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THE STRUCTURE OF LIZARD COMMUNITIES

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Strictly speaking, a community is composed of all the organisms that live together in a particular habitat. Community structure concerns all the various ways in which the members of such a community relate to and interact with one another, as well as community-level properties that emerge from these interactions, such as trophic structure, energy flow, species diversity, relative abundance, and community stability. In practice, ecologists are usually unable to study entire communities, but instead interest is often focused on some convenient and tractable subset (usually taxonomic) of a particular community or series of communities. Thus one reads about plant communities, fish communities, bird communities, and so on. My topic here is the structure of lizard communities in this somewhat loose sense of the word (perhaps assemblage would be a more accurate description); my emphasis is on the niche relationships among such sympatric sets of lizard species, especially as they affect the numbers of species that coexist within lizard communities (species density).

So defined, the simplest (and perhaps least interesting) lizard communities would be those that contain but a single species, as, for instance, northern populations of *Eumeces fasciatus*. At the other extreme, probably the most complex lizard communities are those of the Australian sandridge deserts where as many as 40 different species occur in sympatry (20). Usually species densities of sympatric lizards vary from about 4 or 5 species to perhaps as many as 20. Lizard communities in arid regions are generally richer in species than those in wetter areas; therefore, because almost all ecological studies of entire saurofaunas have been in deserts (18, 20, 25), this paper emphasizes the structure of desert lizard communities. As such, I review mostly my own work. Other studies on lizard communities in nondesert habitats are, however, cited where appropriate.

Historical factors such as degree of isolation and available biotic stocks (particularly the species pools of potential competitors and predators) have profoundly shaped lizard communities. Thus one reason the Australian deserts support such very rich lizard communities may be that competition with, and perhaps predation pressures from, snakes, birds, and mammals are reduced on that continent (20).

Climate is also a major determinant of lizard species densities. The effects of various other historical factors, such as the Pleistocene glaciations, on lizard communities are very difficult to assess but may be considerable.

One of the strongest tools available to ecologists is the comparison of ecological systems which are historically independent but otherwise similar. Observations on pairs of such systems allow one to determine the degree of similarity in evolutionary outcome. Moreover, under certain circumstances such natural experiments may even allow some measure of control over such historical variables as the Pleistocene glaciations. For example, faunas of independently evolved study areas with similar climates and vegetative structure should differ primarily in the effects of history upon them.

This paper consists of two major sections. In the first, "Patterns Within Communities," I briefly review fundamental aspects of community structure and lizard niches to establish a frame of reference and to lay the groundwork for the remainder of the paper. Next I discuss ways of quantifying these niche relationships. In the second section, "Comparisons Between Communities," I use these methods to examine and compare three independently evolved desert-lizard systems in some detail; this section is not a review of the literature but a quantitative summary of much of my own research over the last ten years.

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PATTERNS WITHIN COMMUNITIES

The number of species coexisting within communities can differ in four distinct ways: (*a*) More diverse communities can contain a greater variety of available resources, and/or (*b*) their component species may, on the average, use a smaller range of these available resources (the former corresponds roughly to "more niches," "a larger total niche space," or "more niche dimensions," and the latter to "smaller niches"). (*c*) Two communities with identical ranges of resources and average utilization patterns per species can also differ in species density with changes in the average degree of overlap in the use of available resources; thus greater overlap implies that more species exploit each resource (this situation can be described as "smaller exclusive niches" or "greater niche overlap"). (*d*) Finally, some communities may not contain the full range of species they could conceivably support and species density might then vary with the extent to which available resources are actually exploited by as many different species as possible (that is, with the degree of saturation with species or with the number of so-called empty niches). MacArthur (11) summarized all but the fourth of the above factors with a simple equation for the number of species in a community N

$$N = \frac{R}{\bar{U}}\left(1 + C\frac{\bar{O}}{\bar{H}}\right) \qquad 1.$$

where R is the total range of available resources actually exploited by all species, $\bar{U}$ the average niche breadth or the range of resources used by an average species, C a measure of the potential number of neighbors in niche space, increasing more

or less geometrically with the number of niche dimensions (below), and $\overline{O}/\overline{H}$ the relative amount of niche overlap between an average pair of species. MacArthur improved Equation 1 to handle situations in which resources are not distributed uniformly

$$D_s = \frac{D_r}{\overline{D}_u}\left(1 + \overline{C}\,\overline{a}\right) \qquad 2.$$

where D_s is the diversity of species in the community, D_r is the overall diversity of the resources exploited by all species, $\overline{D}_u$ is the mean diversity of utilization or the niche breadth of an average species, $\overline{C}$ measures the average number of potential niche neighbors as before, and $\overline{a}$ is a measure of the average amount of niche overlap (MacArthur called this the mean competition coefficient). I return to Equation 2 below after considering various aspects of the niche relationships of lizards and how they can be quantified. Results presented here, however, depend in no way upon the validity of MacArthur's equation.

Niche Dimensions

Animals partition environmental resources in three basic ways: temporally, spatially, and trophically; that is, species differ in times of activity, the places they exploit, and/or the foods they eat. Such differences in activities separate niches, reduce competition, and presumably allow the coexistence of a variety of species (8, 11). Among lizards these three fundamental niche dimensions are often fairly distinct and more or less independent of each other, although they sometimes interact; for example, the mode of foraging can influence all three niche dimensions. For convenience I first treat each major niche dimension separately (below) and then briefly examine ways in which they interact. Rather than refer to "the trophic and temporal dimensions of the niche," etc, I use verbal shorthand and speak of the food niche, time niche, etc.

All else being equal (number of species, niche breadths, niche overlaps, etc), a greater number of effective niche dimensions results in fewer immediate actual neighbors in niche space; moreover, pairs of potential competitors with high overlap along one niche dimension may often overlap relatively little or not at all along another niche dimension, presumably reducing or eliminating competition between them.

TIME NICHE To the extent that being active at different times leads to exploitation of different resources, such as prey species, temporal separation of activities may reduce competition between lizard species. Perhaps the most conspicuous temporal separation of activities is the dichotomy of diurnal and nocturnal lizards, which are entirely nonoverlapping in the time dimension. However, more subtle temporal differences in daily and seasonal patterns of activity are widespread among lizards, both within and between species. In the North American Sonoran desert, for example, *Uta stansburiana* emerge early in the day and comprise the vast majority of the lizards encountered during the cool morning hours (Table 1). Later, small *Cnemido-*

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Table 1 Statistics on time of activity of four species of lizards in the Sonoran desert, expressed as time[a] since sunrise, during the period when temperatures are rising. All means are significantly different (t - tests, $P < .01$).

