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# Ecology and Evolution of Communities

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*The Belknap Press of Harvard University  
Press*

Cambridge, Massachusetts, and London,  
England

1975

AN 20 071

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Library of Congress Catalog Card Number 74-27749  
ISBN 0-674-22444-2  
Printed in the United States of America

## 12 Niche Relations of Desert Lizards

Lizards have proven to be especially suitable subjects for investigation of competition, community structure, and species diversity. Data on diets, microhabitats, reproductive tactics, and times of activity are readily obtained. Since much of the empirical base of modern ecology comes from data on birds, it may be judicious to examine other nonavian taxa. In many ways, lizards may be closer to a modal animal than birds; they are terrestrial, poikilothermic ("cold-blooded"), and generally lack parental care (Schoener, 1975). Moreover, most lizards are primary and/or secondary carnivores, relatively high in the trophic structure of a community, and should therefore often encounter relatively keen competition. Finally, lizards span a wide range of the *r-K*-selection continuum, which may make them particularly suitable for testing many current theoretical developments in population biology (Pianka, 1972).

### Study Systems and Methods

I have devoted much of the past decade to studying lizard faunas on some 30-odd desert study areas at similar latitudes on three continents (Pianka, 1967, 1969a, 1971, 1973). These sites vary widely in total number of lizard species. For example, 14 areas in western North America (Great Basin, Mojave, and Sonoran des-

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erts) support from 4 to 11 species, another 10 study areas in the Kalahari Desert of southern Africa support from 11 to 18 species of lizards, and 8 sites in the Great Victoria Desert of Western Australia support from 18 to 40 sympatric lizard species. In terms of the numbers of species they support, or species densities, the lizard communities of the Australian deserts are probably the richest on earth. I designed my research to elucidate the factors determining species diversity.

My assistants and I walked slowly through these desert habitats making observations on their saurofaunas. We spent more than 40 months in the field, observing lizards over their entire annual period of activity. Microhabitat and time of activity were recorded for the majority of undisturbed lizards encountered active above ground at their own volition. Most lizards were collected, and their stomach contents and reproductive condition analyzed.<sup>1</sup> These data were also augmented with both museum specimens and data from the literature. For this paper, I use 15 basic microhabitat categories: subterranean; sunny places in the open, in grass, in bushes, in trees, in other sunny loca-

<sup>1</sup>Resulting collections of some 5,000 North American lizards, over 6,000 Kalahari animals, and nearly 4,000 Australian ones, representing some 90-odd species, are now lodged with the Los Angeles County Museum of Natural History.

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tions; shaded places in the open, in grass, in bushes, in trees, in other shaded locations; and four additional categories that describe whether lizards are found perched high or low in sun or in shade. Low perches are those within 30 centimeters of the ground, high perches are all those higher than this. Lizards at the interface of two or more microhabitats were assigned partial representation in each. Using just these 15 very crude categories allows separation of many species: for example, some lizard species frequent the open spaces between plants, whereas others tend to stay much closer to cover. Because time of activity shifts seasonally with changes in ambient temperature, all times of activity are expressed either as time since sunrise or time since sunset. I use 14 hourly categories for diurnal species here (limitations on human endurance dictated only 8 categories for nocturnal species). Any bias introduced through the shorter night-time sampling period is similar on different areas and among the three continental desert-lizard systems. In the following analysis, I use 20 very crude prey categories: spiders, scorpions, solpugids, centipedes, ants, wasps and other hymenopterans, grasshoppers and crickets, roaches (blattids), mantids and phasmids, ant lions, beetles, termites, bugs (Homoptera-Hemiptera), flies (Diptera), pupae, insect eggs, all insect larvae, miscellaneous insects not listed above including unidentified ones, all vertebrate material including sloughed skins, and plant materials (floral and vegetative). The proportional volumetric representation of each food category is used

in the following analysis. Even these very crude categories allow reasonably good separation of many lizard species by foods they eat. When prey items are analyzed by either numbers or size, separation is much less than when these 20 taxonomic volumetric categories are used.

This body of data from three basically rather similar, but independently evolved, subsets of natural communities allows detailed analysis of the niche relations and community structure of entire lizard faunas, including estimation of species diversities, diversities of resources actually exploited by entire lizard faunas, and both niche breadths and overlaps in saurofaunas that vary widely in species diversities and diversities.

Species densities and diversities of the lizard faunas on 28 study sites are listed in Table 1. Lizard species diversities were calculated from the relative abundances of various species in the above-mentioned collections. These estimates are biased to the extent that different species may not have been collected in proportion to their true relative abundances; however, they are the best available estimates. In any case, lizard species diversity is very strongly correlated with the estimated number of lizard species ( $r = 0.84$ ,  $P < 0.001$ ).

### Composition of Lizard Communities

Some major aspects of the niche relations and organization of lizard communities within each of the continental desert-lizard systems are summarized according to 5 niche categories in Table 2 and shown

Table 1. Desert lizard faunas at 28 study sites on three continents

Study site	(1) Estimated total number of lizard species	(2) Estimated lizard-species diversity	(3) Annual precipitation		(4) Average overlap			(5) (6) (7) Average overall overlap		(10) Multiplicative Summation (All) (Nonzero) (All)
			Long-term mean	Standard deviation	Food	Place	Time	(8)	(9)	
North America	4	1.4	18.4	5.6	0.49	0.80	0.58	0.20	0.20	0.63
	5	2.3	14.0	5.5	.75	.78	.53	.33	.36	.69
	5	1.8	9.6	4.4	.52	.92	.49	.25	.36	.64
	6	2.9	11.6	6.6	.55	.55	.47	.22	.37	.52
	6	1.9	18.7	10.5	.34	.55	.40	.12	.27	.43
	7	2.3	9.3	5.9	.39	.42	.31	.11	.39	.37
	8	2.1	12.7	9.2	.56	.31	.32	.10	.24	.40
	9	2.7	9.4	6.1	.28	.52	.58	.11	.23	.46
	9	2.8	19.2	8.0	.38	.32	.39	.06	.18	.36
	10	2.7	20.9	7.6	.37	.33	.50	.08	.25	.40
Mean	6.9	2.3	14.4	6.9	.46	.55	.46	.16	.29	.49
Kalahari	11	2.6	22.7	11.3	.92	.35	.28	.18	.41	.52
	13	5.3	21.7	10.3	.36	.39	.30	.08	.26	.35
	13	6.2	22.7	11.3	.56	.47	.34	.13	.36	.46
	14	7.3	16.3	—	.56	.21	.15	.04	.27	.31
	15	7.7	14.5	8.6	.45	.23	.21	.04	.22	.30
	15	8.1	19.0	—	.56	.25	.24	.06	.23	.35
	16	7.0	16.7	7.8	.72	.22	.23	.09	.35	.39
	16	7.3	19.0	9.7	.44	.22	.24	.05	.22	.30
	16	8.3	28.6	9.3	.71	.28	.26	.11	.36	.42
	18	8.2	15.2	7.2	.51	.26	.27	.07	.24	.35
Mean	14.7	6.8	19.6	9.4	.58	.29	.25	.08	.29	.37
Australia	18	8.3	16.0	—	.23	.16	.18	.01	.14	.19
	20	8.5	15.2	—	.18	.36	.13	.01	.02	.22
	28	6.3	21.5	13.4	.25	.32	.16	.03	.21	.24
	30	7.3	23.5	14.0	.23	.24	.19	.02	.19	.22
	31	7.0	15.2	—	.19	.28	.18	.02	.16	.22
	30	10.5	21.3	10.0	.37	.24	.27	.03	.18	.28
	29	9.7	21.9	9.3	.27	.30	.27	.04	.23	.28
	40	11.8	20.2	13.1	.23	.25	.22	.02	.15	.24
Mean	28.3	8.7	19.4	12.0	.24	.27	.20	.02	.16	.24

