig. 1) only *M. tristrami* is found and there it occupies sand dunes as well as other habitat types. This type of geographical and local distribution often has been interpreted as an indication of strong competition. Furthermore, the two species exhibit a large overlap in their diets and microhabitat preferences (Abramsky, 1980). Thus, it was hypothesized that *G. allenbyi* excluded *M. tristrami* from sandy habitats south of Haifa. North of Haifa, Mt. Carmel provides a biogeographical barrier that limits the distribution *G. allenbyi*. Thus, *M. tristrami* is the only species that can (and does) utilize sand dunes there. For these reasons, it was assumed that a removal of *G. allenbyi* from a dune south of Haifa should trigger a density response of *M. tristrami* in that area.

TABLE 3.—*Regression equation of the species. Note that each species prefers different microhabitat type.*

Species	Equation	R^2
G. gerbillus	$y_1 = 11.8 - 28.3 \, V_{12}$	0.62
G. pyramidum	$y_2 = 23.5 - 0.3 \, V_1 - 1.2 \, V_{15}$	0.66
G. allenbyi	$y_3 = -1.9 - 66.7 \, V_{11} - 40.8 \, V_4$	0.94

V_1, nearest neighbor.
V_4, percent soil particles bigger than 1.0 mm. diameter.
V_{11}, percent annual cover.
V_{12}, percent perennial cover.
V_{15}, amount of vegetation between 15 and 30 cm. above ground.

The results of *G. allenbyi* removal, which lasted one year (Fig. 5), did not support the hypothesis that ongoing competition between the two species determine their present local distributions (Abramsky and Sellah, 1982).

Conclusions

What are the factors that seem to determine number of gerbilline species in sand dune habitats of Israel? Two factors, area and mean annual rainfall were significantly correlated with the number of species. The density and the occurrence of the common species were highly correlated with certain types of microhabitats.

Abramsky *et al.* (1985*b*) have used residual analysis to discriminate between the relative importance of rainfall and area in predicting the number of species. The results of the residual analysis suggested that both factors were important. It is not clear how rainfall can determine number of rodent species directly.

However, rainfall is probably an accurate index of size of the annual seed crop on which the gerbilline rodents feed. Seed production was not measured in this study but annual cover was measured, and it would give an index of relative seed abundance in the different locations. Species diversity of gerbilline rodents is limited by annual cover only in a relatively poor location (Figs. 3). Once a certain threshold of annual cover is reached a further increase in productivity is not followed by an additional increase in number of rodent species, or their consuming biomass.

This result may suggest that area has a stronger effect on the number of gerbilline species than previously suggested (Abramsky *et al.*, 1985*b*). However, the relationship between area and number of rodent species is similar to the relationship between annual cover and number of species. Because both relationships can be represented by an asymptotic curve, another factor (or factors) may limit the number of gerbilline species. These other limiting factors could include history, geographical barriers, and the habitat structure. These two factors are not supported by the existing information. A third factor, habitat heterogeneity also may limit the number of rodent species.
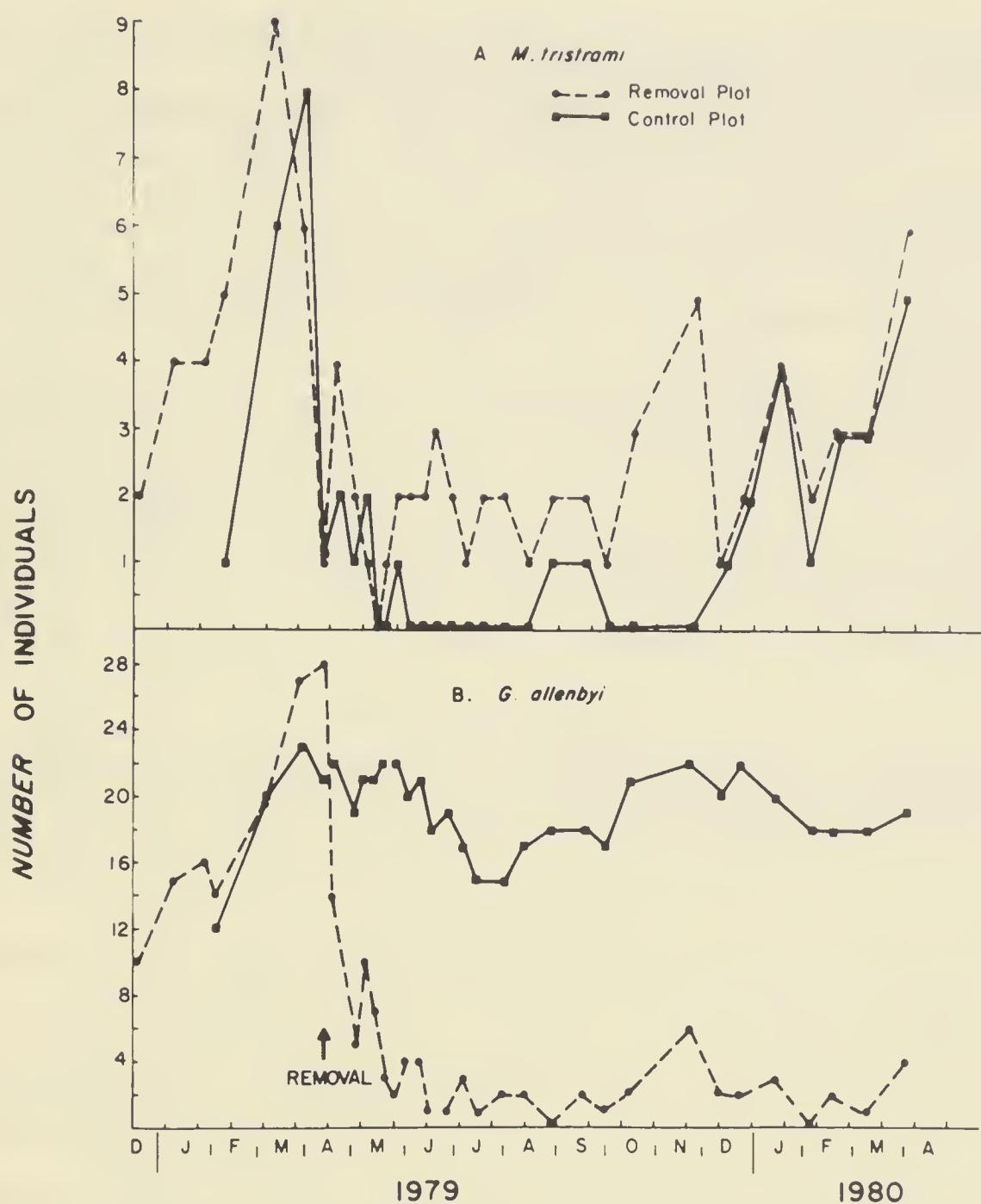
Fig. 5.—Densities of *G. allenbyi* and *M. tristrami* on the control and removal plots. Note that the mean difference of the preremoval densities of *M. tristrami* on the two plots is similar to the difference of the postremoval densities.

Abramsky *et al.* (1985*a*) have shown that gerbilline species in sandy habitats are habitat selectors, that each species seems to specialize on a somewhat different kind of microhabitat, and that the habitat preference is density dependent (Rosenzweig and Abramsky, 1985). Because the form, height, and spacing of perennial plants on all dunes are similar in their general appearance and simple in structure, a finite number of closely related rodent species might be able to coexist in the best microhabitat. Tilman (1982) has shown for plants that when resources are limited species diversity first increases over low resource supplies, then declines as the environment becomes richer. A similar peaked curve of diversity over productivity will result for rodent species competing for limiting number of microhabitat types. Abramsky and Rosenzweig (1984) hypothesized that this

was the case for the nonoverlapping assemblages of rodent species inhabiting the rocky and sandy habitats of Israel.

In some cases, ongoing competition over the same preferred microhabitats seems to determine the distribution and abundance of the species (Rosenzweig and Abramsky, 1986). In other cases, such as in the case of *G. allenbyi* and *M. tristrami* (Abramsky and Sellah, 1982), the process of habitat selection may have resulted in a distinct habitat preference. In such cases, onging competition may no longer be detectable in a relatively short experiment.

What limits the number of coexisting species in the best locations (the peak in Fig. 2) is not exactly known. It is interesting to note, however, that a maximum of five to six coexisting granivorous rodent species were found in this study (including *J. jaculus*) and in the studies reported by Brown (1975) for two different deserts in the United States. A similar maximum number of nongranivorous rodents was also reported for the rocky habitats of Israel (Abramsky and Rosenzweig, 1984).

ACKNOWLEDGMENTS

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ON THE EVOLUTIONARY ECOLOGY
OF MAMMALIAN COMMUNITIES

Nils Chr. Stenseth

ABSTRACT—Various theories for coevolution in competitive and predator-prey communities are reviewed in this paper. Special attention is paid to Red Queen models, and to the integration of population dynamics, island biogeography, and coevolutionary theories. Colonization and extinction processes are linked to population dynamics by joint consideration of simple population growth models and those of island biogeographical theory. The derived predictions are tested using ecological and paleontological data on mammalian communities. On this background, a discussion is presented of what new theoretical developments and data are needed. In particular, we need to integrate processes occuring at different times scales. Both ecological and paleontological data on mammalian communities are badly needed. Ecological data may provide insight into the processes and paleontological data may expose details about the patterns to be explained.

Any existing community is the result of two fundamentally different, but nevertheless interrelated, forces. Ecological forces determine the stability of any assemblange of coexisting species. Evolutionary forces determine which species are able to invade an established community and how these coexisting species are modified through coevolution. In this paper, I discuss various ways of integrating ecological and evolutionary processes; unfortunately such interactions are neglected too often by evolutionary ecologists. Data on mammalian communities may illuminate this issue. Regretably, my discussion will be rather fragmentary. I wish I could provide a clearer picture, but at present this seems impossible.

When discussing ecological and evolutionary processes, it is useful to distinguish three different scales: 1) the ecological time scale refering to fast processes where the only variables often are the species abundances, 2) the gene frequency time scale refering to slower processes where the number of species and the nature of the interactions between them are treated as constants, but the species are evolving, and 3) the speciation-extinction time scale, which refer to even slower processes. Basically, these time scales correspond to Valentine's (1972) classification of the types of changes occurring in communities: 1) changes that alter the proportional representation of species present in the community, 2) changes that alter the quality of species present, and 3) changes that alter species diversity in the community. My classification also corresponds somewhat to the one suggested by Rummel and Roughgarden (1983, 1985) and referred to as invasion and coevolution-structured communities.

These distinctions are to some degree artificial. In particular, as gene frequencies change on the gene frequency time scale, the relative abundances of species will change, and this in turn will alter the strengths

of interspecific interactions. Nevertheless, we often treat these interactions as constants on this time scale, and as variables only on the speciation-extinction time scale. Some simplification of this kind seems necessary if progress is to be made, because it enables us to study separately the processes occurring on different time scales—for a discussion, see Stenseth and Maynard Smith (1984) and Stenseth (1985). However, treating such simplifications too literally may become disastrous. For instance, distinction between island biogeography and population dynamics is unfortunate to much of modern ecological theory.

In the following sections, I discuss various ways of intergrating theories refering to different time scales. In the first section, I discuss the integration of population dynamics theory with island biogeographic theory; there I refer to ecological data on mammalian communities. Then, I consider the integration of population dynamics theory and macroevolutionary theory; there I refer to data on rates of speciation in groups of species with density cycles as well as in groups with stable densities. Finally, I discuss mammalian data on frequency distributions in fossil communities, and suggest how observed differences may be interpreted on the basis of population dynamical insights on the species composing these communities. None of these discussions is conclusive. Nevertheless, I hope they suggest new ways of studying mammalian communities.

Island Biogeography and Population Dynamics

In studies on island biogeography (see MacArthur and Wilson 1967), we only rarely consider population dynamics of species. On the other hand, in studies of population dynamics, we only rarely discuss the effects of community structure and subdivision of space on the dynamics of species. In fact, within the framework of theoretical ecology, conceptual developments in island biogeography and population dynamics have been cruising side by side for several decades. Post and Pimm (1983) and Rummel and Roughgarden (1983, 1985) have begun a fragmentary integration of these two theories, but no synthesis exists. Nevertheless, island biogeography and population dynamics relate closely to each other. Invasion concerns competition for access to an already established community (for example, MacArthur, 1972; Roughgarden, 1974; Hastings, 1986). Furthermore, the persistence of a species in a community is a function of population size and population stability (see MacArthur and Wilson, 1967).

Stenseth (1988) and Stenseth and Sannes (1988) have analyzed two slightly different but complementary models integrating population dynamics and invasion-extinction dynamics of species in a community. The essential aspects of the first model follow. Let S be the number of species in the community. If the mean density of the S coexisting species is denoted x, a dynamic model describing changes in x and S may be given by

$$dx/dt = (B - D) \cdot x \tag{1}$$
$$dS/dt = I - E \cdot S, \tag{2}$$

where B is the average specific birth rate and D is the average specific death rate for the species in the community, I is the total rate of species immigration into the community (including speciation), and E is the extinction rate per species. As explained below, these rates are, in general, functions of the dynamic variables, x and S, and some feature (H) of microhabitat differences such as productivity or habitat heterogeneity as understood by Abramsky and Rosenzweig (1984). Equation 1 is a standard population dynamic model and Equation 2 is a standard island biogeographical model (see MacArthur and Wilson, 1967; Maynard Smith, 1974). However, the component functions are defined so as to merge these two areas of ecological theory. In fact, the main new feature of this model lies in the definition of these functions.

Let $B = B_0 - k_b \cdot x$, where B_0 is the average specific birth rate in the absence of competition; I assume the parameter k_b to be directly proportional to S and inversely proportional to H. That is,

$$B = B_0 - a \cdot (S/H) \cdot x, \tag{3}$$

where a is a positive constant. Furthermore, let $D = D_0 + k_d \cdot x$ where D_0 is the average specific death rate in the absence of competition; I assume the parameter k_d to be directly proportional to S and inversely proportional to H. That is,

$$D = D_0 + b \cdot (S/H) \cdot x, \tag{4}$$

where b is a positive constant.

For the island biogeographic model in Equation 2 assume that $I = I_0 - k_i \cdot S$ where I_0 is the maximal rate of species immigration into the community. As in the theory of MacArthur and Wilson (1967) I assume the parameter k_i to be inversely proportional to H. That is,

$$I = I_0 - c \cdot H^{-1} \cdot S, \tag{5}$$

where c is a positive constant.

In order to integrate population dynamics and island biogeography dynamics, I assume that extinction, E is proportional to the turnover rate of individuals, $D/(B + D)$. That is,

$$E = d \cdot D/(B + D), \tag{6}$$

where d is a positive constant.