Species	$\bar{X}$[b]	S.E.[c]	s[d]	N[e]	95% Confidence Limits of Means
Uta stansburiana	3.67	0.06	1.39	470	3.55–3.79
Cnemidophorus tigris	4.11	0.05	1.33	669	4.01–4.21
Callisaurus draconoides	4.60	0.09	1.32	204	4.42–4.78
Dipsosaurus dorsalis	5.83	0.27	1.71	40	5.29–6.37

[a]in hundredths of an hour
[b]arithmetic mean
[c]standard error of the mean
[d]standard deviation
[e]sample size (number of lizards)

phorus tigris appear, while still later larger *C. tigris* emerge. As air and substrate temperatures rise with the daily march of temperature other species such as *Callisaurus draconoides* and *Dipsosaurus dorsalis* become active (Table 1). Similar patterns of gradual sequential replacement of species during the day occur in Australian skinks of the genus *Ctenotus* (21) and in lacertid lizards in the Kalahari desert of southern Africa (25). Daily patterns of activity also change seasonally with later emergence during cooler winter months than in warm summer ones (4, 13, 21, 23, 27, 30, 31, 46). Species with bimodal daily activity patterns during warm months (early and late in the day) often have a unimodal activity period during cooler months (13, 21, 30, 31, 46). Such seasonal changes in the time of activity presumably allow a lizard to encounter a similar thermal environment and microclimate over a period of time when the macroclimate is changing. Standardizing times of activities to "time since sunrise" (diurnal species) or "time since sunset" (nocturnal species) corrects for such seasonal shifts in time of activity and greatly facilitates comparison among species (Table 1) as well as comparisons between communities (below). Body temperatures of active individuals often reflect the time of activity reasonably well (21), although body temperature can be strongly affected by microhabitat(s) as well (4, 13, 14, 21, 26, 30, 32, 44). Thus species that emerge earlier in the day frequently have lower active body temperatures than those that emerge later; indeed, body temperature can sometimes be used as an indicator of time (21) or thermal (36, 41, 43) niche. The anatomy and size of a lizard's eyes are another useful indicator of its time niche; large eyes and elliptical pupils almost invariably indicate nocturnal activity (48).

PLACE NICHE The use of space varies widely among lizard species. A few are entirely subterranean (fossorial), many others are completely terrestrial, while still others are almost exclusively arboreal. Various degrees of semifossorial and semiarboreal activity also occur. Microhabitat differences among species are often pronounced even within these groups. Thus some terrestrial species forage primarily in the open spaces between plants, whereas others forage mainly under or within

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plants, the plants sometimes having a particular life form. Similar subtle differences in the use of various parts of the vegetation also occur among arboreal lizard species, especially *Anolis* (35, 36, 39, 41, 43). Some lizard species are strongly restricted to a rock-dwelling (saxicolous) existence. In addition to such microhabitat specificity, various species have specialized in their habitat requirements. Thus different sets of species of Australian desert lizards are restricted to sandridge, sandplain, and shrubby habitats respectively (21, 28). As defined here the place niche is more inclusive than Rand's (35) structural niche, as it includes both habitat and microhabitat preferences. Exactly where in the environmental mosaic a lizard forages, as well as its mode of foraging in that space, is perhaps its most important ecological attribute.

Lizards that exploit space in different ways have evolved a variety of morphological adaptations for the use of space (21, 30, 33, 37); such anatomical traits are often accurate indicators of their place niche. Thus fossorial species typically have either very reduced appendages or none at all. Diurnal arboreal lizards are usually long-tailed and slender. Terrestrial species that forage in the open between shrubs and/or grass clumps generally have long hind legs relative to their size, while those that forage closer to cover or within dense clumps of grass usually have proportionately shorter hind legs (21, 30, 33). Lamellar structure often reveals arboreal or terrestrial activity as well as the texture of the substrate exploited (1). Moreover, terrestrial geckos have proportionately larger eyes than arboreal ones (33, 48).

FOOD NICHE Most lizards are insectivorous and fairly opportunistic feeders, taking without any obvious preference whatever arthropods they encounter within a broad range of types and sizes. Smaller species or individuals, however, do tend to eat smaller prey than larger species or individuals (6, 21, 33, 38, 39, 43); also, differences in foraging techniques (below) and place and time niches often result in exposure to a different spectrum of prey species. Rather few lizard species have evolved severe dietary restrictions; among these are the ant specialists *Phrynosoma* and *Moloch* (17, 31, 32), termite specialists such as *Rhynchoedura* and *Typhlosaurus* (7, 33), various herbivorous lizards which include *Ctenosaurus, Dipsosaurus, Sauromalus,* and *Uromastix,* and secondary carnivores such as *Crotaphytus, Heloderma, Lialis,* and *Varanus* which prey primarily upon the eggs and young of vertebrates and the adults of smaller species (17, 19, 22, 24). All the above foods are at least temporarily very abundant making food specialization advantageous (12). Just as lamellar structure and hind leg proportions reflect the place niche of a lizard, head proportions, jaw length, and dentition frequently prove to be useful indicators of the food niche (6, 21, 38), especially of the sizes and kinds of prey eaten.

Another, somewhat more behavioral, aspect of a lizard's food niche concerns the way in which it hunts for prey. Two extreme types of foragers have been recognized (17, 40, 42): a lizard may either actively search out prey (widely foraging strategy) or wait passively until a moving prey item offers itself and then ambush the prey (sit-and-wait strategy). Normally the success of the sit-and-wait method requires a fairly high prey density, high prey mobility, and/or a low energy demand by the

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predator (40, 42). The effectiveness of the widely foraging tactic also depends on the density and mobility of prey and the predator's energy needs, but in this case the distribution of prey in space and the searching abilities of the predator may take on considerable importance (40, 42). Clearly, this dichotomy is artificial and these two tactics actually represent pure forms of a variety of possible foraging strategies. However, the dichotomy has substantial practical value because the actual foraging techniques used by lizards are often strongly polarized. Thus most teids and skinks and many varanid and lacertid lizards are very active and widely foraging, typically on the move continually; in contrast, almost all iguanids, agamids, and geckos are relatively sedentary sit-and-wait foragers. These differences in the mode of foraging presumably influence the types of prey encountered, thus affecting the composition of a lizard's diet.