Lizard species diversity is given in column 1 simply as the total number of species, and in column 2 as the number of species weighted by relative abundances by use of Simpson's Index  $\Sigma 1/p_i^2$ , where  $p_i$  is the proportion of the total number of individuals in species  $i$  and the summation is over all  $i$  species. Columns 3 and 4 are the mean and standard deviation (in centimeters) of annual rainfall, respectively (moisture availability is critical in these deserts). Three components of niche overlap are given separately in columns 5-7 (see text for formula), and the components are combined in three different ways in the last three columns: by multiplying all three together (column 8), by multiplying just the non-zero components together (column 9), and by averaging the three components (column 10). The values in the last 6 columns are community averages of all possible combinations of species pairs.

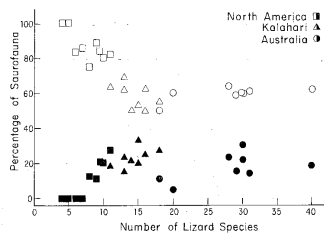
diagrammatically in Figure 1. Even these extremely crude categories reflect some of the differences between continents in the importance of various components of their lizard faunas. For example, fossorial (subterranean) lizards and arboreal nocturnal species are entirely absent from North American communities, but contribute an average of three to four species per area in the two deserts of the southern hemisphere. Moreover, although the average number of species of diurnal terrestrial lizards does not differ greatly in North America and the Kalahari (5.4 and 6.3 species, respectively), there are considerably more diurnal terrestrial species in Australia (14.4 species). However, when expressed as a percentage of the entire saurofauna, diurnal terrestrial species actually constitute a smaller fraction of the

total saurofauna in the two deserts of the southern hemisphere. The percentage contribution of all diurnal species, both arboreal and terrestrial, to the total fauna decreases with lizard species density (Figure 1). The increased relative importance of nocturnality in the Kalahari and the Australian deserts probably stems largely from historical factors (see below), although my interpretation remains speculative. Among all arboreal lizards (nocturnal plus diurnal species), both the numbers of species and the percentage contribution to the total saurofauna tend to increase with lizard species density (Figure 1 and Table 2); however, even within the diverse Australian desert system, arboreal species are less well represented on areas with low diversity (Figure 1), which are structurally simple.

Table 2. Intercontinental comparisons of desert saurofaunas by niche categories

Niche category	North America			Kalahari			Australia		
	$\bar{X}$	(range)	%	$\bar{X}$	(range)	%	$\bar{X}$	(range)	%
Diurnal	6.3	(4-9)	86	8.2	(7-10)	56	17.0	(9-25)	60
Terrestrial	5.4	(4-7)	74	6.3	(5.5-7.5)	43	14.4	(9-21.5)	51
Arboreal	0.9	(0-3)	12	1.9	(1.5-2.5)	13	2.6	(0-5.5)	9
Nocturnal	1.0	(0-2)	14	5.1	(4-6)	35	10.2	(8-13)	36
Terrestrial	1.0	(0-2)	14	3.5	(3-5)	24	7.6	(6-9)	27
Arboreal	0	—	0	1.6	(0.5-2.5)	11	2.6	(1-4)	9
Fossorial	0	—	0	1.4	(1-2)	10	1.1	(1-2)	4
All terrestrial	6.4	(4-8)	88	9.8	(9-11)	67	22.0	(15-30.5)	78
All arboreal	0.9	(0-3)	12	3.5	(2-5)	24	5.2	(1-9)	18
Totals	7.4	(4-11)	100	14.7	(11-18)	101	28.3	(18-40)	100

Lizard species fall into five crude categories in their foraging activities: diurnal and terrestrial, diurnal and arboreal, nocturnal and terrestrial, nocturnal and arboreal, and below ground (fossorial). The table gives the average number  $\bar{X}$  and range of numbers of lizard species, and the percentage of the total saurofauna, in each category on each continent. Semiarboreal species are assigned half to arboreal and half to terrestrial categories. Notice that the proportion of species in each category differs among continents; that North America is poorest in all five categories; and that Australia is richest in all categories except for fossorial lizards, which reach slightly higher species densities in the Kalahari Desert.



**Figure 1** Percentages of diurnal (open symbols) and arboreal (solid symbols) lizard species plotted against the number of lizard species coexisting on various study areas in the three continental desert-lizard systems. Note changes in the proportions of diurnal and arboreal species with different numbers of lizard species.

Lizards are predominantly insectivorous. Most are rather opportunistic feeders and consume a wide variety of arthropods with little evident preference. However, differences in foraging technique and time and place of activity often result in exposure to different spectra of prey types. Some lizard species have evolved pronounced dietary restrictions; for example, *Phrynosoma* and *Moloch* are ant specialists in North America and Australia, respectively. Both the Kalahari and the Australian deserts support termite-specialized species; these include *Typhlosaurus*, *Rhynchoedura*, and certain species of *Diplodactylus* (Huey et al., 1974; Pianka and Pianka, 1976). The North American genus *Dipsosaurus* is almost entirely herbivorous, whereas *Crotaphytus* is a secondary carnivore, preying mostly on other lizards (*Varanus* in the Australian deserts also eat largely other lizards). Foods of all these dietary specialists are

at least temporarily very abundant, which makes specialization economically feasible (MacArthur and Pianka, 1966).

Temporal separation of activities may reduce competition between lizard species, provided that being active at different times leads to exploitation of different resources, such as basking sites or prey species. In addition to the conspicuous dichotomy of nocturnal versus diurnal lizards used in Table 2, a much more subtle temporal separation of daily and seasonal patterns of activity is widespread among lizards (Pianka, 1973; Schoener, 1974). In principle, niche separation resulting from temporal differences should be reflected in differential use of resources such as food and microhabitats; however, the crude prey and microhabitat categories employed here are most unlikely to subsume all such differences resulting from temporal separation of activity. Time of activity is therefore treated as a "resource" in the following analysis.