Analysis of this model (Stenseth, 1988) suggests that the number of species in the community at its equilibrium continues to increase toward an asymptote with increasing H. However, the stability of this equilibrium, measured by how fast the equilibrium is reattained after a perturbation, decreases with increasing H. These two features lead to a humped curve of species diversity with increased habitat heterogeneity (Fig. 1). Interestingly, this pattern resembles the one found by Abramsky and Rosenzweig (1984), who demonstrated that the number of coexisting rodent species in different desert habitats (one rocky and one sandy) first rose quickly, then fell more slowly along a gradient of increasing rainfall, where rainfall was assumed to determine the habitat heterogeneity of the area (see Fig. 2 in Abramsky,
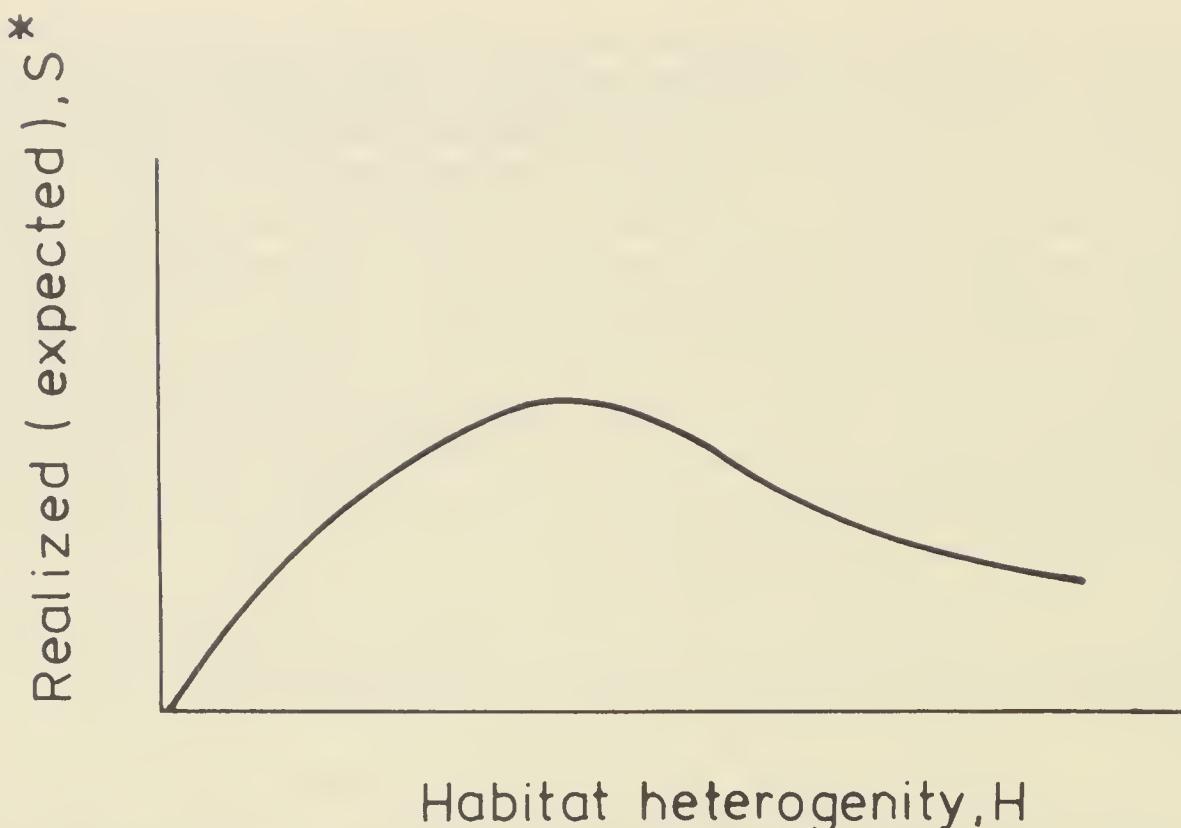
FIG. 1.—Expected relation between species number, S*, and habitat heterogeneity, H (modified from Stenseth, 1988).

this volume). A similar pattern was predicted by Tilman (1982, 1985). A clearer understanding of these patterns has important implications for community ecology (Lawton, 1984).

The model analyzed by Stenseth (1988) and summarized above may be criticized as an oversimplified representation of the real world. Stenseth and Sannes (1988) numerically analyzed models for both competition communities and for food webs with competitive as well as trophic interactions. It is encouraging that similar patterns were produced by all these models. This suggests that the prediction depicted in Figure 1 is theoretically sound.

One main conclusion derived from the Stenseth-Sannes models is that communities never become resistant to invasion by new species even though an equilibrium number species always exists. As more species become established in a community it becomes increasingly more difficult to invade. That is, species turnover is negatively related to the number of species in the equilibrium community. The former result is in sharp constrast to the one drawn by G. Sugihara (unpublished data). Our second result is, however, consistent with Post and Pimm (1983) and both results are consistent with empirical findings (Crawley, 1986).

Even though further theoretical work is necessary, data are even more desperately needed to test available theory. Mammalian communities are, in this context, useful to study. They are fairly easy to observe and we are beginning to understand the relation between their dynamics and various features of habitat (for example, Stenseth, 1980).

TABLE 1.—*Number of species per genus in mammals. Data compiled from Honacki et al. (1982). Parentheses give the number of species within the listed genera.*

Taxon	Average no. species per genus
Mammals	3.2
Rodents	4.3
Arvicolidae	6.4
Microtines[1]	
Group I (most genera)	13.3
Clethrionomys (7)	
Microtus (45)	
Lemmus (4)	
Dicrostonyx (10)	
Arvicola (5)	
Pitymus (23)	
Synaptomys (2)	
Group II (the cyclic genera)	16.5
Clethrionomys (7)	
Microtus (45)	
Lemmus (4)	
Dicrostonyx (10)	

[1]Microtines is, according to Honacki *et al.* (1982), not an acceptable taxonomic category. Here I am only interested in having a larger grouping including the "cyclic genera" as a subgroup; for that purpose the two groupings should do. All genera listed as "Microtines" here are also included in the larger category—Arvicolidae.

POPULATION DYNAMICS AND MACROEVOLUTION

The ecological setting determines the selective pressures and hence, rates of evolution (for example, Maynard Smith, 1982; Stenseth, 1985, 1986). More variable ecological conditions (both biotic and abiotic) lead to more rapid evolution of the coexisting species within a community; moreover the rates of speciation and extinction will be higher (see Maynard Smith, 1976 and Stenseth and Maynard Smith, 1984). This suggests we should observe both higher speciation rates and higher extinction rates in cyclic small rodents that undergo dramatic density changes between years.

At least three pieces of evidence support this prediction. First, as shown in Table 1, there are more species per genera in the cyclic mammals (group II) than in the groups with both cyclic and noncyclic species (group I and Arvicolidae). Obviously the genus *Microtus* biases the microtine group upwards. Notice, however, that most of the "cyclic" genera do have more than the average number of species per rodent genus. This suggests that speciation and extinction rates are positively related to ecological change in small mammals. Generation times differ between the various groups listed in Table 1. There is no reason to believe that such differences could account for the differences in number of species per genus. Second, it can be shown on the basis of data compiled by Van Valen (1973) that rodent species "survive" in the paleontological record for a shorter time than do other

mammalian species. This may occur because rodents are exposed to a more variable environment over time with respect to density and general ecological conditons (see arguments in Stenseth, 1985). This is indeed consistent with the data in Table 1. Third, the rate of karyotypic evolution in a genus may be estimated by the standard deviation of chromosome numbers within the genus. Árnason (1972) pointed out that the rate of karyotypic evolution is low in cetaceans and pinnipeds, and particularly low compared to the high rate of karyotypic evolution in Insectivora and Rodentia. Wilson *et al.* (1977) further showed that small mammals have, on average, a higher rate of karyotypic evolution than large mammals. Finally, Bush *et al.* (1977) demonstrated that vertebrates with a high tendency to speciate have a higher rate of karyotypic evolution than vertebrates with a low tendency to speciate. This suggests that karyotypic evolution is of profound phenotypic importance. Bengtsson (1980) was able to corroborate the findings reported by Wilson *et al.* (1977) and Bush *et al.* (1977), as was, to a certain extent, Patton and Sherwood (1983). On this basis and on the above presented theoretical background, I suggest that rodents have a higher rate of karyotypic evolution than other mammals due to variable population dynamics.

In this section, I have discussed mainly population dynamics within a given species or a taxonomic group of species. If my argument is correct, we would also expect to find high rates of evolution in those species that are ecologically closely related to cyclic small rodents. I do not know of any relevant data for testing this prediction.

The Red Queen Views Mammalian Communities

The essential aspect of the Red Queen hypothesis (Van Valen, 1973) is that the coexisting species in an ecosystem represent a major component of any particular species' environment. Any evolutionary change in one species will be experienced as a change in the environment of others. Typically, the change experienced by any species will involve an increase in the evolutionary lag of a species (see Maynard Smith 1976), because most species usually are assumed to be close to their local adaptive peaks (Stenseth and Maynard Smith, 1984). An arbitrary change in the environment will usually move a species further away from its adaptive peak.

In a previous work (Stenseth, 1979), I discussed some data on mammals in the light of this hypothesis. On the basis of a general community model (see Stenseth 1979), I predicted that there should be a negative correlation between species diversity and environmental variablity. As can be seen from Table 2, this finds some support in the literature on mammalian communities. Furthermore, I predicted that in equilibrium communities, a log-normal abundance or species-area curve (May, 1975; Engen, 1978) is to be expected, whereas in nonequilibrium communities, the species abundances should fit a logarithmic series. Brown (1971, see also Brown, 1975) speculated that the boreal small mammal fauna of the Great Basin of North

TABLE 2.—*Relation between diversity (S*) and environmental stability. Significance at one percent level is indicated by ** and at five percent level by *. After Stenseth (1979).*

Fauna	Location	Estimate for S*	Estimate for stability	Correlation (sample size in parenthesis)	Source
Mammals	West Coast United States	Number of species	Temp. range	−0.955** (n=7)	MacArthur (1975: fig. 6)
Desert rodents	Sandy flat-land, United States	Number of species	Inverse of predictable productivity	−0.820** (n=10)	Brown (1975: table 1)
	Rocky hills, United States	Number of species	Inverse of predictable productivity	−0.519 (n=4)	
Small mammals	Fennoscandia	Shannon-index	Standard deviation of logtransformed densities	−0.551 (n=10)	Myllymäki et al. (1977)
Small mammals	Northern Fennoscandia	Shannon-index	Standard deviation of logtransformed densities	−0.415 (n=4)	Hansson et al. (1978: fig. 3)
Small mammals	North American grasslands	Shannon-index	Between year variation in diversity relative to average diversity	−0.414 (n=9)	Grant and Birney (1979: table 2 and fig. 1)

America is supersaturated (see also Diamond's (1972) discussion of these data). He further suggested, on paleontological evidence, that the mountains were colonized by a group of boreal species during the Pleistocene. Subsequent isolation of the mountains by desert has left each with an enriched mammal fauna. Consistent with this view and the Red Queen's prediction, a logarithmic series is observed for the species abundances (see Stenseth, 1979). This suggests that both the biotic and the abiotic components of the environment are likely to play important roles in shaping the rodent community.

Van Valen's (1964) data on Eocene mammals are relevant also for testing these predictions (see Deevey, 1969, for other groups) (Table 3). Unfortunately, the data are of a nature that makes statistical analysis impossible. However, the log-normal distribution of these fossil mammals is consistent with paleontological evidence suggesting that the Eocene was characterized by a relatively constant diversity (see Bakker, 1975). If the Red Queen hypothesis is intrinsically consistent, we should, assuming that my interpretation is correct, expect to see that the corresponding survivorship curve is a straight line. And so it is (see Stenseth, 1979).

CONCLUSION

I have discussed models that incorporate both fast ecological processes and slow evolutionary processes. By so doing, I have been able to interpret

TABLE 3.—*Abundance-models for various biota. LN denotes a log-normal distribution and LS denotes a logarithimic series distribution.*

Source	Fauna	Location of geological period	Type of abundance distribution
Van Valen (1964: figs. 3-4)	Fossil mammals	Earliest Eocene	LN?
Van Valen (1964: fig. 1)	Fossil mammals	Middle Pliocene	LS
Fleming (1975: fig. 12.1)	Small mammals	Panamá	LN
Fleming (1975: fig. 12.1)	Rodents	Central Africa	{ Lower montane wet forest, subtropical most forest, banana plantations } LN { Subtropical wet forest } LS?

both ecological and paleontological observations on mammalian communities.

This paper documents attempts at integrating different temporal and spatial scales. Colonization and extinction processes are linked to population dynamics by joint consideration of simple population growth models and those of island biogeographical theory. This provides an alternative explanation of the rapid increase and subsequent decline in species diversity along productivity gradients as predicted by Tilman's (1982) resource partitioning theory. Abramsky and Rosenzweig's (1984) work on the geographical ecology of Israeli desert rodents is cited as a possible empirical example of this pattern. Similarly, I discuss macroevolution in the context of population dynamics and the Red Queen hypothesis. Species that experience the most variable ecological environments (especially if those conditions are reflected or caused by variable population dynamics) should have higher rates of evolution than other species, and so too should the communities of which they are a part. This prediction is, to a certain extent, supported by data on numbers of species per genera, rodent extinction rates, and karyotype evolution. Preliminary data on patterns of species diversity with different levels of environmental variation and distributions of abundance also support the Red Queen predictions.

It is *quite* encouraging that a variety of predications derived from theories integrating ecology and evolution seem to fit available data. Even though we do not know in detail how ecology and evolution mutually affect each other, we seem to be on the right track.

Much further work is needed. Most of all, we need data. My gut feeling is that data on cyclic small rodents could play an exceedingly important role in the integration of ecology and evolution. The changes in population dynamics are so extensive in this group that evolutionary effects are likely to

be prounounced and easily detectable. Many important data of the kind needed in this context are collected in Heaney and Patterson (1986).

ACKNOWLEDGMENTS

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THE TROPHIC STRUCTURE AND SPECIES RICHNESS OF ASSEMBLAGES OF ARBOREAL MAMMALS IN AUSTRALIAN FORESTS

S. R. Henry, A. K. Lee, and A. P. Smith

Abstract.—Forty species of arboreal and scansorial mammals (32 marsupials, eight rodents) occur in Australian forests. Temperate eucalypt forests support 17 species, tropical eucalypt forests 13 species, warm temperate rainforests seven species, cool temperate rainforests seven species, and tropical rainforests, despite their small area and fragmented nature, support 19 species. Arboreal-scansorial rodents are virtually confined to tropical forests.