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INTERACTIONS BETWEEN THE TIME, PLACE, AND FOOD NICHES Place niches and food niches of lizards change in time, both during the day and with the seasons. In the early morning, when ambient air and substrate temperatures are relatively low, lizards typically locate themselves in the warmer microhabitats of the environmental mosaic, such as depressions in the open sun or the sunny side of a rock, slope, sandridge, or tree trunk. Often an animal orients its body at right angles to the sun's beams, thereby maximizing heat gained from the sun. Later in the day as environmental temperatures rise the same lizards usually spend most of their time in the cooler patches in the environmental mosaic, such as shady spots underneath shrubs or trees (4, 26, 27, 41). Finally, as the surface gets still hotter many lizards retreat into cool burrows; certain species, such as *Amphibolurus inermis,* climb up off the ground into cooler air and face into the sun, minimizing their heat load due to solar irradiation (4, 26). Thus time of activity strongly affects a lizard's place niche and its habitat and microhabitat requirements may dictate periods when the animal can be active.

Similarly, the composition of the diet of many lizards changes as the relative abundances of different types of prey fluctuate with the seasons (and probably within a day). Nocturnal lizards clearly encounter a different spectrum of potential prey items than diurnal lizards, and those that forage in different places usually encounter different prey. The mode of foraging or the way in which a lizard uses space can influence both its place and food niches; thus widely foraging species typically have broader place niches than sit-and-wait species, while the latter type of foragers often tend to have broader food niches than the former. Recall that pairs of lizard species with high overlap along one niche dimension, say microhabitat, may have low overlap along another niche dimension such as foods eaten, effectively reducing interspecific competition between them.

Niche Breadth and Niche Overlap

In addition to the differences in times of activity and use of space and foods noted above, lizard species differ in the spans of time over which they are active as well as the ranges of spatial and trophic resources they exploit. As outlined above, such differences in niche breadth may have a considerable impact upon the structure and

diversity of lizard communities. Following MacArthur (11), niche breadth along any single dimension is here quantified using Simpson's index of diversity

$$B = 1/\sum_{i}^{n} p_i^2 \qquad 3.$$

where p_i represents the proportion of the ith time period (or microhabitat or food type) actually used; B varies from unity to n depending upon the p_i values. Niche breadths based on a different number of p_i categories can be compared after standardizing them by dividing by n. Overall niche breadth along several niche dimensions can be estimated either as the product or the geometric mean of the breadths along each component dimension (recall that the lower bound on B is one) or by the arithmetic mean of the latter breadths.

Niche overlap also varies among lizard species and between communities. Overlap along any single niche dimension can be quantified in a wide variety of ways (2, 5, 10, 21, 34, 39, 47). Here I use still another measure of overlap, based upon Levins' (10) formula for α

$$\alpha_{jk} = \frac{\sum_{i}^{n} p_{ij}\, p_{ik}}{\sum_{i}^{n} p_{ij}^2} \qquad \alpha_{kj} = \frac{\sum_{i}^{n} p_{ij}\, p_{ik}}{\sum_{i}^{n} p_{ik}^2} \qquad 4.$$

where p_{ij} and p_{ik} are the proportions of the ith resource used by the jth and the kth species respectively. The above equations have been used to estimate the so-called competition coefficients (10, 11, 47), and give different α values for each partner in a niche overlap pair provided that niche breadths (the inverse of the denominators in Equation 4) differ. Here I use the following multiplicative measure of overlap

$$O_{jk} = O_{kj} = \frac{\sum_{i}^{n} p_{ij}\, p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}} \qquad 5.$$

where the p_{ij} and p_{ik} are defined as before (I am indebted to Selden Stewart for suggesting this equation). Equation 5 is symmetric and gives a single overlap value for each niche overlap pair; it can never generate values less than zero or greater than one [Equation 4, however, does give one α value (of a pair) that is greater than unity provided niche breadth and overlap are high]. Overall niche overlap along several niche dimensions can be estimated by the product of the overlaps along each component dimension (10, 21), although this procedure may either overestimate or underestimate overall overlap (H. S. Horn, personal communication; R. M. May, unpublished). Thus if niches are completely separated along any single niche dimension both niche overlap along that dimension and overall niche overlap are zero.

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COMPARISONS BETWEEN COMMUNITIES

During the last decade I have studied in some detail three independently derived and evolved, but otherwise basically comparable, sets of desert lizard communities at similar latitudes in western North America, southern Africa, and Western Australia. Here I use data from these studies to quantify and compare various parameters of lizard niches. Although lizards were studied on 32 different study areas (below) I lump data from various study areas within each continental desert-lizard system here for brevity and clarity (a more detailed area by area analysis will be undertaken elsewhere). A few allopatric species pairs are thus treated as though they are sympatric, but the vast majority of the species considered are sympatric on one or more study areas.

The number of sympatric lizard species on 14 North American desert study areas varies from 4 to 11, with either 4 or 5 sympatric species in the northernmost Great Basin desert, 6–8 species in the more southern Mojave and Colorado deserts, and 9–11 species in the still more southerly Sonoran desert (16–18). (The analysis to follow includes only 10 southern North American desert study areas.) Ten study areas in the Kalahari desert of southern Africa support 12–18 sympatric species of lizards (25). In the Western Australian desert 18–40 species of lizards occur together in sympatry on eight different study sites (20, 21, 33). In addition to such censuses of lizard species densities, I gathered supporting data on the physiography, climate, vegetation, and faunas of each of the 32 desert study areas (15–18, 20, 21, 25, 28–31).

The actual diversity of lizards observed on all sites within each desert-lizard system, estimated using the relative abundances of the various species in my collections (below) as p_i's in Equation 3, are: North America = 3.0 (28% of the maximum possible diversity of 11), Kalahari = 12.5 (60% of the maximum possible diversity of 21), and Australia = 19.0 (32% of the maximum possible diversity of 59). (These are crude approximations of the actual lizard diversities, both because real relative abundances doubtless differ somewhat from the relative abundances in my samples and because not all species actually occur in sympatry.)