#### Ecological Equivalents

Animals that fill similar ecological niches in different, independently-evolved, faunas are termed ecological equivalents. Examples among birds are discussed elsewhere in this volume (Cody, Chapter 10; Karr and James, Chapter 11). Some such convergent evolutionary responses of lizards to the desert environment are evident among the three continents (Table 3). For example, as mentioned above, the North American and Australian deserts support a cryptically-colored, thornily-armed, ant-

**Table 3.** Some approximate ecological equivalents in the three continental desert-lizard systems.

North America	Kalahari	Australia
<i>Phrynosoma</i>	—	<i>Moloch</i>
<i>Callisaurus</i>	—	<i>Amphibolurus scutulatus</i>
<i>Dipsosaurus</i>	—	<i>Amphibolurus inermis</i>
<i>Crotaphytus</i>	—	<i>Varanus eremius</i>
—	<i>Typhlosaurus</i>	<i>Rhodona</i>
—	<i>Mabuya occidentalis</i>	<i>Ctenotus pantherinus</i>
—	<i>Mabuya variegata</i>	<i>Ablepharus butleri</i> , <i>Ctenotus piankai</i>
—	<i>Chondrodactylus</i>	<i>Nephruus</i>
—	<i>Colopus</i>	<i>Diplodactylus stenodactylus</i>
—	<i>Pachydactylus rugosus</i>	<i>Diplodactylus strophurus</i>
—	<i>Pachydactylus capensis</i>	<i>Heteronotia</i>
<i>Sceloporus</i>	<i>Agama</i>	<i>Amphibolurus barbatus</i>
<i>Cnemidophorus</i>	<i>Eremias lugubris</i> , <i>Nucras</i>	various <i>Ctenotus</i> spp.
<i>Uta</i>	<i>Eremias lineo-ocellata</i>	<i>Amphibolurus isolepis</i>

Species are aligned so that approximate ecological counterparts on different continents appear in the same row but in different columns. North America and Australia have four counterparts missing from the Kalahari. Seven niches are filled with roughly convergent species in Australia and the Kalahari, but only three have obvious counterparts on all three continents. See text for further details.

specialized species: *Phrynosoma* occupies this niche in the North American deserts (Pianka and Parker, 1975), and *Moloch* fills it in Australia (Pianka and Pianka, 1970). Similarly, each of these desert systems has a medium-sized lizard-eating lizard (*Crotaphytus wislizeni* in North America and *Varanus eremius* in Australia) and long-legged species that frequent the open spaces between plants (*Callisaurus* in North America, *Amphibolurus scutulatus*, *A. cristatus*, and *A. isolepis* in Australia). A number of species pairs in the Kalahari and Australia are also convergent: for example, the subterranean *Typhlosaurus* and *Rhodona* have somewhat similar ecologies, as do the agamids *Agama hispida* and *Amphibolurus barbatus* and several pairs of gecko species (*Chondrodactylus* and *Nephruus*, *Colopus*

*wahlbergi* and *Diplodactylus stenodactylus*, and *Pachydactylus capensis* and *Heteronotia binoei*). However, few convergences are apparent among all three desert systems (Table 3). Even the above-mentioned convergent pairs of species exhibit marked ecological differences when subjected to close scrutiny (e.g., Pianka and Pianka, 1970). Indeed, there is considerable disparity among the ecologies of most species in the three continental desert-lizard systems.

#### Environmental Variability

Water is a master limiting factor in deserts. A convenient result is that long-term mean annual precipitation provides a reasonably good estimate of average annual productivity. Furthermore, year-

to-year variation in annual precipitation should generate temporal variability in food availability, and standard deviation in annual precipitation should therefore reflect environmental variability. Brown (Chapter 13) uses the same climate index to predict the diversity of desert rodent species. Table 1 lists precipitation statistics and lizard species densities for the various study areas. Interestingly, the number of lizard species is positively correlated with both long-term mean precipitation and the standard deviation in annual precipitation ( $r = 0.42$ ,  $P < 0.05$  and  $r = 0.68$ ,  $P < 0.001$ , respectively). Long-term mean and standard deviation in precipitation are themselves strongly correlated ( $r = 0.70$ ,  $P < 0.001$ ). To attempt to separate variables, I computed partial correlation coefficients. When effects of long-term mean precipitation are held constant, the correlation between lizard species density and the standard deviation in precipitation remains significant ( $r = 0.54$ ,  $P < 0.01$ ). However, when standard deviation in precipitation is partialled out, the number of lizard species is no longer significantly correlated with long-term mean annual precipitation ( $r = 0.02$ ). This result suggests that productivity, per se, does not promote diversity, but rather that variability in productivity does. More productive areas might be expected to support a greater number of species; at first glance, it is more difficult to see how increased variability in itself might promote diversity. I reconsider this puzzling correlation later, after examining the niche relationships of the lizards.

### Historical Factors

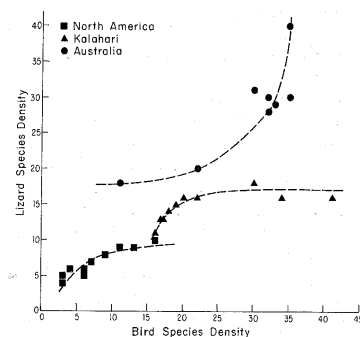
These lizard faunas have clearly been influenced profoundly by various historical factors, such as degree of isolation and available biotic stocks, particularly those of potential competitors and predators. One reason the Australian deserts support such very rich saurofaunas is that competition with, and perhaps predation pressures from, snakes, birds, and mammals are probably reduced on that continent. Climate doubtless shapes lizard faunas and regulates their species densities as well. Effects of other historical variables, such as the Pleistocene glaciations, on lizard communities are very difficult to evaluate, but could well be as considerable as they are in birds (as Cody, Chapter 10, and Diamond, Chapter 14, indicate; see also below).

An extremely powerful ecological technique is comparison of historically independent but otherwise basically comparable ecological systems. The degree of convergence between such independently-evolved systems reflects the extent to which evolutionary outcome is determined by the interaction between a given animal's body plan and a particular physical environment. Both Cody (Chapter 10) and Karr and James (Chapter 11) make use of the same type of comparisons. The degree to which evolutionary pathways are determinate is of considerable interest, since independent evolution of similar patterns strongly suggests common underlying selective forces. Moreover, such a convergence, if ob-

served, indicates that general theories explaining niche relations and community structure can eventually be formulated (Cody, 1973; Recher, 1970). In appropriately selected situations, such "natural experiments" may actually allow some measure of control over historical factors such as the Pleistocene glaciations. Thus, differences between faunas of independently evolved areas with similar climates and vegetation structures presumably reflect their different histories.

