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Niche Segregation in Desert Lizards

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Ecologists have long been fascinated by the possibility of an upper limit on the degree of ecological similarity between coexisting species. Such thinking has generated a rich literature and has led to the notion of "competitive communities," in which species have reached an equilibrium with their resources and rates of resource consumption are exactly balanced by their respective renewal rates. This appealing view of community structure has produced numerous useful concepts, including the principle of competitive exclusion (Gause, 1934; Cole, 1960; Hardin, 1960; Patten, 1961; DeBach, 1966), character displacement (Brown and Wilson, 1956; Hutchinson, 1959; Schoener, 1965; Grant, 1972), limiting similarity (MacArthur and Levins, 1967; Fenchel and Christiansen, 1976), species packing (MacArthur, 1969, 1970, 1972), and maximal tolerable niche overlap (Pianka, 1972; May and MacArthur, 1972; May, 1974).

The term *niche* has been, and doubtlessly will continue to be, used in a wide variety of ways (see, e.g., Whittaker and Levin, 1975). The niche concept has gradually become closely linked to the phenomenon of interspecific competition, however, and has recently been increasingly identified with resource utilization patterns (Levins, 1968; MacArthur, 1968, 1970, 1972; Schoener and Gorman, 1968; Pianka, 1969, 1973, 1974, 1975; Colwell and Futuyma, 1971; Roughgarden, 1972, 1976; Vandermeer, 1972; Pielou, 1972; May and MacArthur, 1972; May, 1974, 1975; Cody, 1974; Schoener, 1968,

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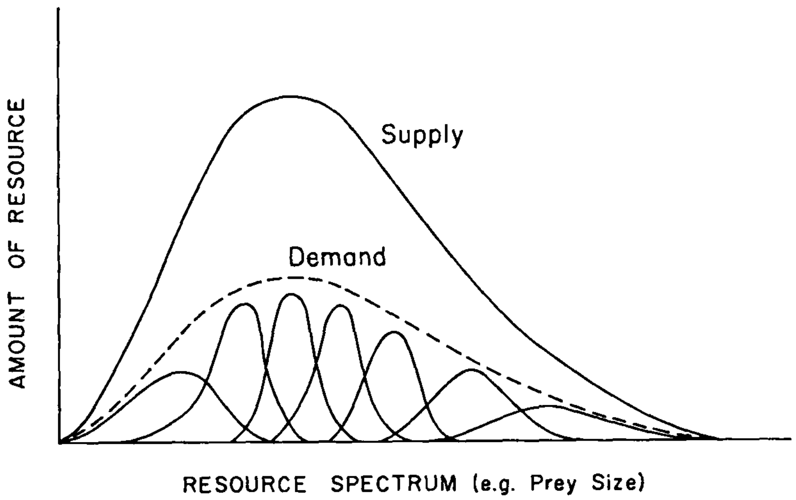

Fig. 1. The vertical axis can be expressed either as the amount of resource available at an instant or as the rate of resource consumption and/or renewal along a spectrum of resources. A positive correlation between resource abundance and turnover rate is assumed for convenience. The uppermost curve represents supply as measured by standing crop along the resource continuum, and the lower curves represent utilization by 7 hypothetical species. Species toward the tails of the spectrum have broader utilization curves because their resources are less abundant. The sum of the species utilization curves is the over-all demand (dashed curve). At equilibrium, resources are consumed at the same rate they are renewed along the entire continuum. Moreover, minimization of interspecific competition results in a relatively constant ratio of demand to supply along any given resource continuum as shown. Analogous arguments can be made for discrete resource categories.

1975a, 1975b). Thus niche relationships among potentially competing species are often visualized and modeled with bell-shaped utilization curves along a resource gradient, such as height above ground or prey size (fig. 1). The sum of the utilization curves of component species represents the total demand along the resource spectrum. When expressed as rates, this demand curve is equal to the rate of resource consumption and/or renewal. The supply curve, on the other hand, is a measure of the instantaneous availability of various resources as measured by their standing crops. Along any given resource continuum, pressures (both ecological and evolutionary) leading to the avoidance of interspecific competition dictate that the ratio of demand to supply must be constant. Hence, all resources should be used in proportion to their availability, and the intensity of competition does not vary among resources. See MacArthur (1969, 1970) for an alternative but related treatment.

Although this emphasis upon resource use is operationally very convenient and will be employed here, it does neglect reproductive tactics and reproductive success, which clearly must eventually be integrated into niche theory (Pianka, 1976a).