Time of activity and microhabitat were recorded for most active lizards encountered. Table 2 lists the average numbers of species in five basic time and/or place niches in each desert system (see also below). Wherever possible, lizards were collected; these specimens[1] allowed analysis of stomach contents. Twenty basic prey categories, corresponding roughly to various orders of arthropods, were distinguished. Both the numbers and volume of prey items in each category were recorded for every stomach.

I used these data on time of activity, microhabitat usage, and stomach contents for the following analyses of the time, place, and food niches of desert lizards. The numbers of lizards active at different times were grouped by species into 22 hourly categories expressed in time since sunrise for diurnal species (14 categories) and time since sunset for nocturnal ones (limitations on human endurance allowed only 8

[1]Some 5000 North American lizards, over 6000 Kalahari lizards, and nearly 4000 Australian ones, all of which are now lodged in the Los Angeles County Museum.

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Table 2 Average numbers of species of lizards in five basic niche categories on study areas in the three desert systems. The percentage of the average total number of species in each system is also given.

Niche Category	North America[a]		Kalahari[b]		Australia[c]	
	$\overline{X}$	%	$\overline{X}$	%	$\overline{X}$	%
diurnal terrestrial	5.7	69	6.3	43	14.4	51
diurnal arboreal	1.2	14	1.9	13	2.6	9
nocturnal terrestrial	1.4	17	3.5	24	7.6	27
nocturnal arboreal	0.0	0	1.6	11	2.6	9
fossorial	0.0	0	1.4	10	1.1	4
totals	8.3	100	14.8	101	28.3	100

[a]10 different southern study areas

[b]10 study areas

[c]8 study areas

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nocturnal hourly categories); these 22 time categories were used as p_i's in the above equations. Fifteen basic microhabitat categories were recognized and used as p_i's. Time and place niche breadths and overlaps were calculated for desert lizards in these three independently evolved systems of lizard communities using Equations 3 and 5 and the above data on the numbers of lizards active at different times and in different microhabitats. The overall span or diversity of time of activity of all the lizards in each continental desert system (D_r in Equation 2), as well as the microhabitats used by them, were estimated using Equation 3 and the proportions of each time period or microhabitat type as computed from grand totals summed over all lizard species. Stomach content data (prey items by volume[2]) allowed similar calculations of food niche breadths and overlaps, as well as the average and overall diversity of foods eaten by all lizards, $\overline{D_u}$ and D_r, in each of the above deserts. Mean niche breadths of all the species in a given community ($\overline{D_u}$ in Equation 2) were also calculated for the time and place niches. Average niche overlap along each niche dimension in any particular community was calculated as the arithmetic mean of all interspecific overlaps (calculated from Equation 5); products of these values were also computed to estimate overall niche overlap.

Diversity of Resources Used by Lizards

The overall diversity of times of activity of all lizards (D_r for the time niche) in each desert-lizard system was computed using Equation 3 and the proportional representation of the 22 hourly time categories among all species (recall that these categories are expressed in hours since sunrise or sunset and that they therefore correct

[2]Prey items in the same 20 categories by numbers of items, rather than their volumetric importance, and prey in 34 size categories (irrespective of type) were also examined, but are not considered further here because there is very little niche separation in either of these two aspects of the food niche.

somewhat for seasonal shifts in activity patterns). Overall diversity of time of activity thus computed is quite low in North America (5.9 or only 27% of the maximum possible value of 22) and nearly twice as large in the Kalahari and Australia (11.6 and 11.7 respectively, or about 53% of the possible maximum). A major factor contributing to the greater diversity of time of activity in the Kalahari and Australia is the increased numbers of nocturnal lizards in the southern hemisphere (Table 2), although the diversity of time of activity of diurnal lizards is also somewhat higher in these two deserts than in North America. Lizards are active year around in the Kalahari and Australia and they were sampled over the entire year, while the seasonal period of activity is shorter in North America and lizards were sampled only over a six-month period. Whatever the reason(s) for this difference between the desert systems, the more diverse communities of the Kalahari and Australia certainly exhibit much greater temporal variation in their times of activity on both a daily and a seasonal basis than the less diverse North American lizard community.

Overall microhabitat diversity, computed using Equation 3 and the 15 basic microhabitat categories as exploited by all the lizards in each system, represents D_r for the place niche; again, it is very low in North America (3.3 or only 22% of the maximal value of 15), where the vast majority of lizards were first sighted in the open sun, and considerably higher in the Kalahari (8.8 or 59% of maximum) and Australia (8.2 or 55% of maximum). These differences in the diversity of microhabitats actually used by lizards are due partly to an increased incidence of arboreal and subterranean lizards in the two deserts of the southern hemisphere (Table 2), although more animals are also first sighted in the shade of various types of plants (Table 3). Nocturnality is much more prevalent in the Kalahari and Australia (Table 2) and contributes to the increased use of shade in these lizard communities (nocturnal lizards were arbitrarily assigned to shade categories in Table 3, although this somewhat confounds place and time niches).

Somewhat surprisingly, the overall diversity of foods eaten by all the lizards[3] in a community, or D_r for the food niche, is lowest in the Kalahari (4.4 or 22% of the maximal value of 20), intermediate in Australia (7.4 or 37% maximum), and highest in the least diverse lizard communities of North America (8.7 or 44% of maximum). The low diversity of foods eaten by Kalahari lizards stems from the preponderance of termites in the diets of these lizards (Table 4). Examination of Table 4 shows that the proportions of various prey categories actually eaten by lizards differ markedly among the desert systems. For example, although termites are a major food item in all three deserts, their fraction of the total prey eaten by all lizards is considerably higher in the Kalahari (41.3%) than in either of the other deserts (16.5 and 15.9%). Prominent prey in the Australian desert are vertebrates (24.8%), especially lizards, and ants (16.4%). By volume, beetles constitute 18.5% of the food eaten by North American desert lizards, 16.3% of that eaten by Kalahari lizards, but only 7.3% of the Australian desert lizard diet.

[3]Computed using Equation 3 and the proportion of the total volume of food in each of 20 prey categories in the stomachs of all the lizards collected in a series of communities from each desert-lizard system.

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Table 3 Microhabitats actually used by all lizards in three different desert systems. Nocturnal lizards assigned to shade categories. Numbers (*N*) and percentages (%).