Historical events have shaped lizard faunas in other ways as well. Australian desert lizards have clearly usurped some of the ecological roles occupied by other taxa in the other two desert systems. Thus pygopodid and varanid lizards in Australia replace certain snakes and mammal carnivores (Pianka, 1969a). The mammalian fauna is conspicuously impoverished in Australia, and the snake fauna less so. Clearly such usurpation of the ecological roles of other taxa has expanded the diversity of resources and the overall niche space exploited by Australian desert lizards. However, these snake-like and mammal-like lizards contribute only a very minor amount to the increased lizard species density of Australia, ranging from one to four species on various study areas. Hence there are many more "lizard-like" lizards in Australia than in the other two continental systems. In addition to such conspicuous usurpation of ecological roles, more elusive but important competitive interactions with bird faunas doubtless occur. For example, proportionately more species of ground-

dwelling insectivorous birds exist in the Kalahari than in Australia, suggesting that competition between lizards and birds is keener in southern Africa (Pianka, 1971; Pianka and Huey, 1971). With increases in total community species density (birds plus lizards), the number of lizard species increases faster than bird species in Australia, whereas in North America and the Kalahari, bird species density increases faster than lizard species density (Figure 2). Reasons for this difference among the continental systems are elusive and interpretation must remain conjectural (Pianka, 1971, 1973). One relevant and salient fact is that there are very few migratory birds in Australia, whereas a



**Figure 2** Lizard species density plotted against bird species density for 28 desert study sites on three continents. The number of bird species increases faster than the number of lizard species in North America and in the Kalahari, whereas in Australia the species density of lizards increases faster than that of birds.

fair number of migrant bird species periodically exploit the North American and the Kalahari deserts. Clearly, competitive pressures from migrants must influence lizard faunas of the latter two desert systems in an adverse manner.

The most diverse, and perhaps the most interesting, lizard communities presently extant occur in deserts (a possible exception is the *Anolis* communities of the Caribbean islands). Indeed, lizards may actually capitalize on scant and variable amounts of primary production, and this could contribute to their relative success over birds in arid regions (Pianka, 1967).

Still other differences in the composition of lizard communities of these three continents presumably have a historical basis as well. Southern Africa is renowned for its diverse termite fauna, which in turn has probably facilitated evolution of termite-specialized subterranean lizards (Huey and Pianka, 1974; Huey et al., 1974). Similarly, the higher incidence of arboreal and nocturnal lizard species in the Kalahari and Australia, as compared with North America, is probably related to fundamental differences in the niches occupied by other members of these communities, such as arthropods, snakes, birds, and mammals. The high diversity of nocturnal lizards in the two southern-hemisphere deserts could be due to one or more of the following factors: (1) The effects of the Pleistocene glaciations are generally acknowledged to have been stronger in the northern hemisphere (cf. Cody's results in Chapter 10). This could have had its effect on the evolution of nocturnal lizards;

however, present-day climates in at least the southern parts of the northern hemisphere's deserts seem to be quite adequate for nocturnal lizards. Indeed, the eublepharine gecko *Coleonyx* has made a successful existence as a nocturnal terrestrial lizard in these deserts. The absence of an arboreal gecko from the flatland desert habitats of the Sonoran desert is puzzling, especially in view of the fact that rock-dwelling geckos (*Phyllodactylus*) are found within the system. Indeed, a successful climbing gekkonid could probably invade this desert system, given an opportunity (Pianka, 1973). (2) Of course, the various desert systems could differ in the diversity and abundance of available nocturnal resources, such as nocturnal insects. (3) The ecological role of arboreal nocturnal lizards could be filled in North America by other taxa, say spiders. Differences in the numbers and/or densities of insectivorous and carnivorous nocturnal snakes, birds, and mammals might also play a role.

#### Components of Species Diversity

Saturated communities can differ in species diversity in only three ways, which are not mutually exclusive (MacArthur, 1965, 1972). (1) The diversity of available resources determines the variety of opportunities for ecological diversification within a community. Communities with fewer different resources will support fewer species than those with a greater variety of resources, all else being equal. (This corresponds to a "smaller overall niche space" or "fewer niches.") (2) As the

diversity of utilization of resources by an average species increases, the number of species that can coexist within a community must decrease. (This corresponds to "larger niches.") (3) Two communities similar in both the above respects can still differ in species diversity if they differ in the average extent to which resources are shared, or the amount of niche overlap. A community with greater overlap will support more species than one with less overlap simply because more species use each resource. (This corresponds to "smaller exclusive niches.")

Briefly, diversity should increase with the range of available resources and the extent of tolerable niche overlap, but decrease as niche breadths of component species become larger.

MacArthur (1972) derived the following intriguingly simple approximate equation for the species diversity of a community:

$$D_s \cong \frac{D_R}{D_U} (1 + C\bar{\alpha}) \quad (1)$$

where  $D_s$  is the diversity of species,  $D_R$  is the diversity of resources used by the entire community,  $D_U$  represents the diversity of utilization (niche breadth) of each species,  $C$  measures the number of potential competitors or "neighbors in niche space" (a function that increases more or less geometrically with the number of subdivided niche dimensions), and  $\bar{\alpha}$  is the "mean competition coefficient" (I prefer to consider this the mean niche overlap). The relevance of this equation to species diversity of desert rodents is discussed by Brown in Chapter 13.

Although his derivation is essentially tautological and requires the perhaps unrealistic assumption that all niche breadths are equal (identical  $D_U$ 's for all species), MacArthur's community equation does focus attention on the importance of niche breadths and overlaps in considerations of species diversity. MacArthur (1972, p. 185) stated that "people have seldom even measured single components in these equations." It should prove profitable to estimate the various terms in eq. 1 for real communities. Here I present such estimates of  $D_s$ ,  $D_R$ ,  $D_U$ , and  $\alpha$  for the above-mentioned lizard communities, and I examine interrelationships among these components and with the above climatological estimates of productivity and climatic variability. While I use MacArthur's elegant equation as a launch, my results do not depend upon its validity (though they may serve to test it).

#### Niche Dimensions

Like most animals, desert lizards subdivide resources in three major ways; they differ in what they eat, where they forage, and when they are active. Ecological differences in each of these three niche "dimensions" should reduce competition and facilitate coexistence of a variety of species.

With most lizard species, it would be virtually impossible to evaluate the degree of interdependence of these three niche dimensions (trophic, spatial, and temporal); however, in some relatively sedentary fossorial skinks (genus *Typhlosaurus*),

we have attempted to assess the degree to which foods eaten depend upon microhabitat (Huey et al., 1974). These two niche dimensions appear to be largely independent in *Typhlosaurus*. Moreover, some diurnal and nocturnal species pairs consume many of the same prey types, sometimes the same prey species (though they are usually captured in different ways). Thus there appears to be a substantial degree of independence among the niche dimensions I have chosen to use here (see also Schoener, 1974, 1975). In still other cases, however, clear interactions among these three niche dimensions are apparent (Pianka, 1973). Because the vast majority of interspecific pairs of sympatric lizard species have substantial niche separation along one or more of these three dimensions, it is unnecessary to subdivide niche dimensions further.