Eighteen assemblages of arboreal and scansorial mammals (10 Australia, eight elsewhere) are analyzed for species richness and trophic structure. Temperate eucalypt forests are distinguished by a high proportion of folivores and insectivores-exudivores, and a paucity of frugivores and granivores. Tropical eucalypt forests support more partial frugivores but no strict folivores; trophic structure of these assemblages resembles other tropical assemblages rather than other Australian assemblages. Australian tropical rainforests support a depauperate fauna compared to other tropical rainforests, and the trophic structure resembles temperate eucalypt assemblages rather than other tropical assemblages. Marsupial-dominated assemblages in tropical rainforest in New Guinea are similar in species richness to tropical assemblages outside Australia. The low species richness of Australian tropical rainforest is probably due to its small area and fragmented nature. The trophic structure of the Australian assemblages is strongly influenced by the particular suite of food resources available—a paucity of soft fruit and grain, and an abundance of plant and insect exudates.

The Australian continental plate separated from Antarctica in the Eocene and began drifting northward. Eutherians were either absent from Australia at this time, or failed to persist (Archer, 1981), so that the subsequent radiation of marsupials occurred free from eutherian presence (excluding chiropterans) until the early Pliocene (Archer, 1981). It was then that rodents invaded Australia from the north (Watts and Aslin, 1981). This marsupial radiation represents an independent experiment in mammalian evolution that can be compared with the radiations of mammals on other continents.

Morton (1979) compared the desert-dwelling mammalian faunas of Australia and North America, and observed a substantial difference in the trophic structure, with granivorous species dominant in North America and insectivorous species more numerous in Australia. Morton concluded that convergence between the faunas was minimal and that the dichotomy was strongly related to differences in the food resources available in the two regions.

This paper compares the trophic structure and species richness of arboreal and scansorial mammal assemblages in the principal forest formations of Australia and elsewhere. We analyze the macroniches (*sensu* Eisenberg, 1981) of arboreal and scansorial mammals in Australian forests, describe the

TABLE 1—*Species richness of arboreal and scansorial mammals in Australian forest types. Forest areas from Webb and Tracey (1981) and Anon. (1983).*

| Forest type | Latitudinal range (degrees) | Area (ha× 10^6) | Mammal species | | | |
			Total	Endemics	Marsupials	Rodents
Tropical rainforest	11-25	0.76	19	12	15	4
Warm temperate rainforest	21-37	0.6	8	0	7	1
Cool temperate rainforest	37-44	0.5	6	0	6	0
Temperate eucalypt forest	17-44	28.1	19	9	19	0
Tropical eucalypt forest	11-17	6.5	13	9	9	4

trophic structure and diversity of particular assemblages, and compare Australian assemblages with those from other continents.

FORESTS AND ARBOREAL MAMMALS OF AUSTRALIA

Forest covers about six percent of Australia's total land area of 768 million hectares, and more than 84 percent of this comprises plant formations dominated by the genera *Eucalyptus* and *Acacia*. Other formations individually contribute two percent or less (Table 1).

At the time of separation from Antarctica, much of the Australian continent was covered by temperate rainforests, and these remained prominent over most of southern Australia until the late Miocene (Martin, 1981), when the climate became increasingly arid. This trend persisted, with pluvial interludes, until the present (Galloway and Kemp, 1981). As the rainforest retreated toward the present mesic refuges, *Eucalyptus* and *Acacia*-dominated forest became predominant. This process began during the Pliocene (Martin, 1981), and has accelerated during the last 100,000 years in association with an increased frequency of fire (Kershaw, 1981). Thus the dominance by *Eucalyptus* open forests is a relatively recent phenomenon.

The tropical rainforest formations of northern Australia are ancient, and their confined, extant distribution is relatively recent. Tropical rainforest was reduced to isolated refugia for some 70,000 years in the Quaternary, and has expanded to its present extent only in the last 10,000 years (Galloway and Kemp, 1981; Webb and Tracy, 1981).

The origins and patterns of radiation of the arboreal marsupial fauna are not clear. Families of extant arboreal marsupials, the Phascolarctidae, Petauridae, Pseudocheiridae, Burramyidae, and Phalangeridae, were represented in the mid-Miocene (Archer, 1981). Thus, there was probably a diverse arboreal fauna prior to the preeminence of the *Eucalyptus-Acacia* formations.

Fossils assigned to the glider genus *Petaurus* are first recorded from the early Pliocene (Archer, 1984). Five of the six extant gliding marsupials (*Petaurus australis, P. breviceps, P. norfolcensis, Petauroides volans, Acrobates pygmaeus*) are associated almost exclusively with open *Eucalyptus*

forests. This evidence suggests that the evolution of the gliding possums may have coincided with the development of open forests in the Pliocene.

Species Richness in Australian Forests

Forty arboreal and scansorial mammals are found in Australian forests, of which nearly half are found in temperate eucalypt forest and a similar fraction in tropical rainforest (Tables 1 and 2). Thirty-two species or 80 percent of this fauna are marsupials. Murid rodents are found in arboreal and scansorial niches in tropical rainforest, tropical eucalypt forest, and warm temperate rainforest where they comprise 21, 31, and 13 percent of species, respectively. A single arboreal rodent, *Conilurus albipes*, inhabited temperate eucalypt forest in southeastern Australia at the time of European settlement (*ca.* 1800), but is now extinct (Watts and Aslin, 1981).

Endemism is highest in tropical eucalypt forest and tropical rainforest where 69 and 63 percent of species are confined to those forest types, respectively. In temperate eucalypt forest, 47 percent of species are endemic. Warm temperate or cool temperate rainforest share all species with temperate eucalypt forest or tropical rainforest. No species occurs in all forest types, with the possible exception of *Petaurus breviceps*.

Macroniches of Forest-dwelling Scansorial and Arboreal Mammals in Australia

In this analysis, each scansorial and arboreal species is placed into one of 10 trophic categories based upon their principal food items: insectivore (mainly invertebrate prey); insectivore-carnivore (both invertebrate and vertebrate prey); insectivore-exudivore (invertebrates and plant exudates—nectar, sap, gum, and manna—or insect exudates—honeydew and lerp); insectivore-frugivore-granivore (invertebrates, fruit and seeds, or both); insectivore-frugivore-exudivore (invertebrates, fruit, and plant exudates); omnivore (foliage, fruits, seeds, and animal prey); frugivore-insectivore-carnivore (fruit, and vertebrate and invertebrate prey); frugivore-folivore (fruit and foliage); frugivore (fruit); folivore (foliage).

Six of these trophic categories and eight macroniches are occupied by marsupials and rodents in Australia (Table 2).

Comparison of Assemblages

Comparisons are based upon the species composition of 18 assemblages of arboreal and scansorial mammals (Table 3). All assemblages are from forests, defined as a vegetation community dominated by trees, with a projective foliage cover in excess of 30 percent (Specht, 1970). Information on bats is often incomplete and they are excluded from consideration. We endeavored to choose assemblages that were maximally diverse for each particular forest type, and for which we had complete information on species composition. Assemblages outside Australia were selected to cover as

TABLE 2.—*Microniche and habitat preference of forest dwelling arboreal and scansorial mammals in Australia.*

Maroniche	Species	Body weight (grams)	Cool. temp. rainf.	Warm temp. rainf.	Temp. euc.	Trop. euc.	Trop. rainf.
Scansorial insectivore	*Antechinus flavipes*	21-79			x		x
	A. stuartii	17-71	x		x		
	A. bellus	26-66				x	
	A. leo	30-100					x
Arboreal insectivore	*Cercartetus lepidus*	6-9			x		
	Dactylopsila trivirgata	246-390				x	x
Scansorial insectivore-carnivore	*Dasyurus maculatus*	4000-7000	x	x	x		x
	D. geoffroii	705-2075			x		
	D. hallucatus	300-900				x	
	Phascogale tapoatafa	110-235			x	x	
Arboreal insectivore-exudivore	*Acrobates pygmaeus*	10-14			x	x	
	C. nanus	15-43	x	x	x		
	C. caudatus	15-40					x
	Gymnobelideus leadbeateri	100-166			x		
	Petaurus breviceps	95-160	?	?	x	x	x
	P. norfolcensis	200-260			x		
	P. australis	450-700			x		
Scansorial omnivore	*Melomys burtoni*	45-65				x	
	Mesembriomys gouldii	430-870				x	
	M. macrurus	270-330				x	
	Uromys caudimaculatus	245-720					x
Scansorial frugivore-folivore	*Trichosurus caninus*	2500-4500	x	x	x		
	Dendrolagus lumholtzi	3700-10000					x
	D. bennettianus	13000					x
	Conilurus penicillatus	110-170				x	
	Pogonomys mollipilosus	52-71					x
	Melomys cervinipes	45-110		x			x
	M. sp. nov.	149-164					x
Arboreal frugivore-folivore	*Pseudocheirus dahli*	1280-2000				x	
	Trichosurus vulpecula	1500-4500	x	x	x		x
	T. arnhemensis	1100-2000				x	
	Wyulda squamicaudata	1400-1600				x	
	Phalanger orientalis	1500-2200					x
	P. maculatus	1500-3600					x
Arboreal folivore	*Petauroides volans*	900-1700			x		
	Phascolarctos cinereus	4100-13500			x		
	Pseudocheirus archeri	1075-1350					x
	P. herbertensis	700-1450					x
	P. peregrinus	700-1100	x	x	x		x
	Hemibelideus lemuroides	810-1270					x

wide a range of trophic structures as possible, rather than to comprehensively analyze assemblages from a large number of forest types. Thus, trophically divergent tropical assemblages outnumbered northern temperate

TABLE 3.—*Location, forest types, and species richness of arboreal/scansonalmammal assemblages. Letters identify forest types in Fig. 1.*

Assemblage number	Forest type	No. of species	Location	Reference
1 A	Temperate eucalypt (dry)	8	Reef Hills, Victoria	MacFarlane et al., 1982
2 A	Temperate eucalypt (moist)	10	Atherton, Queensland	Russell, 1980, and personal communication
3 A	Temperate eucalypt (moist)	10	Glengarry, Victoria	Henry, 1985
4 A	Temperate eucalypt (moist)	8	Cambarville, Victoria	Smith et al., 1985
5 A/D	Temperate eucalypt/warm (moist) temperate rainforest	11	Mt. Boss, New South Wales	A. Smith and A. Dunning, unpublished
6 B	Tropical eucalypt	8	Alligator River, Northern Territory	Calaby, undated
7 B	Tropical eucalypt	7	Coburg Peninsula, Northern Territory	Calaby and Keith, 1974
8 C	Cool temperate rainforest	3	Gordon River, Tasmania	Hocking and Guiler, 1983
9 D	Warm temperate rainforest	6	Petroi, New South Wales	Harden, 1977
10 E	Tropical rainforest	12	Atherton, Queensland	Russell, 1980 Strahan, 1983 Winter, 1983
11 E	Tropical rainforest	24	Mt. Kaindi, New Guinea	Gressit and Nadkarni, 1978
12 F	Cool temperate rainforest	3	Puerto Blest, Argentina	Pearson and Pearson, 1982
13 G	Temperate conifer/hardwood	12	Charlevoix Co., Michigan, United States	Fleming, 1973
14 H	Tropical gallery forest	8	Antserananomby, Madagascar	Sussman, 1977
15 I	Tropical rainforest	22	Cristobal, Panamá	Fleming, 1973
16 I	Tropical rainforest	37	Cocha, Cashua, Perú	Terborgh et al., 1984
17 I	Tropical rainforest	28	Kuala Lompat, Malaysia	Chivers, 1980
18 I	Tropical rainforest	40	Makokou, Gabon	Delany and Happold, 1979; Emmons, 1980

assemblages, which tended to be trophically uniform and about which complete information was difficult to obtain.

Data on diets were obtained from the literature describing the assemblages and Fleming (1973), Menzies and Dennis (1979), and MacDonald (1984). Details of the composition of these assemblages are held by the authors.

We performed cluster analyses on the assemblages to determine where the affinities of the Australian assemblages lay in terms of species richness and trophic composition. The data used in cluster analysis were determined by scoring 1.0 for each species and dividing the score equally between all food types eaten by the species. Six food types were recognized: invertebrates (I), vertebrates (V), exudates (E), grain (G), fruit (Fr), and foliage (F). Thus omnivores, for example, were scored 0.25 I, 0.25 G, 0.25 Fr, and 0.25 F, whereas folivores were scored 1F. We recognize that this is an arbitrary division; ideally the analysis requires specific information on diet composition of each species in each assemblage, but this is not available.

Total scores were calculated for each food type in each assemblage. A cluster analysis was performed on these scores to compare species richness in relation to food type in each assemblage. The totals for each food type were then summed for each assemblage and the percentage contribution of each good type to the total score was calculated. A cluster analysis was performed on these data to compare trophic structures. The data for both comparisons were clustered by the unweighted pair group method using arithmetic averages on squared Euclidean distance (Sneath and Sokal, 1973).

Results and Discussion

In the analyses of species richness and trophic structure (Fig. 1), the five temperate eucalypt assemblages cluster together. They contain eight to 11 species, dominated by insectivore-exudivores (three to four species) and folivores (two to five species—Fig. 2a-2e). Eucalypts and the associated myrtaceous and proteaceous understory shrubs flower profusely and can produce large quantities of nectar. Some eucalypts are unusual in that phloem ducts continue to produce sap when severed (Henry, 1985), and a number of acacias produce copious gum from sites of insect damage (Smith, 1982). In southern and eastern Australia, nectar, sap, or gum, or one of the other exudates (honeydew, manna) can be available throughout the year (Smith, 1982; Henry and Craig, 1984). Leaves are available year-round in temperate eucalypt forest. In addition to the three strict folivores, the two frugivorous-folivorous species tend towards folivory in southern Australian eucalypt forest where succulent fruits are small and in low abundance.

The other temperate forest assemblage at Charlevoix does not cluster with temperate Australian assemblages, but is distantly related to the tropical assemblages. The omnivores and the insectivores-granivores in this assemblage feed extensively on the seeds of hardwoods and conifers. Strict granivory is rare among marsupials and rodents in Australia (Lee and Cockburn, 1985), and they may be excluded from this macroniche by competition from birds and ants (Morton, 1979).