Microhabitat Category	North America *N*	North America %	Kalahari *N*	Kalahari %	Australia *N*	Australia %
Subterranean	0	0.0	579	12.1	17	0.5
Terrestrial						
open sun	1335	45.3	890	18.6	596	19.0
grass sun	92	3.1	155	3.2	314	10.0
bush sun	883	30.0	547	11.4	192	6.2
tree sun	103	3.5	126	2.6	31	1.0
other sun	95	3.2	6	0.1	14	0.4
open shade	49	1.7	546	11.4	547	17.4
grass shade	2	0.1	274	5.7	525	16.6
bush shade	165	5.6	765	15.9	221	6.9
tree shade	30	1.0	179	3.7	81	2.6
other shade	72	2.4	18	0.4	43	1.3
Arboreal						
low sun	12	0.4	125	2.6	56	1.5
low shade	6	0.2	109	2.3	224	7.0
high sun	50	1.8	200	4.2	91	2.0
high shade	51	1.8	276	5.8	250	7.7
TOTALS	2945	100.1	4795	100.0	3202	100.1

Table 4 Major prey items in the stomachs of all lizards in three different desert systems by volume in cubic centimeters.

Prey Category	North America volume	North America percentage	Kalahari volume	Kalahari percentage	Australia volume	Australia percentage
spiders	50	1.6	36	3.1	54	3.4
scorpions	23	0.7	33	2.9	22	1.4
ants	307	9.7	155	13.6	261	16.4
locustidae	364	11.5	70	6.1	138	8.7
blattidae	100	3.2	4	0.4	37	2.3
beetles	587	18.5	187	16.3	117	7.3
termites	525	16.5	473	41.3	253	15.9
homoptera-hemiptera	31	1.0	15	1.3	30	1.9
lepidoptera	68	2.1	16	1.4	9	0.5
all larvae	384	12.1	41	3.6	80	5.0
Miscellaneous arthropods	225	7.0	76	6.6	107	6.7
vertebrates	246	7.8	26	2.3	395	24.8
plants	262	8.3	13	1.2	89	5.6
TOTALS	3172	100.1	1145	100.0	1592	99.9

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To give each niche dimension equal weight the above estimates of D_r were standardized by dividing by the number of p_i categories and multiplying by 100, thus expressing the diversity of use of resources as a percentage of the maximal possible resource diversity along a given niche dimension. The overall diversity of resources used by all lizards in all three niche dimensions was then computed as the product of the above three standardized D_r values divided by 1000. So estimated, overall diversity of resources used is lowest in North America (25.9), intermediate in the Kalahari (68.9), and highest in Australia (107.5); moreover, these estimates of the size of the lizard niche space are directly proportional to observed lizard diversities in the various deserts (above).

Differences in Niche Breadth

Niche breadths for the food, place, and time niches, as well as their products (overall niche breadth) were calculated for 91 species of desert lizards in 10 families on the three continents. Frequency distributions and averages of all the species in each desert-lizard system are shown for each niche dimension in Figure 1; these mean niche breadths represent the average diversity of utilization of each niche dimension, or $\overline{D}_u$ in Equation 2, by the lizards in a given system. In all three deserts average time niche breadths are very similar, though their frequency distributions differ

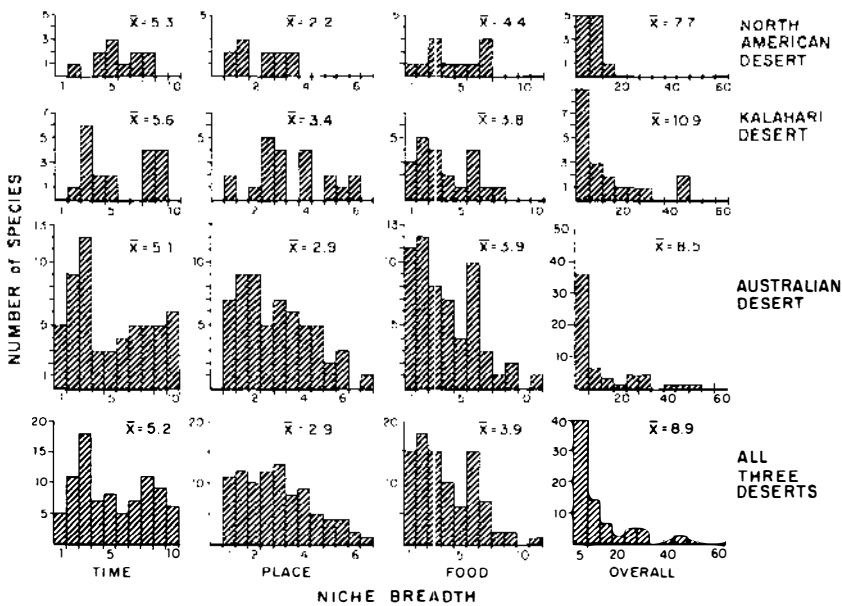

Figure 1 Frequency distributions of niche breadths of 91 species of desert lizards along three major niche dimensions in three deserts. Overall niche breadths, computed as the products of the standardized breadths along each component dimension, weight each niche dimension equally. See text for discussion.

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(Figure 1). The frequency distribution of time niche breadth of North American lizards is fairly continuous, but these distributions are distinctly bimodal in the Kalahari and Australia where most nocturnal species have relatively narrow time niches while diurnal ones generally have comparatively broader time niches. (The narrow time niches of nocturnal lizards are probably an artifact due to the shorter nighttime sampling period; however, this bias is similar in all three deserts and should not generate differences between the desert systems.) Place niche breadths are more evenly distributed than time niche breadths, although the distributions are skewed with more narrow place niches than broad ones (Figure 1); place niches are smallest in North America ($\bar{x} = 2.2$, or 15% of maximal value), intermediate in Australia ($\bar{x} = 2.9$, or 19% of maximum), and broadest in the Kalahari ($\bar{x} = 3.4$, or 23% of maximum). In all three deserts food niche breadths appear to be distinctly bimodal, suggesting a natural dichotomy of food specialists versus food generalists (Figure 1). Average food niche breadth is fairly similar in all three deserts and is largest in North America.