#### Methods of Estimating Niche Parameters

Many different techniques of estimating niche breadths and niche overlaps have been suggested and used (Simpson, 1949; Horn, 1966; MacArthur and Levins, 1967; Levins, 1968; Schoener, 1968; Colwell and Futuyma, 1971; Pielou, 1972; Roughgarden, 1972; Vandermeer, 1972; Pianka, 1969b, 1970, 1973). Throughout this paper, I quantify diversity and niche breadth with the index proposed by Simpson (1949),  $1/\sum p_i^2$ , where  $p_i$  is the proportion of the  $i$ th species or resource category. Overlaps are computed with the following improved version of the equation proposed by MacArthur and Levins (1967) and Levins (1968) for estimating

"alpha" from field data:

$$a_{jk} = a_{kj} = \frac{\sum_i p_{ij} p_{ik}}{\sqrt{\sum_i p_{ij}^2 \sum_i p_{ik}^2}} \quad (2)$$

where  $p_{ij}$  and  $p_{ik}$  are the proportions of the  $i$ th resource used by the  $j$ th and the  $k$ th species, respectively. May (1975) recently gave mathematical rationale for the superiority of this symmetric measure over the original nonsymmetric form. I do not consider values obtained from eq. 2 "competition coefficients," but merely measures of niche overlap (for discussion of the distinction between overlap and competition, see Colwell and Futuyma, 1971 and/or Pianka, 1974a).

In the following analyses I quantify the trophic dimension, using the volumetric representation of prey in the 20 different food categories listed earlier. Similarly, the 15 basic microhabitats listed earlier are recognized for analysis of the spatial dimension of the niche. Time dimension computations are based on 22 hourly time categories, expressed in hours since sunrise or sunset to help to correct for seasonal shifts in the time of activity, as noted above. Each niche dimension is given equal weight by dividing computed diversities by the total number of possible categories, which allows all diversities to be expressed as a proportion of their maximal possible value.

Ideally, a multidimensional analysis of resource utilization and niche separation along more than a single niche dimension

should proceed by considering all resources present as a simultaneous function of all niche dimensions (May, 1975). However, in practice it is extremely difficult or even impossible to obtain such multidimensional utilization data, both because animals move and because they integrate over time. (Stomachs of most lizards contain prey captured in a variety of microhabitats.) To obtain true estimates of multidimensional utilization, one would have to follow an individual animal and record the exact time and place of capture of all prey items. Instead, I must work with three separate unidimensional utilization distributions, for reasons indicated above.

Provided that niche dimensions are truly independent (orthogonal), with any given prey item being equally likely to be captured at any time and in any place, overall multidimensional utilization is simply the product of the separate unidimensional  $p_i$ 's (May, 1975). In this case, estimates of various niche parameters along component dimensions can be multiplied to obtain multidimensional estimates. However, should niche dimensions be entirely dependent upon one another, resource utilization becomes additive, and the appropriate procedure is to sum or average the separate unidimensional estimates of various niche parameters. Since real niche dimensions are presumably seldom, if ever, either perfectly dependent or perfectly independent, neither technique is entirely satisfactory. Recognizing these very considerable difficulties, I estimate multidimensional niche parameters along the three niche dimensions, using both

multiplicative and summation multidimensional estimates for resource diversity, niche breadths, and niche overlaps. May (1975) shows that summation niche overlap actually constitutes an upper bound on true multidimensional overlap; moreover, he points out that multiplicative overall overlaps can both underestimate and overestimate the true multidimensional overlap.

#### Resource Diversity

There are many striking differences among the three continental desert-lizard systems in the relative importance of various resource categories. For example, termites comprise 41.3% of the diet of all Kalahari lizards, but represent only 16.5% and 15.9% of the saurian diet in North America and Australia, respectively. As a result, the diversity of foods eaten by Kalahari lizards tends to be lower than in the other two deserts. Ants increase in importance from North America to the Kalahari to Australia (9.7, 13.6, and 16.4%, respectively), whereas beetles decrease (18.5, 16.3, and 7.3%, respectively). Vertebrates, largely lizards, constitute 24.8% of the diet by volume of Australian desert lizards, but only 7.8% and 2.3% of the food eaten by lizards in North America and the Kalahari, respectively. Whereas 45.3% of all North American lizards were first sighted in the open sun, only about 19% of those in the two southern hemisphere deserts were in the open sun (open shade percentages are, respectively, 1.7, 11.4, and 17.4%). This heavy use of one microhabitat category in North



America results in low values for microhabitat diversity on that continent. The percentage of arboreal animals above the ground increases from 4.2% in North America to 14.9% in the Kalahari to 18.2% in Australia. Many other interesting differences in resource utilization patterns are also evident among the continents (Pianka, 1973).

Diversities of resources actually used along each niche dimension by all the lizards (of all species) in the saurofaunas on the various study sites are plotted against lizard species densities in Figure 3. The diversity of foods eaten by all lizards does not correlate with the number of lizard species when all 28 areas are considered, although the correlation between these two measures is statistically significant within the North American deserts ( $r = 0.77$ ,  $P < 0.01$ ). When all 28 areas are grouped, the diversity of microhabitats exploited by all lizards and the diversity of times of activity of all lizards are both strongly correlated positively with lizard species density (Figure 3). Trends within continental systems are usually less pronounced or nonexistent; lizard species density is significantly correlated with the diversity of microhabitats exploited in both North America ( $r = 0.64$ ,  $P < 0.05$ ) and the Kalahari ( $r = 0.79$ ,  $P < 0.01$ ). None of the correlations between resource diversity and lizard species density is significant for the Australian deserts. Multiplicative and summation estimates of the overall diversity of resources used by lizards are very strongly correlated with one another ( $r = 0.95$ ,  $P < 0.001$ ), and less strongly, but significantly, positively correlated with

lizard species density (Figure 3, lower right).

Thus the diversity of resources actually used by lizards, or the total volume of lizard niche space, tends to be greater in areas with more diverse saurofaunas (Figure 3). This result is not as circular as it might at first seem; the correlations often do not hold up within any single continental desert-lizard system, and thus high lizard diversity on any particular continent is not necessarily associated with high diversity of resource use there.

#### Niche Breadth

To maximize sample sizes and confidence in estimates of niche breadths, I group all individuals of each species from various study areas in the following analysis. (A few species exhibit distinct, usually relatively slight, niche shifts between study areas, but these constitute a definite minority.) Similar relative results are obtained in a more complex area-by-area analysis, except that niche breadths tend to be smaller and more variable, especially for uncommon species.