Australian cool temperate rainforest at Gordon River, with only three species, is closely allied to cool temperate rainforest in Argentina in terms of species richness (Fig. 1 top), but has a trophic structure more closely related to temperate eucalypt forest (Fig. 1 bottom). Cool temperate rainforests are
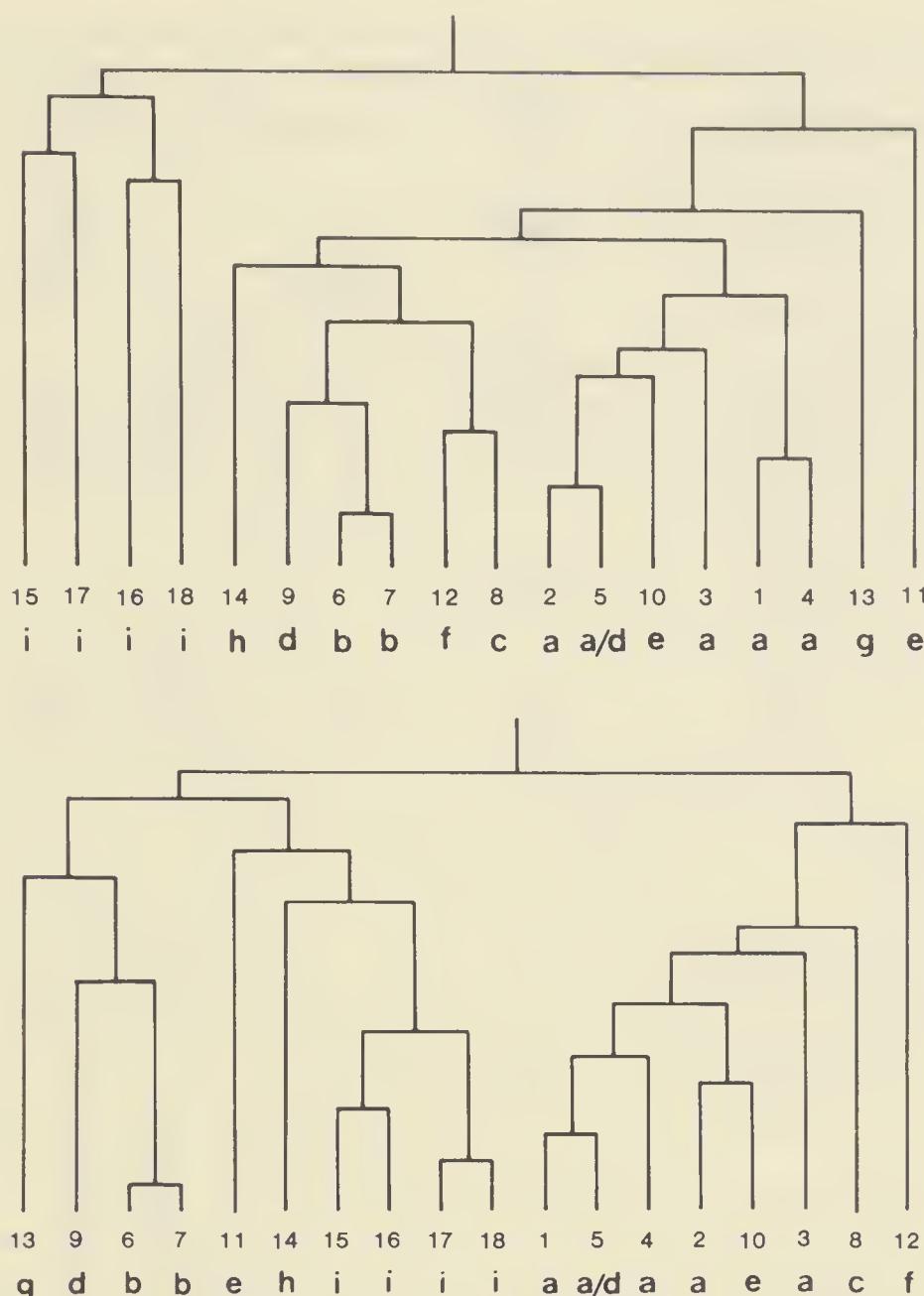
FIG. 1.—Cluster of species richness (top), and trophic structure (bottom), in each assemblage. Numbers refer to assemblage identity numbers in Table 3.

poor in food resources; soft fruits and nectar are scarce, and the seeds of *Nothofagus*, the dominant genus of trees, are small (Glanz, 1982). This probably contributes to the low species richness and trophic diversity of arboreal and scansorial mammals (Fig. 2g, 2h).

As in South America, *Nothofagus*-dominated cool temperate rainforests are ancient in Australia (Kemp, 1984), but although the Argentinian community is highly endemic, the Australian forests lack endemic arboreal mammals. This is probably a consequence of the reduction of the area of this forest type during the Pleistocene, combined with the low abundance and diversity of food resources.

Endemics also are absent from the floristically more diverse warm temperate rainforests of eastern Australia, although the arboreal mammal fauna is richer than in Tasmania. Four trophic categories are occupied (Fig. 2i). All the species at Petroi occur in adjacent *Eucalyptus*-dominated forest
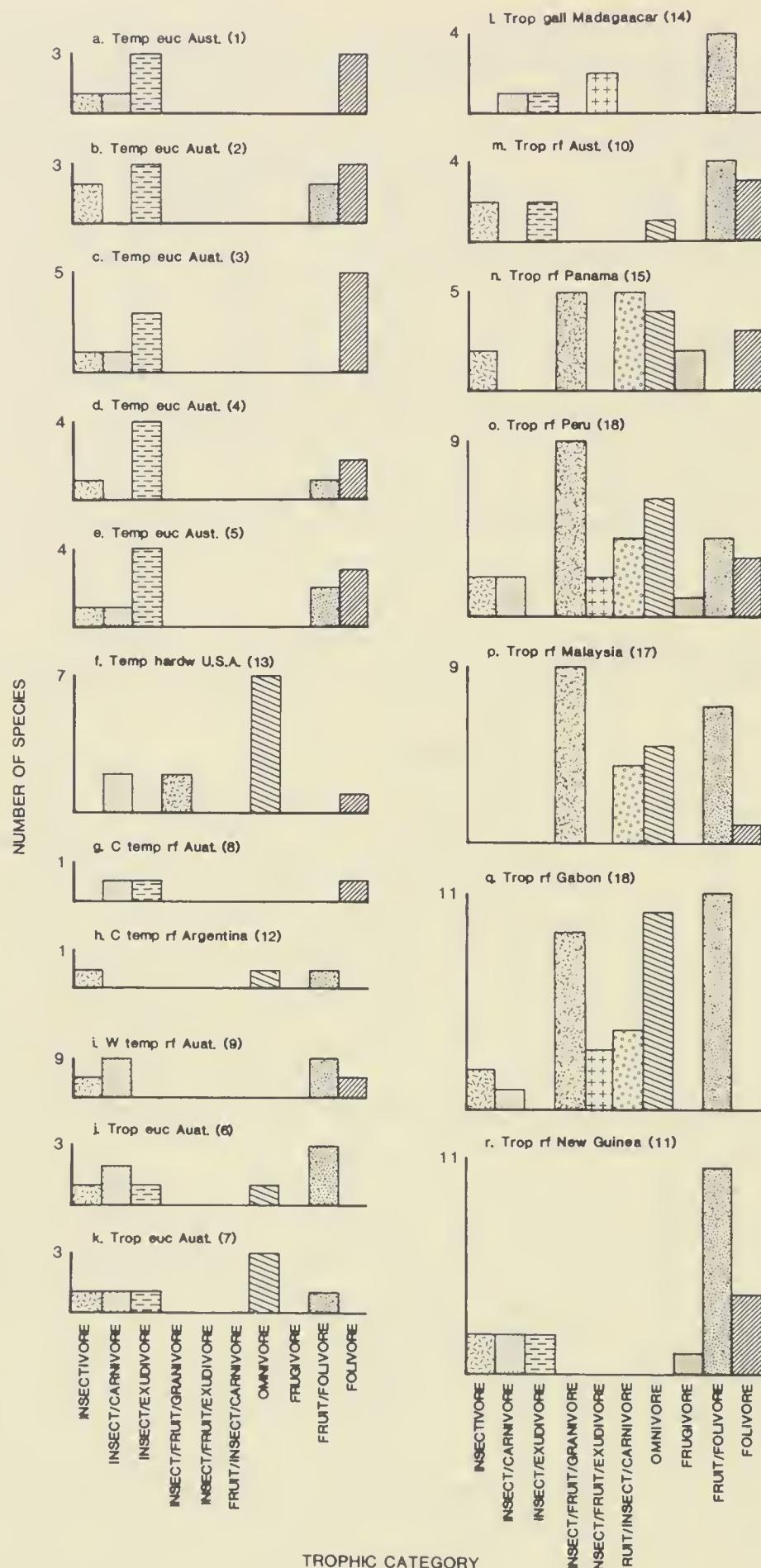
FIG 2.—Trophic structure of assemblages of arboreal and scansorial mammals. Numbers in parentheses refer to assemblage identity numbers in Table 3. Abbreviations of forest types as follows: Temp euc, temperate eucalypt; Temp hardw, temperate hardwood; C temp rf, cool temperate rainforest; W temp rf, warm temperate rainforest; Trop euc, tropical eucalypt; Trop gall, tropical gallery; Aust., Australia.

(Harden, 1977), but no insect and exudate-feeding species enters the warm temperate rainforest and only one exclusively folivorous species is present. The Petroi assemblage clusters with the tropical eucalypt assemblages (Fig. 1), and the trophic structure of these three assemblages is more closely related to tropical assemblages elsewhere than to other Australian assemblages.

Strict folivores are absent from both tropical eucalypt assemblages (Fig. 2j, 2k), but several rodents and *Trichosurus arnhemensis* feed on foliage as well as fruit (Watts and Aslin, 1981; Kerle, 1984). Frugivorous mammals are more abundant in these forests than in temperate eucalypt forests, and there is a greater abundance and variety of trees and shrubs that produce succulent fruits (Kerle, 1984). Species that take some fruit constitute between 57 and 80 percent of these assemblages, which is high for Australian assemblages, but similar to the proportion of fruit-feeding species in the Madagascan assemblage (75 percent—Fig. 21) and the tropical rainforest assemblages in New Guinea (52 percent), Panamá (77 percent), Perú (81 percent), Gabon (85 percent) and Malaysia (96 percent).

The Australian tropical rainforest assemblage with 12 species (Fig. 2m) clusters closely to temperate eucalypt assemblages (Fig. 1), rather than to other tropical assemblages. This assemblage lacks granivorous species and only 45 percent of species eat fruit, a lower proportion than in other tropical assemblages. As in temperate eucalypt forests, the Atherton tropical rainforest does support a high proportion of exclusively folivorous species (27 percent of the fauna), compared to only four to nine percent in Panamá, Perú, Malaysia, and Gabon (Fig. 2n-2q).

Richness of mammal and bird species generally increases with decreasing latitude (Fleming, 1973; Orians, 1969), but in Australia, temperate eucalypt forest supports as many arboreal mammal species as tropical rainforest. However, the tropical rainforest of Australia is both small in area and fragmented; a more useful comparison is the rainforest assemblage from New Guinea. New Guinea has a substantial area of tropical rainforest and a diverse fauna of arboreal marsupials and rodents (Ziegler, 1982). Mid-altitude (2000-2362 meters) elaeocarp-*Nothofagus* mixed rainforest and mossforest at Mt. Kaindi supports 24 arboreal and scansorial species, comprising 13 species of marsupials and 11 rodents (Gressit and Nadkarni, 1978), and thus has a richness of species similar to tropical rainforest assemblages in Panamá and Malaysia, although it clusters, albeit distantly, with the Australian assemblages (Fig. 1 top).

The trophic structure of the New Guinea assemblage (Fig. 2r) is relatively distant from any other assemblage. Compared to tropical rainforests outside Australia, it supports a relatively small proportion of species that feed on fruit (52 percent) and a high proportion of exclusive folivores (19 percent). There are few omnivores and granivores. In this regard, it resembles the Atherton rainforest assemblage.

The scarcity of fruit and large seeds is probably an important reason for the virtual absence of rodents from scansorial and arboreal niches in temperate eucalypt forests and cool temperate rainforests in Australia. Rodents have radiated into the scansorial frugivore-folivore and omnivore niches in tropical rainforest and tropical eucalypt forest, but marsupials have maintained a firm grasp on other arboreal niches, even in New Guinea where rodents make up a larger proportion of the fauna. At Mt. Kaindi, for instance, rodents comprise 11 of the 24 species but are still predominantly scansorial frugivore-folivores.

The species richness of arboreal mammals in Australian temperate forests is similar to species richness in corresponding forests in North and South America. The trophic structure of Australian arboreal mammal assemblages in temperate eucalypt forests is distinguished from assemblages elsewhere by the lack of fruit and seed-eating species and the prominence of insectivore-exudivores and folivores. The isolation of the Australian zoogeographic region has prevented eutherian taxa, which occupy niches similar to arboreal marsupials, from invading Australia. Thus, the competitive ability of arboreal marsupials in the face of eutherians with similar adaptations remains unknown.

Acknowledgments

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PATTERNS IN THE STRUCTURE AND DIVERSITY OF MARSUPIAL CARNIVORE COMMUNITIES

C. R. Dickman

Abstract—In Australia, species densities of small (less than 250 grams) carnivorous marsupials are highest in the central arid zone, where up to nine species overlap, and lowest (zero to one species) in certain nonarid coastal and subcoastal areas. In the nonarid areas, the highest species densities (six) occur in structurally complex forests or layered woodland. It is suggested that, because most carnivorous marsupials are generalist predators of invertebrates, these latter habitats offer maximum opportunity for separation of foraging niches and hence for reduction of dietary overlap. In the arid zone, the highest species densities occur in hummock grass-desert complexes. Although some separation of foraging niches is apparent with species exploiting prey at different depths in soil cracks, weather and unpredictable shortfalls in the food supply may so reduce local populations that overlaps in foraging niche and diet are tolerated. Large carnivorous marsupials (more than 500 grams) are absent from the arid zone, perhaps due to the lack of shelter, the unpredictability of the food resource, or preemption of the carnivore niche by dingoes and goanna monitor lizards. Interspecific differences in body size probably enhance local community diversity by allowing species to partition prey by size. However, this may be less marked if species show strong sexual dimorphism in size and consequent expansion of niche width, because this precludes packing of additional species into the community. Competition is implicitly assumed to shape the structure and species composition of many carnivorous marsupial communities. This assumption was confirmed in one community by experimentally manipulating the population densities and resource use of the member species.