Because species with broad niches along one dimension often, though by no means always,[4] have narrow niches along another dimension, overall niche breadths are strongly skewed with the majority of species having rather narrow overall niches (Figure 1). Nevertheless, a few species in the Kalahari and Australia with broader than average niches along all three niche dimensions have extremely broad overall niches (Figure 1). Average overall niche breadth is smallest in North America (7.7), intermediate in Australia (8.5), and largest in the Kalahari (10.9). However, overall niche breadths, as well as average overall niche breadths, do not differ strikingly between the desert systems; indeed, if anything, overall niches tend to be slightly larger in the more diverse communities, rather than smaller as might have been anticipated.

Niche Dimensionality

Any given niche dimension's potential to separate niches, and thus its potential effectiveness in reducing interspecific competition, should be roughly proportional to the ratio of the overall diversity of use of that niche dimension divided by the diversity of utilization by an average species, or $D_r/\bar{D}_u$. Table 5 summarizes much of the above discussion and lists the ratios of $D_r/\bar{D}_u$ for each major niche dimension in the three desert-lizard systems. Estimates for each niche dimension are also multiplied to give overall estimates (products of the standardized estimates for each component dimension). Thus measured, the dimension with the greatest apparent potential to separate niches in North America is food, which, by the same criteria, is a comparatively negligible niche dimension in the Kalahari; conversely, by these standards place and time niches seem to have a much greater potential to separate niches of Kalahari lizards than North American ones (Table 5). All three niche dimensions, especially place and time, appear to have the potential to separate niches of Australian lizards. The products of the $D_r/\bar{D}_u$ ratios for all three dimen-

[4]Product moment correlation coefficients among niche breadths along various dimensions range from –0.38 to 0.40 and are generally weak and seldom statistically significant.

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Table 5 Estimates of various niche parameters (see text and Table 6).

Desert and Niche Dimension	D_r	$\overline{D}_u$	$D_r / \overline{D}_u$	$\overline{C}$	Mean Overlap (all pairs)	Mean Overlap (nonzero pairs)
North America						
time	25.4	24.2	1.05	3.0	0.58	0.86
place	22.0	14.6	1.51	3.0	0.34	0.55
food	43.7	22.0	1.98	1.2	0.46	0.49
overall	25.9	7.7	3.34	-9.5	0.09	0.23
Kalahari						
time	52.7	25.4	2.07	11.7	0.43	0.78
place	58.9	22.8	2.58	13.3	0.29	0.38
food	22.2	18.8	1.18	14.9	0.64	0.64
overall	68.9	10.9	6.34	12.2	0.08	0.27
Australia						
time	53.3	23.1	2.31	22.9	0.32	0.54
place	54.8	19.1	2.87	19.2	0.29	0.35
food	36.8	19.3	1.90	28.4	0.32	0.36
overall	107.5	8.5	12.62	17.3	0.03	0.13

sions (Table 5), which should be proportional to the overall potential for niche separation, increase from North America (3.3) to the Kalahari (6.3) to Australia (12.6), as might be expected. Hence, as measured by $D_r/\overline{D}_u$, the potential for niche partitioning seems to be greater in more diverse lizard communities; moreover, this potential is directly proportional to actual lizard diversities observed.

Differences in Niche Overlap

Figure 2 shows the frequency distributions of niche overlap values for all interspecific pairs along each niche dimension in the three desert systems (calculated using Equation 5). Estimates of overall overlap, computed as the products of the overlap along the three niche dimensions, are shown at the right of the figure. Although there are some striking differences and trends in overlap patterns,[5] among both niche dimensions and deserts, overall overlaps are uniformly low in all three deserts (Figure 2 and Tables 5 and 6). The vast majority of interspecific pairs overlap very little or not at all when all three dimensions are considered. This is demonstrated by low overall overlap values and by the size of the "zero" classes of overall overlap in the various deserts (Tables 5 and 6). Table 5 gives averages both for all overlap pairs and for only those pairs which overlap somewhat (that is, all pairs other than those with zero overlap) for each niche dimension and for overall overlap estimates. Provided average niche breadth ($\overline{D}_u$) remains relatively constant, the number of possible nonoverlapping pairs increases markedly as overall niche space (D_r) increases. Hence the average niche overlap of pairs with some overlap is of interest as it should reflect the limiting similarity and/or maximal tolerable overlap

[5]For instance, distributions of time niche overlap are distinctly bimodal in all three deserts (particularly North America and the Kalahari), reflecting the nonoverlapping times of activity of nocturnal and diurnal species.

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Table 6 Summary of overall niche overlap patterns (see text and Table 5).

Desert System	Total Number of Overlap Pairs	Number of Zero Overlap Pairs	Zero Overlap Pairs as % of Total	Number of Nocturnal-Diurnal (ND) Pairs	ND Pairs as % of Zero Overlap Pairs	Number of Non-ND Pairs with Zero Overlap	Non-ND Pairs with Zero Overlap as % of Zero Overlap Pairs	Non-ND Pairs with Zero Overlap as % of all Overlap Pairs
North America	55	37	67%	18	49%	19	51%	35%
Kalahari	171	101	59%	78	77%	23	23%	13%
Australia	1596	1255	78%	680	54%	575	46%	36%

in each desert system. Although a substantial number of nonoverlapping pairs are nocturnal-diurnal species pairs, many non-nocturnal–diurnal pairs also do not overlap (Table 6). The proportion of such zero overlap pairs is distinctly lower in the Kalahari desert, where only 23% of the non-nocturnal–diurnal pairs do not overlap, than in North America and Australia (51 and 46% respectively). Furthermore, the average overlap among all nonzero overlap pairs tends to be somewhat greater in the Kalahari and North America than in Australia, suggesting that maximal tolerable niche overlap is lower in the latter desert (Table 5).

Although niche overlap values are far from normally distributed (Figure 2), arithmetic means [especially of the nonzero overlap values (Table 5)] do reflect differences between the various niche dimensions and deserts. Average overlap in microhabitat is low and generally similar in all three deserts, while average overlaps in the time and food niches are considerably more variable (Figure 2 and Table 5). Average time niche overlap is high in North America, while both average food and time niche overlaps are high in the Kalahari. In Australia, average niche overlap values are low along all three niche dimensions (Table 5). As a result, overall overlap is distinctly lower in Australia than in the other two desert systems. Thus overall niche overlap seems to vary inversely with lizard species diversity.