Niche breadths, standardized by dividing by the number of resource categories, were computed for 86 lizard species along with two estimates of overall niche breadth (summation and multiplicative). Niche breadths along particular dimensions and overall breadths vary considerably among species. Certain specialized species, described above, have very narrow niches along a particular niche dimension. Breadths along various dimensions appear to be independent (as judged by nonsignificant correlation coefficients

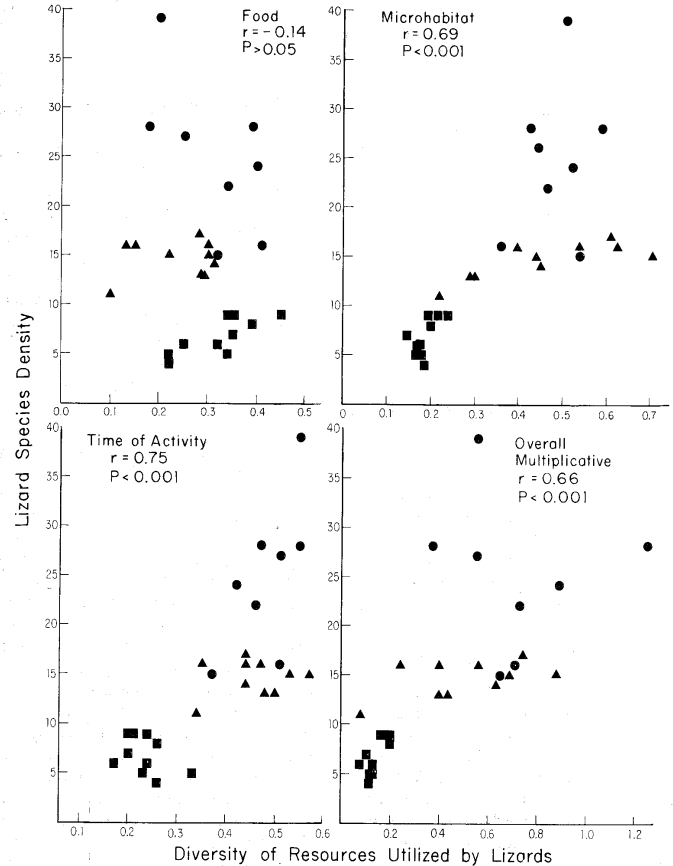


Figure 3 Four plots of the diversity of resources utilized by entire saurofaunas against their lizard species densities. Symbols coded by shape represent different continents, as in previous figures. Three niche dimensions (trophic, microhabitat, and time of activity) are shown, as well as their product, in-

tended to reflect the overall diversity of resources exploited along all three niche dimensions. Note that, except for the trophic dimension, diversity of resources used by lizards tends to increase with the number of species. See text.

between dimensions), except that the diversity of microhabitats used by various species is weakly but significantly correlated with the diversity of time of activity ( $r = 0.39$ ,  $P < 0.001$ ).

The average diversity of use of foods and microhabitats by the component species varies among continental systems. For example, the diversity of use of the trophic dimension by an average species is low in the Kalahari where many species consume a lot of termites, while the spatial niche dimension is narrow in North America where many animals are first sighted in the open sun. Average diversities of utilization of the three niche dimensions are less variable in Australia. Confidence limits on means within continental desert-lizard systems overlap broadly (Table 4), however, so that no statistically significant variation in niche breadth is evident among continents. Because summation and multiplicative overall niche breadths are quite strongly cor-

related ( $r = 0.88$ ,  $P < 0.001$ ), I use multiplicative values hereafter.

Species diversity should increase with the ratio of the diversity of utilized resources ( $D_R$  in eq. 1) over the diversity of utilization by an average species. I calculated average niche breadths for the species actually occurring together on each study area ( $\bar{D}_U$  for various subsets of species). Thus estimated, mean overall niche breadths within each continental system vary inversely with the number of lizard species, as might be expected, although these inverse relationships are not statistically significant. Somewhat surprisingly, however, when all 28 areas are grouped, the only evident relationship is a positive correlation of niche breadth with estimated lizard-species diversity ( $r = 0.57$ ,  $P < 0.01$ ). There is also a positive correlation between overall mean  $D_U$  and  $D_R$  ( $r = 0.52$ ,  $P < 0.05$ ), but this disappears when the effects of lizard species diversity are held constant by partial correlation.

Table 4. Average niche breadths of desert lizards on three continents

Niche dimension	North America	Kalahari	Australia
Trophic	0.232 (0.168–0.296)	0.198 (0.196–0.312)	0.214 (0.202–0.278)
Spatial	.146 (.108–.184)	.228 (.186–.270)	.201 (.177–.225)
Temporal	.241 (.167–.295)	.254 (.148–.258)	.240 (.180–.248)
Overall summation	.206 (.178–.234)	.237 (.205–.269)	.218 (.196–.240)
Overall multiplicative	.077 (.045–.109)	.138 (.078–.198)	.112 (.078–.146)

This table shows what proportion of the total range of a particular resource axis is used by the average lizard species in the three continental desert systems. The three main resource axes are food, space or microhabitat, and time of foraging activity. Each entry gives the mean and 95% confidence limits (in parentheses) of average niche breadth along the given axis on the given continents. Notice that lizards of all three continents have very similar temporal niche breadths, but that North American lizards have broader diets and narrower habitat ranges than lizards elsewhere. Kalahari lizards have the broadest habitat ranges and the narrowest diets, and Australian lizards are intermediate in both respects.

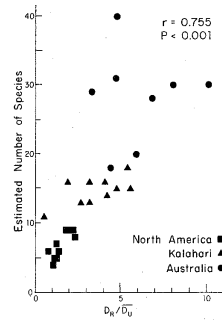


Figure 4. Ratios of the overall multiplicative diversity of resources used by all lizards  $D_R$  over the average niche breadth of the species on a given study area  $\bar{D}_U$  are plotted against the number of lizard species. This ratio reduces variance in lizard species density by some 58%.

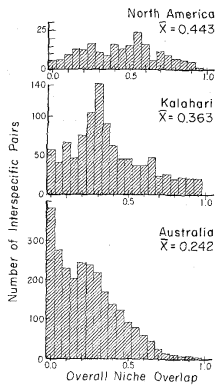
As expected, ratios of  $D_R/\bar{D}_U$  are strongly positively correlated both with lizard species densities (Figure 4) and with lizard diversity ( $r = 0.71$ ,  $P < 0.001$ ). Overall  $D_R$  values alone account for 49% of the variation in lizard species density ( $r^2 = 0.487$ ), whereas the ratio of overall  $D_R$  over mean overall niche breadth ( $D_R/\bar{D}_U$ ) reduces variance in species densities by some 58% ( $r = 0.76$ ,  $r^2 = 0.578$ ). When the effects of niche breadth are removed by partial correlation,  $r$  remains similar (0.73), demonstrating that niche breadth contributes little further to the latter correlation, given knowledge of  $D_R$ . Hence, variations in niche breadth appear to be of relatively minor importance in considerations of diversity in these lizard communities. Increased lizard-species densi-

ties do not stem from conspicuously reduced niche breadths, but rather are closely associated with larger overall niche space ( $D_R$ ).

#### Patterns of Niche Overlap

Species pairs with high overlap along one niche dimension often, though certainly by no means always, overlap little along another. Correlation coefficients of overlaps between dimensions are seldom significant, however. The average extent of overlap along the various dimensions varies among deserts (Table 1). For example, overlap in microhabitat is high in North America where many lizards frequent the open sun, whereas dietary overlap is extensive in the Kalahari where most lizards eat considerable numbers of termites. Overlap tends to be low along all three niche dimensions in Australia (Table 1).