Carnivorous marsupials occur in a wide range of habitats throughout continental Australia and Tasmania, and number at least 50 species. Most, belonging to the family Dasyuridae, are active generalist predators of arthropods, worms, and small vertebrates, and range in size from two grams (*Ningaui timealeyi*) to five to six kilograms (*Dasyurus maculatus*). However, the largest extant dasyurid, the Tasmanian devil, *Sarcophilus harrisii* (eight kilograms), is exceptional in feeding principally on carrion, whereas the smaller (450 grams) numbat, *Myrmecobius fasciatus* (family Myrmecobiidae), is a specialized termite eater.

Communities of carnivorous marsupials usually comprise only two to four species, but more diverse assemblages of five to six species are not unknown (Calaby, 1966). In some of these communities, body-size ratios (Fox, 1982a) and patterns of resource partitioning (Dickman *et al.*, 1983) suggest that interspecific competition plays a role in shaping community structure; in others, harsh weather or unpredictable fluctuations in the food supply (Morton, 1982) may be more important. In the present paper, I will first describe broad geographical patterns in marsupial carnivore diversity throughout Australia, and describe some factors that appear, *a priori*, to influence community membership. I will then review experimental studies

that test hypotheses about community structure (all concern interspecific competition), and suggest directions for further research.

Geographical Patterns in Marsupial Carnivore Diversity

In an attempt to identify broad regional patterns in community diversity, I compiled maps of species densities by overlaying transparencies of the distributions of individual species. If small (less than 250 grams) carnivorous marsupials are considered, species densities are generally highest in arid central Australia (six to nine species overlap), and lower around the periphery of the continent (Fig. 1a). In contrast to North American mammals (Simpson, 1964) and to all species of small mammals inhabiting heath and forest areas in eastern Australia (Fox, 1985), there is a further trend towards faunal impoverishment at lower latitudes, which reaches an extreme in two areas of northern Australia where no marsupial carnivores have been recorded (Fig. 1a). Extant large carnivorous marsupials (more than 500 grams) number only five species, but again show a trend towards increasing species density in southerly latitudes. In contrast to their smaller relatives, however, all species occur in the forested coastal regions of mainland Australia and in Tasmania (Fig. 1b).

In temperate eastern parts of Australia, a major predictor of small mammal diversity is the structural diversity of the vegetation (Fox, 1985), whereas in tropical Australia precipitation, evapotranspiration, soil fertility, and an index of plant growth are important predictors of small mammal diversity in different habitats (Braithwaite *et al.*, 1985). Precipitation also appears to be an important determinant of the regional and local species diversity of North American shrews (G. L. Kirkland, personal communication), and of rodent species diversity in Israel (Abramsky and Rosenzweig, 1984). To investigate the relationship of small carnivorous marsupial diversity to precipitation, I correlated species densities with median annual rainfall at intervals of 100 kilometers along random transects from Alice Springs in central Australia to the edge of the arid zone. No consistent relationship was evident. Only three out of 25 correlation coefficients were statistically significant; two were positive ($r = +0.71$ and $+0.68$), the other negative ($r = -0.80$).

In contrast, comparison of the species density maps with a generalized vegetation map (Fig. 1c) suggests that there is some correspondence of species number with habitat. Thus, more species co-occur in forest, layered woodland, and hummock grass-desert complex than in woodland, savanna, and mallee habitats. Several explanations may account for these findings.

First, consider species densities in the nonarid regions of Australia (see Fig. 1a for definition of arid and nonarid areas). All species are partly or wholly nocturnal, and all appear to be opportunistic in their diet (Strahan, 1983). The highest densities (six) are reached in southern coastal forests, whereas the lowest densities (none to one) occur in low-latitude woodlands. The southern forests are characterized by tall *Eucalyptus* species with a
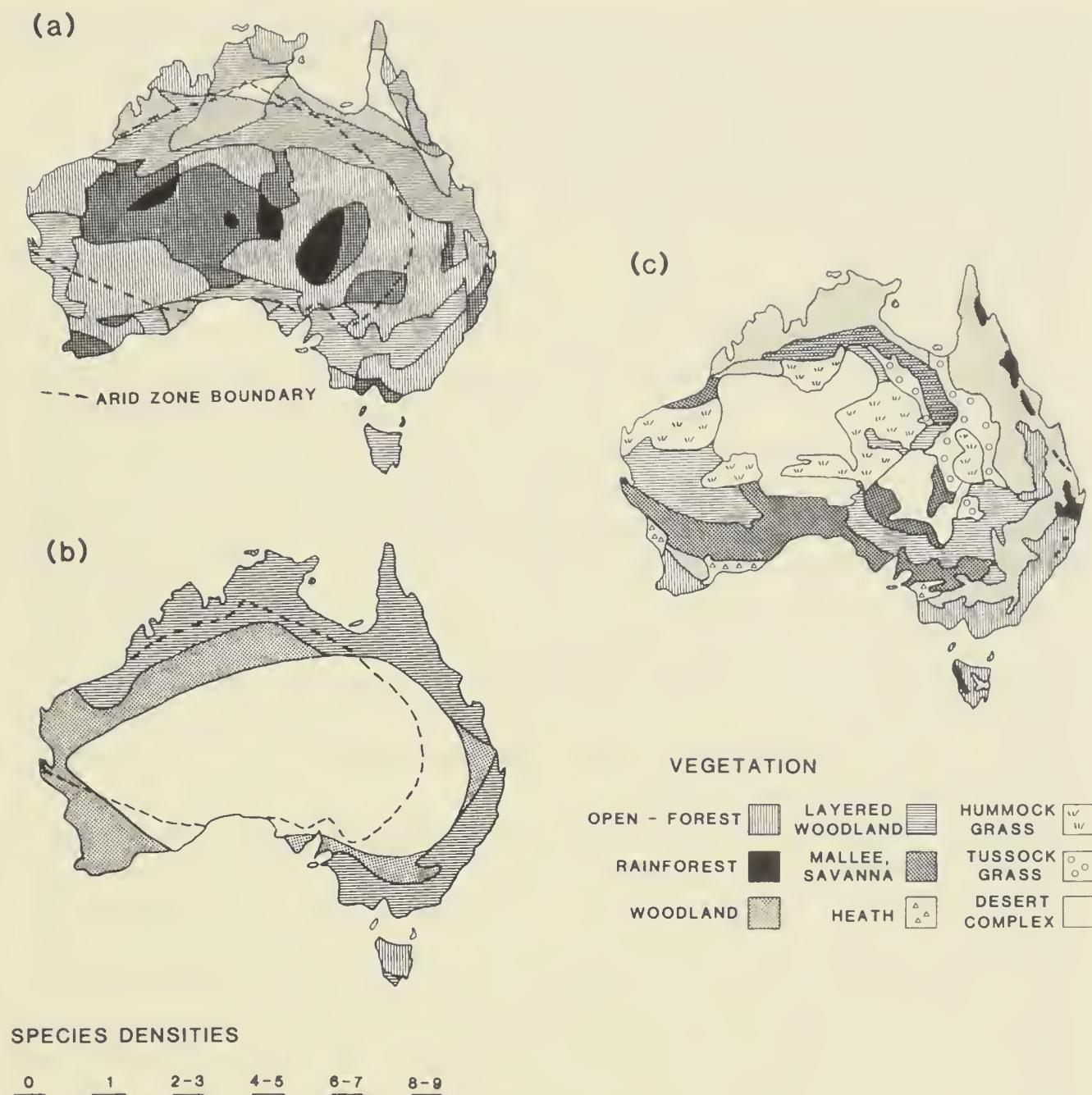
Fig. 1.—Species densities of Australian carnivorous marsupials. (a) species less than 250 grams, (b) species more than 500 grams, and (c) generalized vegetation map (after Moore, 1970). Species density maps were compiled using the pre-European settlement distributions of individual species (Strahan, 1983), including the probably extinct Thylacine *Thylacinus cynocephalus*, but also include the ranges of more recently described species (McKenzie and Archer, 1982; Kitchener *et al.*, 1983, 1984; Van Dyck, 1986). The extent of the arid zone follows Morton (1982) and is shown by a broken line in (a).

complex shrub layer, relatively dense ground level vegetation, and deep leaf litter. The structural diversity of these forests in turn provides a variety of feeding niches that reduce dietary overlap among coexisting species. Although two such niches have been described—for small scansorial dasyurids and for larger soil-fossicking species (Braithwaite *et al.*, 1978)— further specialization might be envisaged for smaller species that forage under tree bark or at different depths in the litter and soil. The northern woodlands, in contrast, are simple in structure and subjected to relatively frequent fires (Kershaw, 1985). Trees are sparse, the understory is dominated

by low, scattered shrubs or grass, and the litter layer is often thin (Specht, 1970). These habitats probably provide little opportunity for separation of foraging niches and hence for reduction in dietary overlap.

Opportunity for separation of foraging niches may increase not only with structural habitat complexity, but also with increased complexity of the abiotic environment. For example, in two northern areas where woodland is interspersed with outcrops of rock (Arnhem Land, Northern Territory and the Kimberley Range, Western Australia), rock-dwelling species (respectively, *Parantechinus bilarni* and the Ninbing *Antechinus*) occur alongside woodland inhabitats and increase the regional species density to five (Fig. 1a). The importance of rocks in maintaining separation of foraging niches has been shown for two further species, *Antechinus stuartii* and *A. swainsonii*, which occur together in the highlands of southeastern Australia (Dickman *et al.*, 1983). At altitudes below 1600 meters both species coexist: the larger species, *A. swainsonii* (approximately 60 grams), forages largely on the forest floor, whereas the smaller *A. stuartii* (approximately 20 grams) forages partly in the trees. Above 1600 meters, the winter snow limits above-ground foraging and usually only the larger species persists. However, *A. stuartii* may still occur in isolated rock tors at altitudes up to 2000 meters, where it has exclusive foraging access to moths (*Agrotis infusa*) in cracks in the rocks (Dickman *et al.*, 1983).

Species densities of small carnivorous marsupials are higher in the arid zone than anywhere else in Australia (Fig. 1a; Morton, 1982), yet the species are still generalist carnivores (Strahan, 1983) and the opportunity there for separation of foraging niches appears, at first sight, to be limited. However, in a study of three sympatric arid zone dasyurids, Read (1984, 1987) noted that the two smallest species (*Planigale gilesi* and *P. tenuirostris*) could exploit prey at different depths in soil cracks that were unavailable to the larger species (*Sminthopsis crassicaudata*), and suggested that this difference facilitated niche separation. Moss (1985) confirmed that captive planigales forage in soil cracks, and showed further than the activity of the two species on the soil surface is inhibited by the presence of *S. crassicaudata*. Other evidence suggests that foraging-niche separation may be less important for species coexistence in the arid zone than in more temperate parts of Australia. The population densities of most arid zone species are usually low (less than one per hectare) and individuals usually occupy continuously shifting home ranges (Morton, 1978; Read, 1984). Droughts, floods, and unpredictable shortfalls in the food supply occur frequently and further reduce and rarify local populations (Denny, 1975; Morton, 1982). These factors would minimize the frequency of encounter, and hence interference competition between individuals of different species (Dickman and Woodside, 1983), and thus allow all animals to occupy the same broad foraging niches.

The absence of large carnivorous marsupials from the arid zone (Fig. 1b) is perhaps due to their inability to use available shelter (for example, soil

cracks—Denny, 1975) and hence reduce the effects of climatic extremes, or to the spatial and temporal unpredictability of invertebrate food (Morton, 1982). The large carnivore niche in arid Australia has perhaps also been preempted by organisms such as goannas, which are physiologically tolerant of temporary food shortages. However, it is also possible that large carnivorous marsupials were replaced by the arrival of dingoes 10,000-4000 years ago (Archer, 1974).

Local Patterns in Community Structure

Usually, regional levels of species diversity (as shown by species density maps) exceed local community diversity because they simplify patterns of spatial (habitat or microhabitat) separation or temporal succession (Fox, 1982b) among the community members. However, local community membership still may depend on separation of foraging niches. Fox (1982a), for example, has noted that sympatric dasyurids differ markedly in body weights and head-body lengths, thus allowing them to partition prey by size. In sympatric *A. stuartii* and *A. swainsonii*, body size differences appear to be maintained in part by differences in when the two species breed (Dickman, 1982). Thus, in localities where the adult head-body lengths of the two species are convergent (by a ratio of less than 1.3), late mating by the smaller species results in an enhanced interspecific difference in size; conversely where the lengths of the two species are divergent (ratio more than 1.3), mating in both species occurs usually at about the same time. This "sympatry effect" accounts for 11.5 percent of the variation in time of mating of *A. stuartii* over its entire geographical range, and 34.5 percent of the variation in the highlands of southeastern Australia (Dickman, 1982, Dickman et al., 1983). Other significant factors are altitude and latitude. In localities where both the head-body lengths and mating times converge, foraging niche separation is reduced and both species become regionally allopatric (Dickman et al., 1983).

Although differences in body size between species may reduce dietary overlap, the differences between some sympatric species pairs exceed the minimum values predicted by the theory of limiting similarity (Fox, 1982a). These species usually have expanded niche widths due to strong sexual size dimorphism, and this precludes the packing of additional species into the community. Sexual dimorphism is considerably less marked in the arid zone than in the coastal and subcoastal forests, due probably to differences in the life history strategies of the species inhabiting these areas (Lee et al., 1982). The reduced dimorphism may, in turn, facilitate closer packing of species in the arid zone, and hence increase community diversity (Fig. 1a).

The Importance of Interspecific Competition

A major assumption underlying the above discussion of community diversity is that patterns of niche separation, especially in the nonarid zone,

are shaped by interspecific competition. But, evidence for competition has been adduced in few Australian studies (Dickman, 1984), and the general importance and prevalence of this phenomenon is currently disputed (for example, Schoener, 1983; Simberloff, 1984). Summarized below are the results of manipulation experiments (Dickman, 1986a) that provide the strongest evidence that competition does indeed occur in marsupial carnivore communities.

Initial competition experiments were designed to establish simply whether competition occurred between the two dasyurids, *A. stuartii* and *A. swainsonii*. Five naturally isolated study areas (four experimental, one control) were set up in tall, open forest near Canberra, Australian Capital Territory; each contained populations of the two species. Removal of the larger species, *A. swainsonii*, resulted in many shifts in the population parameters and resource use of the smaller *A. stuartii*. These included increased numbers, enhanced survival of newly weaned young, increase in movements, home range areas, home range overlaps, use of complex terrestrial habitat, the proportion of large, terrestrial invertebrate prey in the diet, and decreased arboreal activity (Dickman, 1986a). The reintroduction of *A. swainsonii* produced reciprocal shifts in most of these parameters. In contrast, the removal and reintroduction of *A. stuartii* had little evident effect on *A. swainsonii*. It was concluded that competition occurred between the two species, but that the effects of *A. swainsonii* on *A. stuartii* were more marked than the converse situation (Dickman, 1986a).