Numbers of Neighbors in Niche Space

By far the most difficult parameter to estimate in Equation 2 is the number of neighbors in niche space C (indeed, MacArthur did not indicate how one might

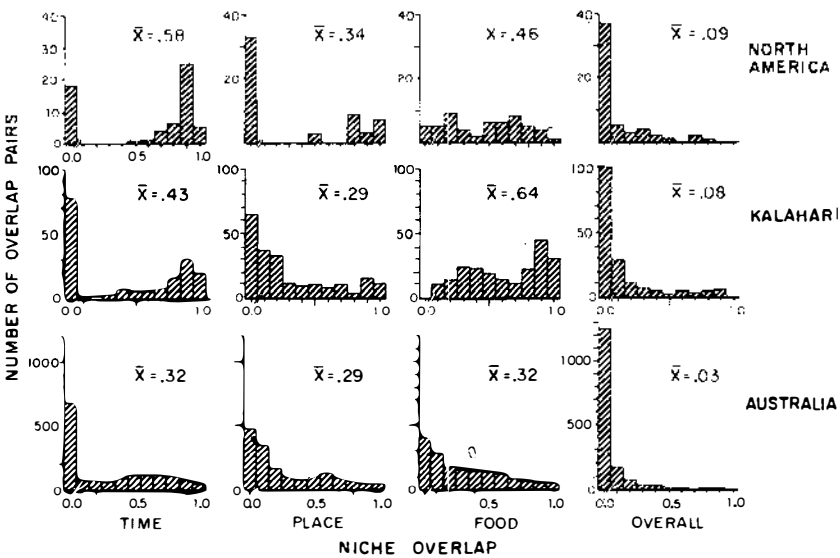

Figure 2 Frequency distributions of niche overlap values of desert lizards along three major niche dimensions in three deserts. See text for discussion.

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attempt to estimate C). This quantity cannot be estimated satisfactorily from my data in an independent way; however, $\overline{C}$ can be calculated by simply rearranging Equation 2 to solve for $\overline{C}$

$$\overline{C} = \frac{\left\{(\overline{D}_u / D_r) D_s - 1\right\}}{\overline{O}} \qquad 6.$$

Values of $\overline{C}$ estimated by substituting various estimates of other parameters (above) into Equation 6 are listed in Table 5. These values appear to be reasonable for any single niche dimension. However, the estimate of the number of neighbors in overall niche space (all three niche dimensions) is actually negative for North America. Estimates of the number of neighbors in overall niche space are much higher and more reasonable in the Kalahari and Australia (Table 5).

As indicated earlier, communities can differ in species diversity with differences in the extent to which they contain as many different species as they can support. The negative estimate of the number of neighbors in overall niche space in North America suggests that lizard diversity in these deserts may actually be lower than it could potentially be, or that these deserts may not be truly saturated with species. Further, the complete absence of any fossorial lizards or any which are both nocturnal and arboreal in North America (Table 2) suggests that these niches either (*a*) do not exist, (*b*) are unoccupied, or (*c*) are occupied but by another kind of animal (see next section). (Indeed, I would be quite surprised if a successful climbing gecko such as the Australian *Gehyra variegata* were unable to invade the North American desert without a simultaneous extinction of another nocturnal animal.)

Reciprocal Relations With Other Taxa

The ecological roles of lizards and various other taxa, especially birds and mammals, are strongly interdependent (9). Thus lizards may capitalize on variability of primary production, and this might be a factor contributing to their relative success over birds in desert regions (18, 20, 25). There are proportionately more species of ground-dwelling insectivorous birds in the Kalahari than there are in Australia (29), suggesting that competition between birds and lizards may be keener in southern Africa than it is in Australia. Figure 3 plots the number of bird species against the number of lizard species on 27 study areas representative of each desert system. As the total number of species increases, the numbers of bird species increase faster than lizard species in North America and the Kalahari, whereas in Australia lizards increase faster than birds. This figure suggests a sharp upper bound on the number of sympatric lizard species in North America and the Kalahari, but no such limit in Australia. Exactly the reverse seems to be true of birds in the three continental desert systems; that is, a distinct upper limit on bird species diversity appears to exist in Australia, but not in either North America or the Kalahari. The reasons for such differences between the three desert systems are elusive and must remain conjectural (9). There are very few migratory bird species in Australia, whereas a number of migratory birds periodically exploit the North American and Kalahari deserts; competitive pressures from these migrants must have their effects upon the lizard

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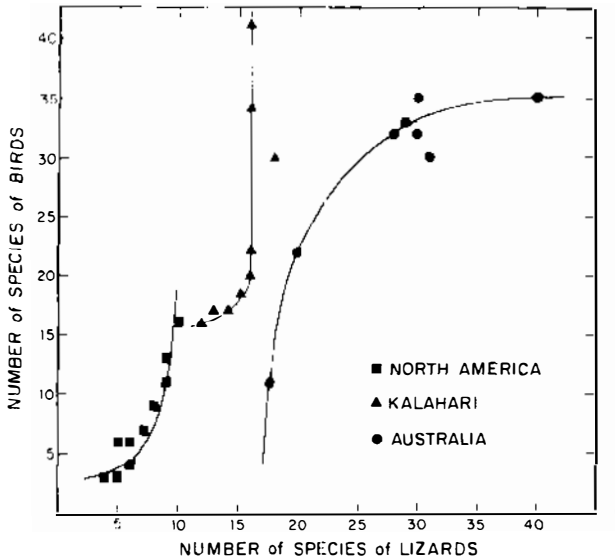

Figure 3 Number of species of birds plotted against the number of lizard species on various study areas within three desert systems. See text.

communities in the latter two desert systems. The higher incidence of arboreal, fossorial, and nocturnal lizard species in the Kalahari and Australia, as compared with North America (Table 2), are probably related to fundamental differences in the niches occupied by other members of these communities such as arthropods, snakes, birds, and mammals (20, 25). These differences in the composition and structure of the various communities presumably have a historical basis. Thus southern Africa has an exceptionally rich termite fauna, which in turn may have allowed the evolution of termite-specialized subterranean *Typhlosaurus* species (7). The prevalence of nocturnality among Kalahari and Australian lizards may arise from variations among systems in either or both of the following: (*a*) differences in the diversity of available nocturnal resources, such as nocturnal insects, or (*b*) differences in the numbers and/or densities of insectivorous and carnivorous nocturnal birds and mammals. The mammalian fauna of the Australian desert is conspicuously impoverished, and the snake fauna less so; in this desert system varanid and pygopodid lizards are ecological equivalents of carnivorous mammals and snakes, respectively, in North America and the Kalahari (20, 25). Such usurpation of the ecological roles of other taxa in the other deserts has expanded the diversity of resources exploited by Australian desert lizards (20).