May (1975) points out the great difficulties in obtaining reasonable estimates of overall multidimensional niche overlap from unidimensional patterns of utilization. In addition to average overlap values for each niche dimension on the various study areas, Table 1 lists the means of all multiplicative overlaps, average summation overlaps (upper bounds on the true multidimensional overlap; see also Figure 5) and means of all pairs of multiplicative (overall) overlap that are nonzero. The latter values might be expected to reflect maximal tolerable niche overlap. Fortunately, all these approaches to estimating multidimensional overlap and/or the upper limit on tolerable overlap yield the

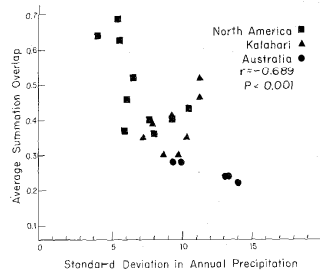


**Figure 5** Frequency distributions of observed overall summation niche overlaps for all interspecific pairs on all study areas within each of the three continental desert systems. These values overestimate true multidimensional niche overlap, but they do constitute upper bounds on the true values. Note that overlap tends to decrease from North America to the Kalahari to Australia. Compare with Figures 6, 7, and 8.

same basic result: namely, overall niche overlap generally *decreases* with increasing lizard species density.

Average overall summation overlaps are also inversely correlated with standard deviation in annual precipitation (Figure 6). However, mean overall summation overlap is even more strongly correlated (again, negatively) with the number of lizard species (Figure 7). When effects of lizard species density are held constant by partial correlation, mean overall summation overlap and the standard deviation in precipitation are no longer significantly

correlated ( $r = -0.28$ ).<sup>2</sup> However, the correlation between lizard species density and overall summation overlap remains significant when the standard deviation in precipitation is held constant by partial correlation ( $r = -0.56$ ,  $P < 0.01$ ). This result suggests that the extent of tolerable niche overlap is *not* a function of the degree of environmental variability, but rather that it is related to the number of competing species [MacArthur (1972) termed this "diffuse competition"]. Exactly comparable results are obtained with multiplicative overall overlap values. Elsewhere I have hypothesized that maximal tolerable niche overlap should vary

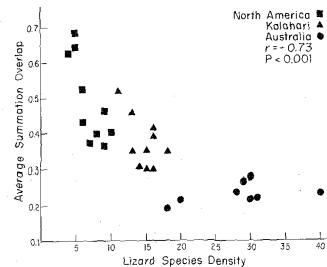


**Figure 6** Average overall summation niche overlap plotted against the standard deviation in annual precipitation for 23 study sites, with climatic data. Although none of the correlations within continental desert systems is significant, the correlation coefficient for all areas is highly significant statistically. When the number of lizard species on the various areas is held constant by partial correlation, however, this correlation disappears.

<sup>2</sup>Averages of the largest tenth of all multiplicative and summation overlaps also decrease significantly with lizard species density (Pianka, 1974b).

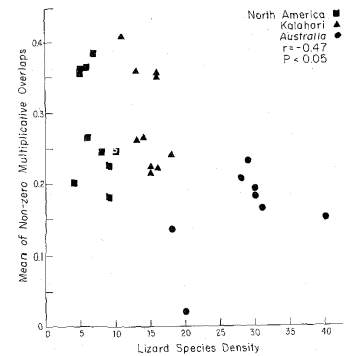
inversely with the intensity of competition (Pianka, 1972); these results support that prediction.

The vast majority of interspecific pairs overlap very little or not at all when overlaps along the three dimensions are multiplied (Pianka, 1973, 1974b). The possible number of such nonoverlapping pairs increases markedly with the size of overall niche space, provided that niche breadths remain relatively constant (demonstrated above). Overlaps between those pairs with some overlap and those with greatest overlap are of most interest, as they are likely to reflect limiting similarity and/or maximal tolerable overlap. Such estimates behave similarly to average summation overlaps, and tend to decrease with increasing lizard species densities (Figures 7 and 8).



**Figure 7** Average summation niche overlap plotted against the number of lizard species for the 28 study areas. The inverse correlation is highly significant ( $r = -0.73$ ,  $P < 0.001$ ). A similar inverse correlation exists between lizard species density and mean multiplicative overall overlap ( $r = -0.67$ ,  $P < 0.001$ ). Three estimates of maximal niche overlap are similarly correlated (see Figure 8).

May and MacArthur (1972) developed an elegant analytic model of niche overlap as a function of environmental variability. Their theory predicts a distinct upper limit on the permissible degree of overlap; moreover, the derivation suggests that maximal tolerable overlap should be relatively insensitive to environmental variability. Leigh (Chapter 2) provides an alternative pathway to this same result. Although the May-MacArthur niche-overlap model assumes a one-dimensional resource spectrum, May (1974) recently expanded the argument without qualitative change to a multidimensional niche space. At first glance, Figure 6 seems at odds with the May-MacArthur prediction



**Figure 8** Mean of all nonzero values of multiplicative overall overlaps plotted against lizard species densities. The averages of the largest tenths of all summation and multiplicative overall overlap values are even more strongly correlated with lizard species densities ( $r_s = -0.63$  and  $-0.62$ , respectively,  $P_s < 0.001$ ).

that maximal overlap should be insensitive to environmental variability. However, overlap values used here are not entirely appropriate for testing the May-MacArthur theory, since this model is expressed in terms of the ratio of niche separation over niche breadth, effectively the inverse of niche overlap scaled by niche breadth. To approximate more closely the conditions of their model, I therefore estimated niche separation as one minus overlap for all interspecific pairs and then expressed these values as ratios of separation over standardized niche breadths. Means and confidence limits of these values are given in Table

5; many distinct differences are apparent both among niche dimensions and among the three desert systems. For example, the ratio of overall niche separation over niche breadth is essentially unity in Australia, but it is significantly greater than one in the Kalahari and significantly lower than unity in North America (Table 5). Plausible explanations for these differences are elusive, but the high overlap in North America could be a result of that continent's relatively low degree of environmental variability and/or reduced intensity of diffuse competition due to lower lizard species densities. Such speculation would be more plausible if the mean for

Table 5. Niche overlap, breadth, and separation of desert lizards on three continents

Niche parameter and dimension	North America	Kalahari	Australia
Overlap/breadth			
(1) Food	2.09 (1.81-2.37)	4.79 (4.37-5.21)	2.18 (2.06-2.30)
(2) Microhabitat	2.51 (1.87-3.15)	1.30 (1.12-1.48)	1.92 (1.84-2.00)
(3) Time	2.33 (1.97-2.69)	1.64 (1.38-1.90)	1.79 (1.69-1.89)
Niche separation			
(4) Food	0.54 (0.48-0.60)	0.36 (0.34-0.38)	0.68 (0.66-0.70)
(5) Microhabitat	.66 (.58-.74)	.71 (.67-.75)	.69 (.67-.71)
(6) Time	.42 (.34-.50)	.65 (.61-.69)	.68 (.66-.70)
(7) Overall (summation)	1.62 (1.48-1.76)	1.72 (1.66-1.78)	2.05 (2.03-2.07)
Separation/breadth			
(8) Food	3.73 (2.87-4.59)	2.51 (2.21-2.81)	5.18 (5.0-5.36)
(9) Microhabitat	5.79 (4.83-6.74)	4.23 (3.85-4.61)	4.60 (4.48-4.72)
(10) Time	2.78 (2.0-3.56)	5.08 (4.48-5.68)	5.11 (4.93-5.29)
(11) Overall	0.50 (0.38-0.62)	1.54 (1.16-1.92)	1.03 (1.00-1.06)