Subsequent manipulation experiments were designed to investigate the effects on *A. stuartii* of reducing and enhancing the numbers of *A. swainsonii*. When the numbers of *A. swainsonii* were reduced, the numbers of *A. stuartii* increased, and movements and arboreal activity decreased (Dickman, 1986b). Individuals also used more complex terrestrial habitat, and ate proportionately more terrestrial invertebrate prey. Increasing the number of *A. swainsonii* produced less marked, but reciprocal, responses in most of these parameters. It was concluded that the intensity of competition on *A. stuartii* depended, in part, on the relative abundance of *A. swainsonii* (Dickman, 1986b).

Throughout the manipulation experiments, samples of invertebrates were obtained in the study areas by pitfall trapping, litter sampling, and sticky trapping. These samples, totalling more than 120,000 specimens, showed that sessile invertebrates in the forest litter were abundant all year round, whereas freely-moving invertebrates captured in pitfall traps on the litter surface and tree trunks became relatively scarce in winter (Fig. 2). Because *A. swainsonii* forages principally in the litter, but *A. stuartii* takes freely-moving invertebrates, it appeared that the latter species could face a seasonal shortage of food. In accordance with the shifts in diet exhibited by *A. stuartii* when the numbers of *A. swainsonii* were manipulated, these findings strongly suggested that food was the object of competition.
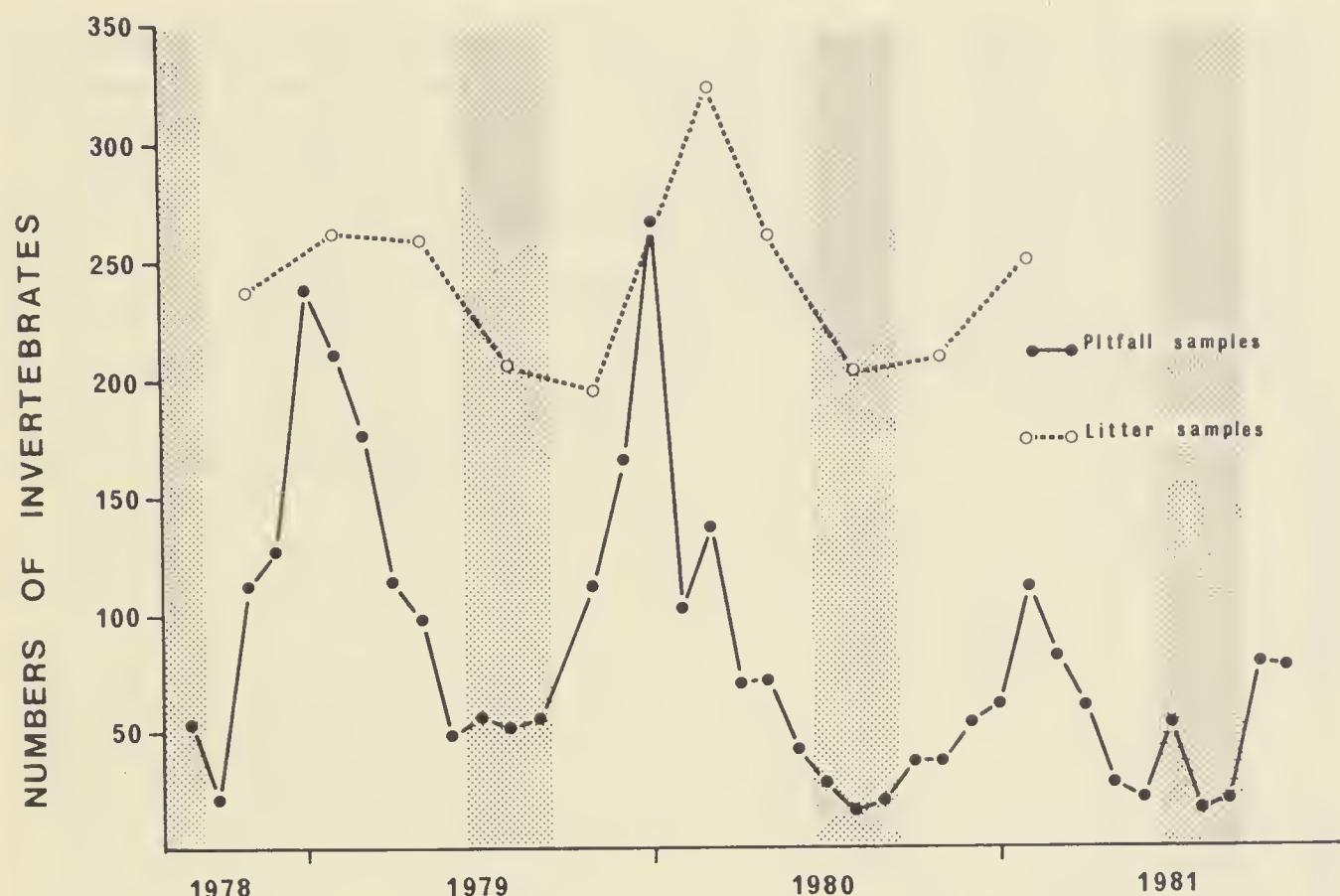
FIG. 2.—Numbers of invertebrates collected in pitfall traps and litter samples in forest near Canberra, Australian Capital Territory. Numbers are means for 20-25 samples (after Dickman, 1983); stippling indicates winter periods.

TABLE 1.—*Effects of supplementary feeding on the population parameters of* Antechinus stuartii. *(a) Percentage monthly survival, (b) mean distances moved between traps (meters), (c) mean body weights (g). After Dickman (1983).*

	Control study area	Experimental study areas	
	No food added throughout study	Food added January-May 1981	Food added January-November 1981
(a)			
Sept-Dec 1980	75.0	75.5	80.0
Jan-May 1981*	75.4	86.4	89.4
June-Nov 1981*	69.8	68.8	84.0
(b)			
Sept-Dec 1980	53.7	56.1	52.3
Jan-May 1981*	42.1	37.2	39.5
June-Nov 1981*	55.7	49.4	39.2
(c)			
Sept-Dec 1980	25.8	25.3	25.9
Jan-May 1981*	18.9	20.1	20.4
June-Nov 1981*	20.9	20.8	23.0

*Denotes periods when a statistically significant difference ($P < 0.05$) occurred between the food-supplemented and control populations.
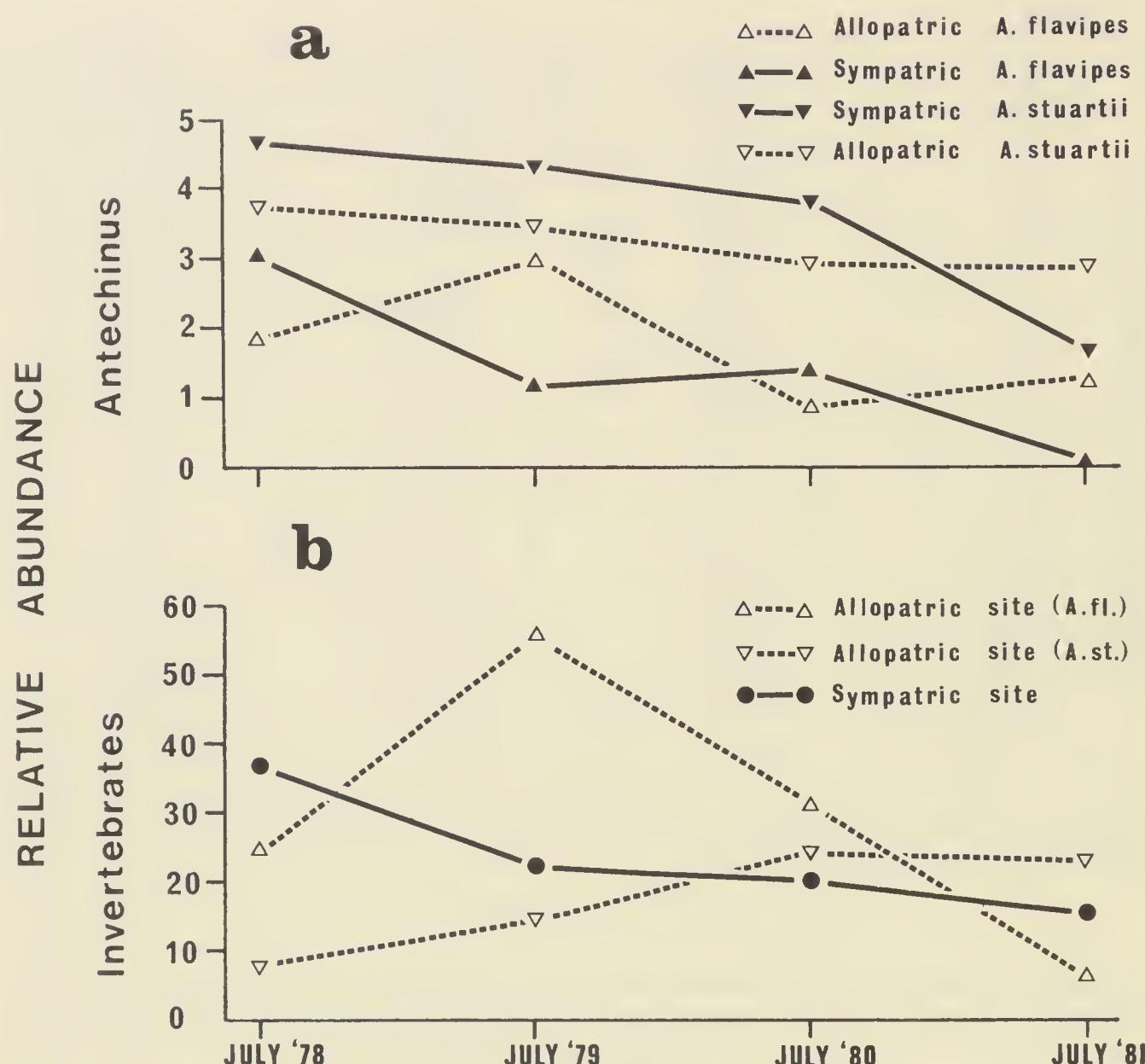
FIG. 3.—Relative abundances of *Antechinus flavipes* and *A. stuartii* and their invertebrate prey in three study areas. (a) *Antechinus* abundance expressed as captures per 100 trap nights, (b) invertebrate abundance expressed as mean numbers per pitfall trap. Study areas and methods of data collection are given in Dickman (1986c).

To test the food competition hypothesis, supplemental food was provided to two populations of *A. stuartii*, but not to a third, control population. The additional food resulted in increases in the survival and body weights of *A. stuartii*, but a decrease in its movements (Table 1). Reciprocal changes were observed in these parameters when supplementary feeding was discontinued in one of the study areas. The findings demonstrated that *A. stuartii* was food limited, and also that competition occurred for this scarce resource.

Food may be the limiting resource in other communities of small carnivorous marsupials. For example, in isolated and semi-isolated patches of open forest north of Canberra, *A. stuartii* occurs alone or in sympatry with a slightly larger congener, *A. flavipes* (approximately 35 grams). In allopatry, the two species take a similar range of prey, but in sympatry they

show marked partitioning of food and habitat: *A. stuartii* occupies structurally more complex habitat and takes more Isoptera than its larger congener, whereas *A. flavipes* forages mostly in rock outcrops and ingests more Araneidae, Blattodea, and larvae than the smaller species (Dickman, 1986c). However, even such partitioning may be possible only when food is relatively abundant. In the face of dwindling invertebrate abundance, particularly Araneidae, over four years due to drought, *A. flavipes* disappeared completely from the one forest patch where it occurred with *A. stuartii*, whereas allopatric populations of both species in nearby patches only declined in size (Fig. 3a, b).

These studies indicate that competition can influence strongly the distribution and abundance of populations, and hence that it may be important in shaping community structure and diversity. The demonstration, moreover, that food limits some carnivorous marsupials further clarifies the importance of foraging niche partitioning in maintaining diversity. Unfortunately, the possible influences of other factors, such as predation, parasitism, or even chance (are communities saturated?), remain unknown. Future studies, therefore, should attempt to carry out manipulation experiments in other, more diverse communities of carnivorous marsupials, and assess the importance of competition and other factors in both arid and temperate zone environments.

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MORPHOLOGICAL PATTERNS IN RODENT COMMUNITIES OF SOUTHWESTERN NORTH AMERICA

James S. Findley

Abstract.—Morphological distance matrices for rodent species in 11 local faunas in New Mexico and Sonora were constructed. Then artificial rodent communities were assembled by drawing species from the regional pool at random, and morphological distance matrices were constructed for these random communities as well. A comparison of random with real communities, using data from which the effect of size had not been removed, revealed that intertaxon distances in the real communities are greater than expected by chance alone. Real rodent communities in the Southwest are not randomly structured morphologically. Possible implications of this finding are discussed.

In this paper, I attempt to answer the question: are morphological differences between syntopic species of rodents in southwestern North America greater than would be the case if the coexisting species were drawn randomly from the available regional pool?

This question is a philosophical descendant of the series of questions engendered by Hutchinson's (1959) seminal Santa Rosalia paper. However, this study differs from those of many of its predecessors in several ways. I am not seeking constant or minimal size-ratios, and indeed am concerned with size only as it may emerge in a multivariate analysis of rodent morphology. Where ecomorphologists often study morphological traits that are believed to have ecological relevance, I have selected a series of measurements that commonly are used in mammalian systematics and for which the ecological importance is mostly undemonstrated. Many studies in the Santa Rosalia tradition have focused on species that are ecologically close, congeners or members of the same feeding guild. I have compared all rodents with a few exceptions noted later. In this way, I hope to avoid biasing my results with guesses about ecology or functional significance of morphology. Although many ecomorphological studies have drawn their data from the literature, I have used only data from specimens collected by myself or by my associates at the Museum of Southwestern Biology, University of New Mexico.

The above question is obviously asked in the context of a resource-limited, competition-based equilibrial view of animal communities. The expectation of that community view is that coexisting species will develop differences sufficient to reduce competition, and hence will differ more from one another that would randomly compared pairs of species that have not been in ecological contact. However, my purpose is only to find out if the morphological pattern in rodent communities is random or not. I do not intend to test any particular paradigm of community organization.