Within-Habitat and Between-Habitat Diversity

Overall species diversities in an area (as opposed to point diversities) can differ in a way that is included neither in Equation 2 nor in the above analysis of niche

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relationships. Thus only the so-called "within-habitat" component of diversity (11, 25) was considered above (indeed, for brevity and clarity, data from various different study areas within each desert-lizard system were lumped for the above analyses). The other way in which communities can differ in species diversity is through differences in species composition from area to area or habitat to habitat within a study area (no study area is perfectly homogeneous); such horizontal turnover in species composition represents the so-called "between-habitat" component of diversity (11). To estimate the amount of between-habitat diversity in each of the above desert-lizard systems I calculated coefficients of community similarity[6] for every pair of lizard communities within each continental desert system (25). Community similarity values are high and rather uniform in the North American desert ($\bar{x}$ = 0.67, S. E. = 0.019, s = 0.153, N = 66) and the Kalahari desert ($\bar{x}$ = 0.67, S. E. = 0.015, s = 0.127, N = 66), indicating little difference between study areas in species composition (i.e. a low between-habitat component of diversity). However, community similarity values are significantly lower (t-tests, $P < 0.01$) in the Australian desert ($\bar{x}$ = 0.49, S. E. = 0.027, s = 0.144, N = 28), demonstrating that this component of diversity is greater in that desert system. Habitat specificity is much more pronounced in Australian desert lizards than it is in North American or Kalahari desert lizards (20, 25, 28). For example, although both the Kalahari and the Australian deserts are characterized by long stabilized sandridges, only a single species [*Typhlosaurus gariepensis* (7)] is specialized to Kalahari sandridges whereas ten lizard species are sandridge specialists in Australia (20, 28).

TAXONOMIC COMPONENTS OF LIZARD SPECIES DENSITY

Because closely related species are often ecologically similar and therefore in strong competition when they occur together, Elton (3) suggested that competitive exclusion should occur more frequently between pairs of congeneric species than between more distantly related pairs of species. Moreover, he reasoned that if this argument is valid fewer pairs of congeneric species should occur within natural communities than in a random sample of species and genera from a broader geographic area which includes several to many different communities. Frequent cases of abutting allopatry (parapatry) of congeners seem to support this argument. Elton examined the numbers of congeneric species in portions of many different natural communities and found evidence for such a paucity of congeners, even in spite of the bias towards an increased number of congeneric pairs due to the possibility of inclusion of two or more communities (and thus abutting allopatric congeneric pairs) in his samples. Although his numerical analysis has since been shown to be incorrect (49), his argument is still reasonable and worthy of consideration. Using a corrected statistical approach, Williams (49) failed to find fewer congeners than expected in a variety of natural communities (indeed, he found more than expected in many). Terborgh

[6]Community similarity (CS) is simply X/N, where X is the number of species common to two communities and N is the total number of different species occurring in either; thus CS equals one when two communities are identical, and zero when they share no species.

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& Weske (45) also used this corrected method to calculate the expected numbers of congeneric species pairs in Peruvian bird communities, and found that these communities were not impoverished with congeneric pairs, thus refuting any increased incidence of competitive exclusion among congeners in this particular avifauna. Similar analyses of the saurofaunas of the Kalahari and the Australian deserts are summarized in Figures 4 and 5. Again, the observed numbers of congeneric pairs are not conspicuously or consistently lower than expected.

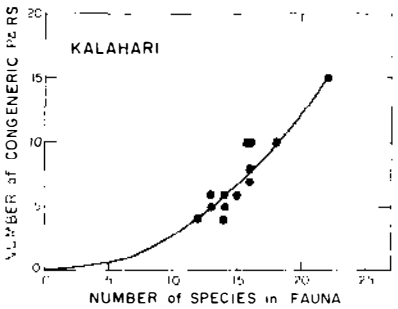

Figure 4 Dots represent the actual numbers of pairs of congeneric species of lizards observed on ten study areas in the Kalahari desert. Curve is the expected number of such pairs in a random subsample of the entire fauna.

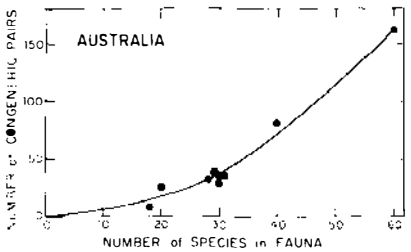

Figure 5 Dots are the actual numbers of pairs of congeneric species of lizards observed on eight Australian desert study areas. Curve represents the number of such pairs expected in a random subsample of the entire fauna.

CONCLUDING REMARKS

Interpretation of the structure of desert lizard communities has become steadily more difficult as the amount of information increases. Early in these studies, I expected to find much more pronounced similarities between these independently evolved, but otherwise basically similar ecological systems. Although a few crude ecological equivalents can be found among the different desert-lizard systems (26, 27, 30, 32), the ecologies of most species are quite disparate and unique. As seen above, the diversity of resources actually used by lizards along various niche dimensions, as well as the amount of niche overlap along them, differs markedly among the desert systems; moreover, the relative importance of various niche dimensions in separating niches varies. Thus food is a major dimension separating the niches of North American lizards, whereas in the Kalahari food niche separation is slight and differences in the place and time niches are considerable. All three niche dimensions are important in separating the niches of Australian desert lizards. Overall niche overlap is least in the most diverse lizard communities of Australia. Differences in diversity between the three continental systems stem from differences in the overall diversities of resources used by lizards or the size of the lizard niche space, as well as from differences in overall niche overlap, but are not due to

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conspicuous differences in overall niche breadths. Factors underlying these observed differences in diversity of utilized resources and niche overlap are poorly understood at present, but probably involve some of the following: (*a*) the degree to which any given system is truly saturated with species, (*b*) differences in the available range of resources among deserts that stem from historical factors, such as diversification of termites, reciprocal relations with other taxa, and the usurpation of their ecological roles, (*c*) differences between desert systems in the extent of spatial heterogeneity and habitat complexity which alter the degree of habitat specificity and the between-habitat component of diversity, and (*d*) other factors, such as possible differences in climatic stability and predictability, which might affect tolerable niche overlap.

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