Each entry gives the mean and 95% confidence limits (in parentheses) for the indicated ratio or parameter, over all study sites on each continent. A simple hypothesis would be that species diversity is directly proportional to niche overlap and inversely proportional to niche breadth, so that the overlap/breadth ratio should be positively correlated with species diversity. Comparison of the first three rows of the table shows this naive deduction to be quite wrong, for North American deserts have high overall values of this ratio but support lizard faunas of low species diversity. Niche separation is estimated as 1 minus niche overlap (rows 4-7). This yields values that are very similar among the three niche dimensions in Australia, with the richest fauna. But niche separation is lowest in North America, again the opposite of simple expectations. The ratio of niche separation over niche breadth is given for each continent in rows 8-10, and the overall value is expressed in the last row. As expected, the Kalahari, with fewer lizard species than Australia, has a higher ratio. Contrary to expectations, North America, with the fewest species, has the lowest ratio. No simple hypothesis explains these results, as discussed in the text.

the Kalahari was intermediate between those for North America and Australia.

If the number of neighbors in niche space ( $C$  in eq. 1) could somehow be estimated independently, MacArthur's equation would generate predicted species diversities that could be compared with observed diversities. Unfortunately, I have been unable to find a satisfactory way to estimate  $C$  independently of the remaining parameters of eq. 1. It does seem likely, however, that the number of neighbors in niche space should be least in North America and greatest in Australia.

In sum, species diversity in rich saurofaunas is *not* facilitated by increased niche overlap; rather, quite the reverse is true: overlap tends to decrease with increasing lizard species density. I interpret this pattern as indicating that competitor species density or diversity influences tolerable niche overlap; a greater number of competing species, or stronger "diffuse competition," demands greater average niche separation among coexisting species. Similarly, Diamond (1973) finds precise altitudinal replacement among competing species only in the most species-rich bird communities. High overlap with fewer competitors could be equivalent to lower overlap with more competitors, since in the former case the coefficients  $a_{ij}$  in the competition expression  $\sum a_{ij}X_j$  (cf. Levins, Chapter 1, eqs. 1-3) are larger and in the latter case the summation is over a larger number of competitors. If so, the actual intensity of interspecific competition per species, or the *total* of the interspecific inhibitory effects, could thus be similar in communities of widely divergent species densities. A first hypothesis might be that

total overlap among sympatric species remains constant; however, total overlap actually *increases* significantly with lizard species density, even though the average amount of overlap between pairs decreases (Pianka, 1974b). Indeed, it is intriguing to speculate that such adjustments of overlap with species density might actually result in a relatively constant level of interspecific competitive inhibition among a community's component species. If so, it is not overlap that remains constant, but rather the degree of competitive inhibition tolerated by the individuals comprising an average species.

#### Synthesis and Conclusions

Earlier I noted that lizard species density is positively correlated with standard deviation in annual precipitation, a measure of environmental variability. Hutchinson (1961) suggested that temporal heterogeneity might actually facilitate coexistence, both by continually altering the relative competitive abilities among members of a community, and by periodically reducing population sizes and thus the intensity of competition. Similar mechanisms might certainly be expected to operate in desert faunas. A difficulty with these interpretations, however, is that the above data on niche relationships make it difficult to avoid the conclusion that competition is in fact actually *keener* in the more diverse lizard communities. Clearly, future improvements in the theory of species diversity will have to include more sophisticated considerations of environmental variability, as Leigh, Chapter 2, shows; furthermore, overlap

will have to be treated as a variable that varies inversely with diversity.

The diversity of resources actually exploited by lizards along various niche dimensions, and the extent of niche overlap along them, varies widely among the three continental desert-lizard systems. As a result, the relative importance of various niche dimensions in separating niches differs among continents. Food is a major dimension separating niches of North American lizards, whereas in the Kalahari niche separation is slight on the trophic dimension and differences in microhabitat and time of activity are considerable. All three dimensions separate niches more or less equally in Australia. Differences in diversity among continents stem largely from differences in the overall diversities of resources exploited by lizards or in the size of the lizard niche space, but are not due to conspicuous adjustments in overall niche breadths. Overall overlap decreases, rather than increases, as lizard diversity increases, so that niche overlap does not enhance diversity, but rather contributes negatively to it. Two of the four parameters in eq. 1 vary consistently with differences in lizard species density:  $D_B$  positively and  $\bar{\alpha}$  inversely. The number of neighbors in niche space,  $C$ , probably influences maximal tolerable niche overlap and  $\bar{\alpha}$ . Mean niche breadth,  $\bar{D}_V$ , however, does not vary much and contributes little to observed differences in lizard diversity. This empirical finding could partially justify MacArthur's assumption that the  $D_V$ 's among members of a community are identical. Moreover, if this result is generally true, niche breadths may not play an important role in future diversity

studies or theoretical developments. Since overlap varies inversely with lizard species density, whereas the number of competitors (or diffuse competition) varies positively, the term  $C\bar{\alpha}$  in eq. 1 may change relatively little with diversity. If so, species diversity should be approximately proportional to the diversity of resources utilized (this implies that eq. 1 can be greatly simplified to  $D_S \propto D_R$ ). In short, only one of the factors in eq. 1 is implicated as a major determinant of the number of species coexisting in these lizard communities: namely, the size of the lizard niche space as measured by the diversity of resources actually exploited by lizards, or  $D_R$ .

To my knowledge, this is the first empirical demonstration that species density is negatively correlated with the average extent of overlap among the members of a community. [Brown and Lieberman (1973) and Brown (Chapter 13, Figure 10) reported positive correlations between overlap and species densities of small mammals, but these could be artifacts of the increased numbers of interspecific pairs in more diverse communities.] I conclude that both species diversity theory and niche overlap theory need to be expanded to incorporate more fully the important phenomenon MacArthur (1972) termed "diffuse competition."

#### Acknowledgments

Robert MacArthur inspired this work and provided me with continual food for thought over the ten years I have been involved in it.

This research has benefited from con-

tacts with so many other persons that it is impossible to list them all here. Some who deserve particular acknowledgment are my field assistants: Nicholas Pianka, William Shaneyfelt, Michael Thomas, Larry Coons, and Raymond Huey. My wife, Helen, has assisted in numerous ways. I thank Virginia Denniston and Glenn Kaufman for much help in data processing and analysis. Michael Egan painstakingly analyzed the contents of thousands of lizard stomachs. Participants in the MacArthur Memorial Symposium, especially the consulting editors, provided useful comment on a preliminary draft of the manuscript. The project was made possible by financial support from the National Science Foundation (grants GB-5216, GB-8727, GB-31006).

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