TABLE 1.—*Sites in southwestern North America at which rodent communities were studied.*

Station	Habitat	Species
1. Chaco Canyon National Monument, New Mexico	Shrub grassland, scattered piñon and juniper	12
2. Mesa west of Albuquerque, New Mexico	Shrub grassland	10
3. Jemez Mountains, New Mexico	Spruce-fir forest	6
4. West foothills, Sandia Mountains, New Mexico	Rocky chaparral, oaks, beargrass	5
5. Sandia Mountains, New Mexico	Spruce-fir forest	6
6. Carrizozo Lava Field, New Mexico	Lava field with juniper-zone vegetation	4
7. White Sands National Monument, New Mexico	Sandy desert grassland	11
8. Upper Animas Valley, Hidalgo Co., New Mexico	Grassland	8
9. Crest of Peloncillo Mountains, Hidalgo, Co., New Mexico	Piñon-juniper-oak, grassland	10
10. Puerto Penasco area, Sonora	Sonoran desert	9
11. San Carlos Bay area, Sonora	Sonora desert	8

Many ecomorphological studies have been found to be deficient in various ways. Good reviews are those of Simberloff and Boecklen (1981) and Wiens (1982). Some studies seem to have demonstrated nonrandom structure (for example, Gatz, 1979; Bowers and Brown, 1982) and others have not (Wiens and Rotenberry, 1980; James and Boecklen, 1984). Differing results may be attributable to different methodologies or to the fact that some organisms exist in structured communities, whereas others do not. Of 31 studies reviewed by Simberloff and Boecklen (1981), seven dealt with mammals (four with bats, three with rodents). Thirty-one data sets were included in these seven studies. Of those, six showed significantly constant ratios and minimum ratios larger than expected by chance according to the tests applied by Simberloff and Boecklen. Bowers and Brown (1982) compared size ratios of coexisting granivorous desert rodents against the null expectation that coexistence of two species was unrelated to the size ratio obtained between them, and were able to reject the null model. These authors confined their attention to the granivore guild, eliminated rare species, with some exceptions, and used weight, as an indication of size. Of course Hutchinson (1959) considered weasels (*Mustela*), voles and mice (*Apodemus, Microtus, Clethrionomys*), and shrews in his original consideration of size ratios, but most ecomorphologic work has been done with birds and other organisms, not mammals.

METHODS AND MATERIALS

Communities.—I selected for study 11 sites in New Mexico and Sonora at which personnel from the Museum of Southwestern Biology have collected intensively over a period of years. Each site comprises an area of reasonably

TABLE 2.—*Species taken at the 11 stations listed in Table 1.*

Onychomys leucogaster	*M. mexicanus*	*Baiomys taylori*
O. torridus	*M. montanus*	*Zapus princeps*
O. arenicola	*Clethrionomys gapperi*	*Perognathus flavus*
Reithrodontomys megalotis	*Geomys bursarius*	*P. penicillatus*
R. fulvescens	*Thomomys talpoides*	*P. intermedius*
Sigmodon hispidus	*T. bottae*	*P. baileyi*
S. ochrognathus	*Peromyscus nasutus*	*P. flavescens*
Neotoma albigula	*P. boylii*	*Dipodomys deserti*
N. cinerea	*P. crinitus*	*D. spectabilis*
N. mexicana	*P. eremicus*	*D. ordii*
N. stephensi	*P. leucopus*	*D. merriami*
N. devia	*P. maniculatus*	
Microtus longicaudus	*P. truei*	

uniform habitat. The areas of the sites vary somewhat, but most are of a size that would be covered by a trapper working on foot out of a base camp. A species is considered to be a part of the local fauna if one or more specimens from that site is preserved in the Museum. Species that I suspect occur at the site but have never been captured there are not included. All rodents recorded at each site, exclusive of members of the families Sciuridae (squirrels) and Castoridae (beavers) make up the total pool of species, 37 in all, which I analyzed morphologically. A description of the sites is contained in Table 1, and depicted in Figure 1, whereas the rodent species included are shown in Table 2. The faunal compositions of the sites were all about equally distinctive.

Measurements.—Ten measurements, as described in Figure 2, were taken of 10 of each of the species listed in Table 2. Mammalogists will recognize most of these except for moment arm of the temporal muscle. The specimens measured were adult animals, half males, half females, captured at one or more of the study sites.

Transformations and analyses.—Measurements were transformed to base 10 logarithms, which have the advantage of normalizing the distribution of measurements, equalizing variances, and preventing dominance of the analysis by large structures at the expense of small ones. The latter problem is an especially serious result of using untransformed measurements.

Using the mean of each measurement for each species, so that each species was represented by 10 measurements that were the means of the 10 log transformed measurements taken from the 10 specimens of that species, I constructed a 37 by 37 symmetric taxonomic distance matrix (Sneath and Sokal, 1973). The distances, which are the elements of this matrix, are the intertaxon Euclidean distances between each pair of species divided by 10, the number of traits measured. Intertaxon distances calculated in this way are greatly influenced by the size of the species being compared. Species of markedly different sizes usually are separated by large distances. Such distances also contain information about shape differences, but because the
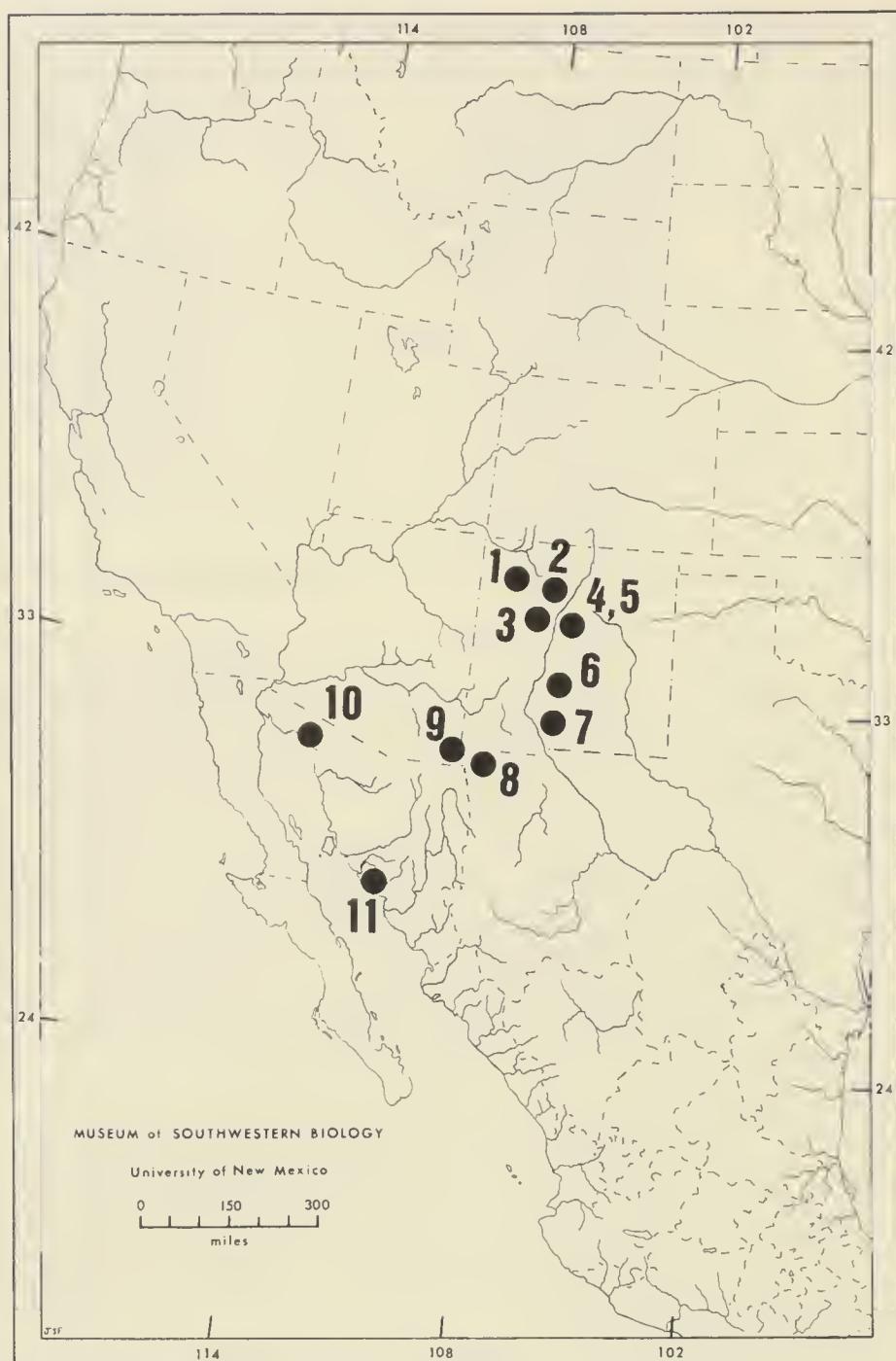
FIG. 1.—Map showing the 11 sites described in Table 1.

difference between, for example, a pocket mouse and a woodrat is overwhelmingly dominated by the size differences between the two, the shape component is not readily apparent. There are several ways of comparing shape, and minimizing the role of size in a comparison. I selected the SIZEOUT procedure (Rohlf *et al.*, 1974). This procedure involves conducting a principal component analysis of the data. Then the effect of the first component, which is generally regarded as a size component, is removed, and distances are recalculated using the remaining significant components (Lemen, 1983). I performed the principal component analysis using a covariance matrix rather than the more conventional correlation matrix, as recommended by Ricklefs and Travis (1980). Species projected on these components are arranged as they are in the original morphological space.
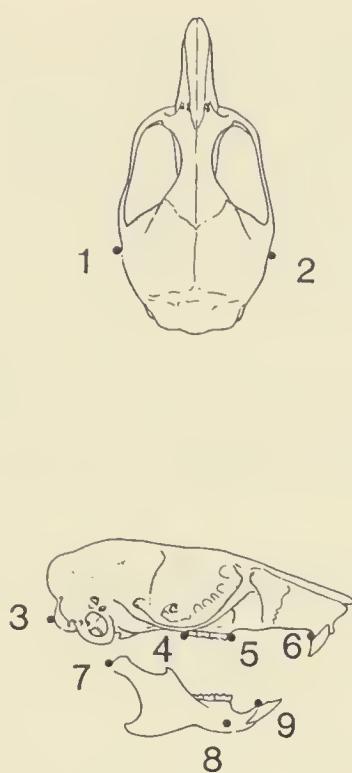
1. condylobasilar length (3-6)

2. diastema (5-6)

3. cheek tooth row (4-5)

4. cranial breadth (1-2)

5. dentary length (7-9)

6. masseteric moment arm (7-8)

7. head and body length

8. tail

9. hind foot

10. ear

Fig. 2.—Description of 10 measurements taken on each specimen.

For each of the 11 communities all the pairwise distances between the species comprising that community were assembled. The sets of distances for each community cannot be analyzed with parametric techniques because the values are neither independent nor normally distributed. I used the median of each distribution as a measure of central tendency. To find the median, all the pairwise distance values for a community were arranged in order from smallest to largest. Counting from the smallest upward, the median is that value below which and above which are found an equal number of values in an assemblage of an odd number of values. In an even-numbered assemblage, the median is a number half-way between the highest value of the lower one-half of the values and the lowest value of the higher one-half of the values.

To generate random communities, I drew species at random from the regional faunal list of 37, and assembled 30 communities of 10 species each and 30 of five each. A given species could not occur more than once in a community, but was not limited as to the number of communities in which it could occur. The real communities under study ranged in size from four to 12 species. Because random communities of increasing size converge in structure on the total pool of 37 species, I judged that construction of larger random communities was not necessary. I compared real and random communities in two ways: 1) the sets of medians of random and real communities were compared by means of the Mann-Whitney U-test, and 2) the entire set of distances from the 11 real communities were compared with the entire set of distances from the random communities and also with the set of distances between all members of the regional species pool by means of the Kolmogorov-Smirnov test.
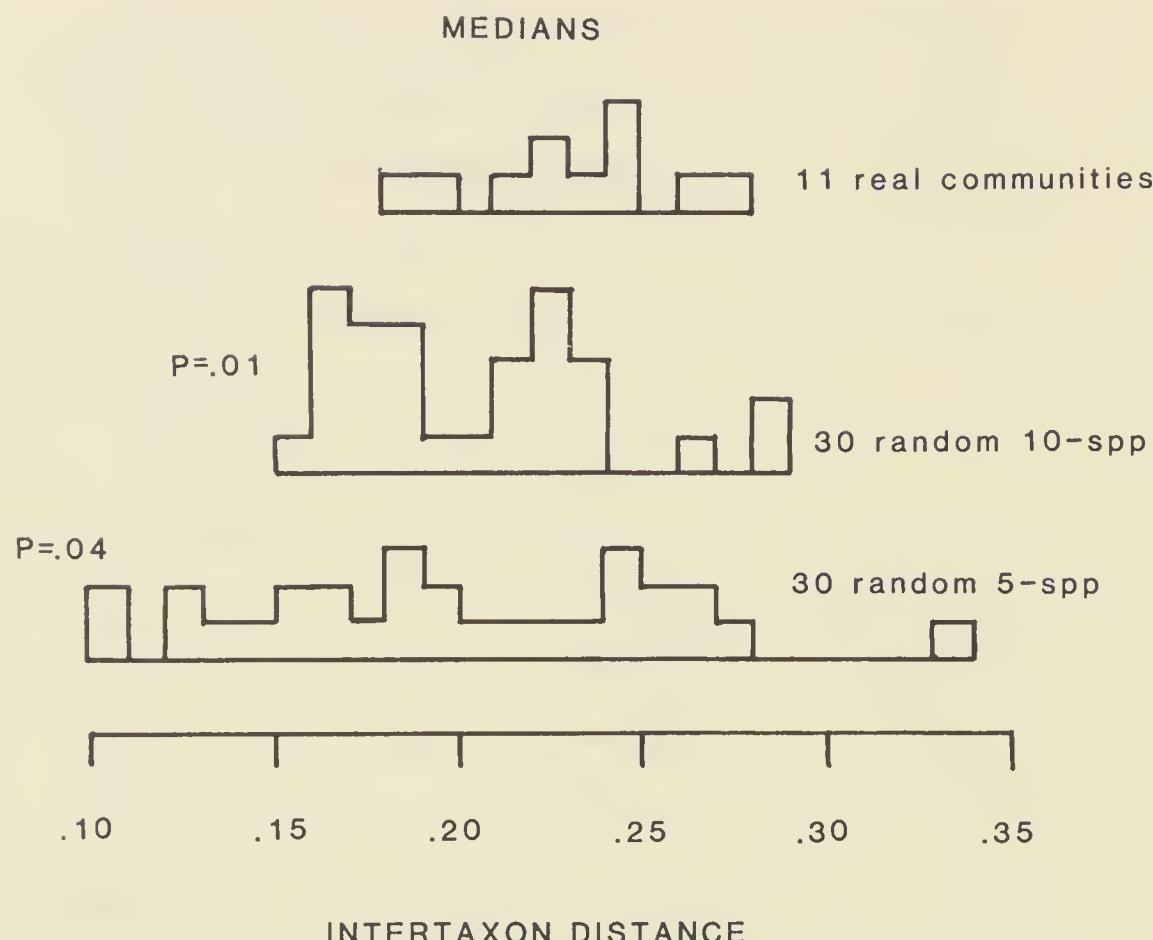
MEDIANS

FIG. 3.—Distribution of medians of intertaxon distances for 11 real communities compared with medians from 30 randomly generated five-species communities and 30 randomly generated 10-species communities.

The null hypothesis to be tested is: intertaxon morphological distances between syntopic species in real communities are not significantly different from distances between species in randomly assembled communities. The alternative hypothesis is that the two sets of distances do differ significantly.

RESULTS

Comparisons of medians of size-included distances.—Distribution of medians of distances from 11 real communities are compared with medians from random five- and 10-species communities in Figure 3. The real communities have significantly larger medians than either set of random communities.

Comparisons of medians of sizeout distances.—These medians are compared in Figure 4. Here, real communities do not differ significantly from those that are random.

Comparisons of all real size-included distances with all random distances.—As in the comparison of the medians, real distances are significantly greater than random distances and at higher levels of significance (Fig. 5).

Comparisons of all real sizeout distances with all random sizeout distances.—Here the difference between real communities and simulated 10-

MEDIANS

11 real communities

30 random 10-spp

p = .06

30 random 5-spp

p = .30

.05   .10   .15   .20

INTERTAXON DISTANCE—SIZEOUT
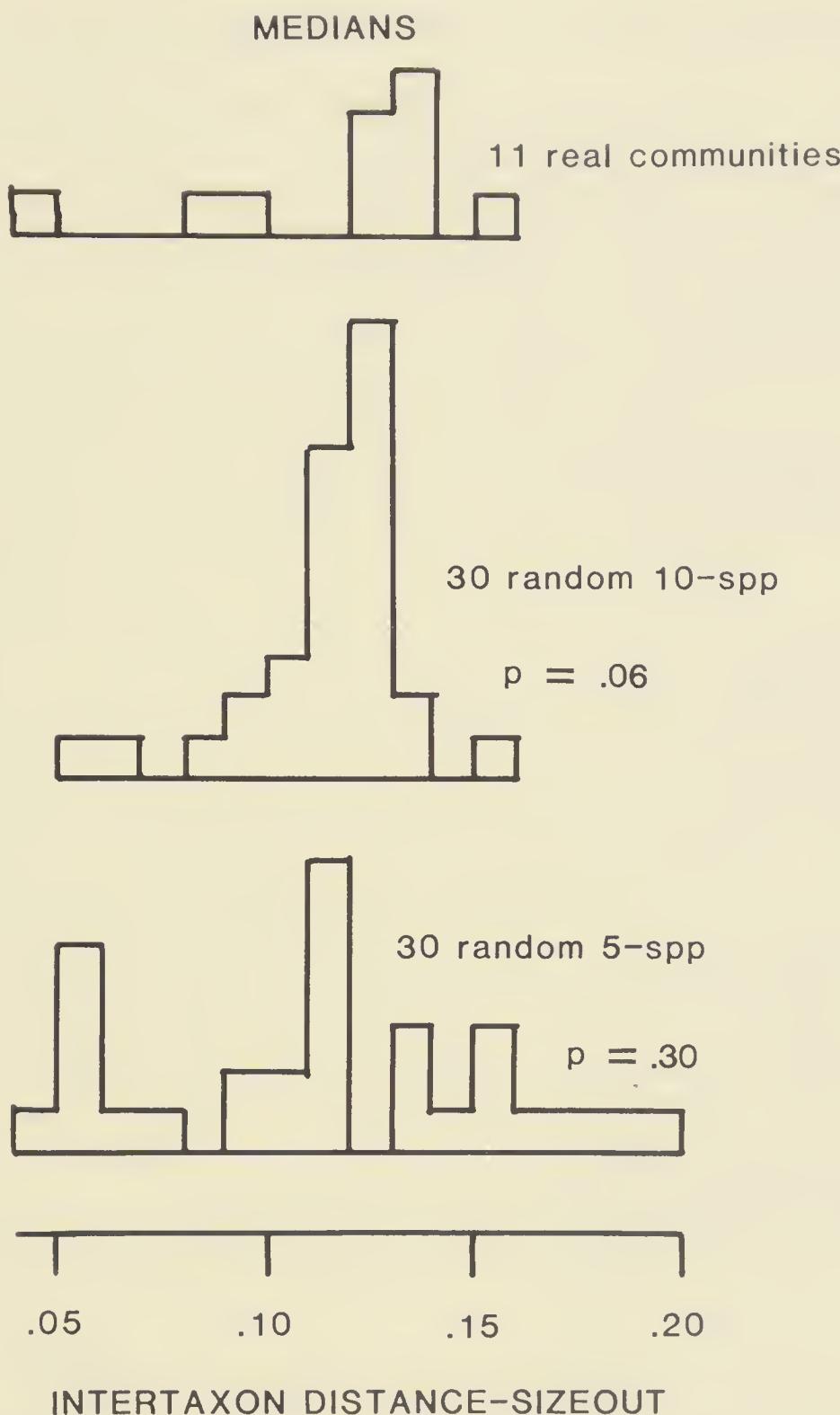
FIG. 4.—Comparisons as in Figure 3, except that size has been removed from the data before distances were calculated.

species communities reaches significance. However, the real communities are not significantly different in any of the other comparisons (Fig. 6).

For the comparisons of random and real communities in which size was included, the null hypothesis is decisively refuted. Species in real communities differ from one another more than expected. For the sizeout comparisons the results are less clearcut. For one comparison, all real with all random distances from 10-species communities, real differences are greater than expected. Species in real communities are clearly arranged in a
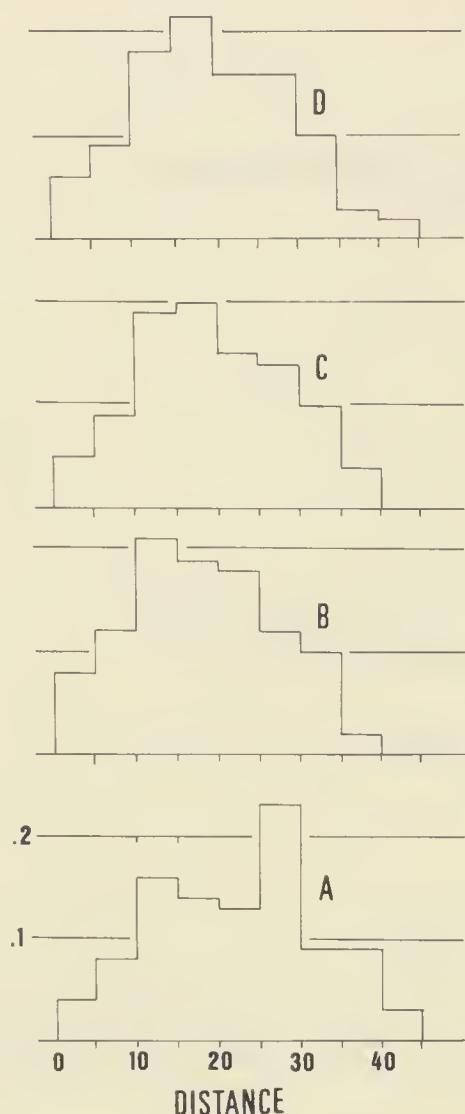
FIG. 5.—Comparisons of frequencies of all intertaxon distances from (A) 11 real communities (n = 349), with (B) all distances from 30 random five-species communities (n = 300), (C) all distances from 30 random 10-species communities (n = 1350), and (D) all distances between the 37 species in the regional pool (n = 666). On the basis of a Kolmogorov-Smirnov test the real communities differ from all the rest at the .001 level.
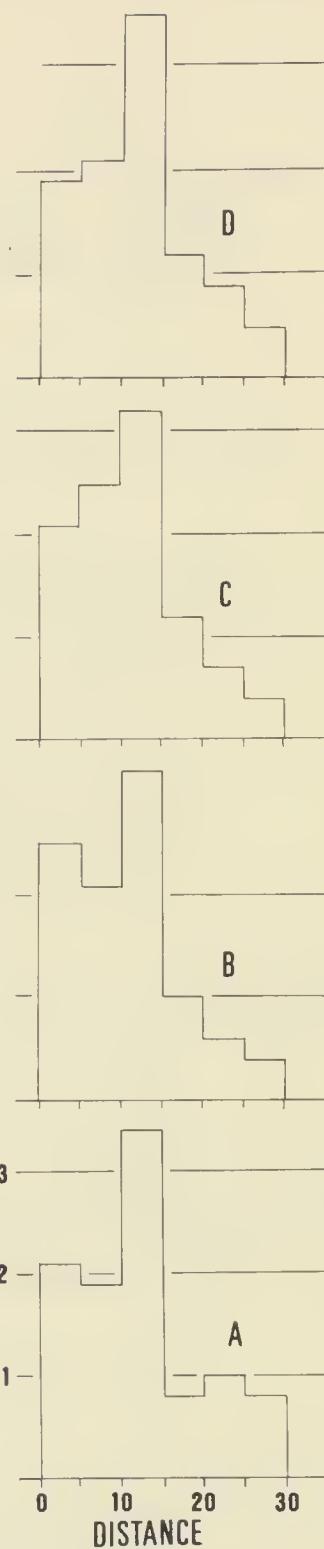
FIG. 6.—Comparisons as in Figure 5, except that size has been removed. A differs from B at the .05 level, but is not significantly different from any other set of values.

nonrandom way morphologically, but the overriding trait may be size rather than shape.

DISCUSSION

It seems clear that these Southwestern rodent communities are not assembled at random, that morphological differences between coexisting

kinds are greater than expected, at least in the space defined by 10 log transformed measurements.

Seemingly shape differences in real communities are no greater than expected by chance. This may really be the case. Size may be the morphological variable of overriding importance in structuring small mammal communities, and shape differences may be a consequence of zoogeographic access or other historical factors rather than of community processes. On the other hand the methods that I have used may not deal adequately with shape differences. It is unlikely that the shape differences between the similarly-sized *Neotoma albigula* and *Dipodomy spectabilis* have nothing to do with their ability to coexist. Methods of dealing with shape that are currently in use (Lemen, 1983; James and Boecklen, 1984) all leave something to be desired, and I hope to address this problem in ongoing studies.

In considering the meaning of these results, one must immediately be suspicious that they follow from some inevitable consequence of the methodology rather than from ecological processes. Williams (1964) and Simberloff (1970) have shown that the ratio of species to genera in assemblages drops with community size, even when the communities are randomly assembled from the regional species pool. Smaller communities have fewer species per genus as a result of this relationship, not because competition makes it difficult for congeners to coexist as Elton (1946) asserted. Because fewer congeners coexist in small communities, a result should be greater distances between species in smaller than in larger communities. I tested for this possibility in my data, first by calculating the correlation coefficient between community size and median intertaxon distance. The coefficient is −.1274, and is not significant. In my data, differences do not decrease significantly with increasing community size. Secondly, I compared the medians of the random five-species communities with those of the random 10-species communities for both the full and the reduced distance matrices. In no case was the difference significant at the .05 level. Ten-species communities are not marked by smaller differences; indeed, to the extent that there is any difference, the opposite is true. The species-to-genus ratio problem is not responsible for the results reported here.

Bowers and Brown (1982) reported nonrandom structure in the seed-eating rodent guild in the Southwest, but this pattern disappeared when members of other guilds were included. Here the nonrandom pattern is well-marked even though all rodent guilds were included. My methods differ in that a suite of measurements was used, I did not delete rare species, and I considered the degree to which each species pair was similar, rather than casting all relationships into two categories (separated by a size ratio greater or less than 1.5) as did Bowers and Brown. Perhaps the pattern detected by them did indeed persist beyond the seed-eating guild, but their methods of assessing resemblance were too coarse to detect it.

If the nonrandom pattern is not artifactual, it may, of course, result from biotic interactions, or from one-on-one responses to resources that are arranged in a nonrandom way. A caveat expressed by many who have commented on ecomorphological results is that evidence for close correspondence between morphological traits and ecological functioning is usually sketchy and uncompelling. At least for mammals, this situation is no longer completely true. Findley and Black (1983) demonstrated some close relationships between external morphology and feeding in an assemblage of East African insectivorous bats. Smartt (1978) showed correspondence between morphology and feeding in several syntopic species of *Peromyscus* in New Mexico. Lemen (1980) found a strong correlation between brain size and climbing ability both between and within some *Peromyscus* species. Finally Smartt and Lemen (1980) showed that intraspecific morphological variation within populations of several species of *Peromyscus* was closely predictive of stomach contents and of foraging site of the individuals involved. For small mammals, then, there is at least some concrete basis for suspecting that details of morphology track ecological functioning.

Not all ecomorphologic studies have revealed nonrandom patterns. For example, although Gatz (1979) detected nonrandom structure in stream fish communities, Findley and Findley (1985) found no relation between coexistence and morphology in butterfly fishes in coral reef habitats. Karr and James (1975) revealed ecomorphological correspondences in diverse bird communities, whereas Wiens and Rotenberry (1980) failed to find the patterns predicted by community theory in sage-steppe birds, and James and Boecklen (1984) concluded that the birds in the community they studied were responding to resources independently of one another.

Perhaps small mammals, like resident tropical birds and stream fishes, but unlike migratory birds and oceanic reef fishes (which have pelagic larvae), have accommodated to each other in ecological and morphological ways such that the structure of their communities is recognizably nonrandom.

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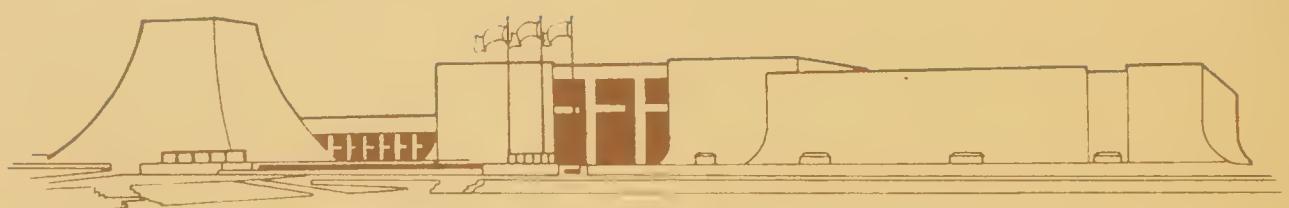
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Patricia G. Dolan