In any case, we focus here on differential use of resources among members of desert saurofaunas. We search for answers to some fundamental questions about community structure, such as the following:

1. *How* are available resources divided among members of an ecological community? Is this segregation nonrandom? If so, how?
2. How much do pairs of species overlap in their use of resources, and how does maximal overlap vary with factors such as environmental variability, intensity of competition, and number of species?
3. Are species evenly dispersed in niche space, or are there clusters of functionally similar species with similar ecologies ("guilds") separated from other such groups by lower overlaps? If so, why? How are such guilds structured?
4. How many, and which, niche dimensions are important in separating species (and hence reducing interspecific competition)? Why?

Competition is the conceptual backbone of much current ecological thought; nonetheless, it remains surprisingly elusive to study and hence is poorly understood (probably because avoidance of competition is always advantageous when possible). Nevertheless, precise mechanisms by which available resources are divided among members of a community must be known before determinants of species diversity and community structure can be fully understood. For these reasons, resource-partitioning among coexisting species, or niche segregation, has attracted considerable interest (for recent reviews, see Lack, 1971; MacArthur, 1972; Cody, 1974; Schoener, 1974; Pianka, 1976b).

We do not attempt to review the now extensive body of theory on niche breadth and overlap (for an entry to this literature, see Whittaker and Levin, 1975); rather, we simply outline methods of quantifying niche overlap and indicate some difficulties that are of particular concern in the present context.

The basic raw data for analysis of niche overlap is the resource matrix, which is simply an m by n matrix indicating the amount (or rate of consumption) of each of m resource states utilized by each of n different species. From this matrix, one generates an n by n matrix of overlap with ones on the diagonal and values less than unity as off-diagonal elements. Overlap is sometimes equated with competition coefficients ("alphas") because overlap is much easier to measure. However, the caveat is often issued that overlap need not result in competition unless resources are in short supply. Indeed, extensive overlap may well be possible when there is a surplus of resources (low demand/supply), whereas maximal tolerable overlap may be much less in more saturated environments. Because the ratio of demand over supply must be constant along any *particular* resource gradient, intensity of competition should be directly proportional to the actual overlap observed along that resource spectrum. But caution must be exercised in comparing patterns of niche overlap along different resource axes or between different communities.

Throughout this paper, we quantify niche breadth with the diversity index of Simpson (1949) and niche overlap with the symmetrical overlap index of Pianka (1973, 1974). (The precise formula used to measure overlap is somewhat arbitrary since all overlap indices generate values ranging between zero and one with various degrees of departure at intermediate values.)

Niche overlap theory is usually framed in terms of a single niche dimension. As such, each species has only two neighbors in niche space, and overlap matrices contain many zeros and only two positive entries on the off-diagonal per row. Real plants and animals, however, differ in their use of just one resource only infrequently; rather, pairs of species often show moderate niche overlap along two or more niche dimensions. Complementarity of niche dimensions also occurs, with pairs that have high overlap along one niche dimension overlapping little on another dimension and vice versa (Schoener, 1974, 1975). As the effective number of niche dimensions rises, the number of neighbors in niche space increases more or less geometrically. Moreover, overlap matrices contain fewer off-diagonal elements of zero, and the variance in observed overlap usually falls, both within rows and over the entire matrix. Niche dimensionality also strongly affects the potential for "diffuse" competition arising from the total competitive effect of all interspecific competitors (MacArthur, 1972). Note that the over-all effect of relatively low competitive inhibition per species summed over many other species could well be as strong or even stronger than much more intense competitive inhibition (per species) by fewer competing species. Thus an increased number of niche dimensions, by generating a greater potential for immediate neighbors in niche space, can intensify diffuse competition.

We now discuss some problems and consequences of multidimensional niche relationships. Imagine that height above ground and prey size are the two critical niche dimensions that species use differentially and thus avoid or reduce interspecific competition (fig. 2). Analysis of resource utilization and niche separation along more than a single niche dimension should proceed through estimation of proportional *simultaneous* utilization of all resources along each separate niche dimension. These define a three-dimensional resource matrix, with each entry representing the probability of capture of a prey item of a given size at a particular height by each of the species present. Obtaining such multidimensional utilization data is extremely difficult, however, because animals move and integrate over both space and time. Accurate estimates of an animal's true use of a multidimensional niche space could be obtained only by monitoring continually an individual's use of all resources (even then, the degree to which prey individuals move between microhabitats will affect competition in obscure but vitally important ways!). Because such continual observation is often extremely tedious or even impossible, one usually approximates from separate unidimensional utilization distributions (fig. 2 and 3). Just as the three-dimensional shape of a mountain cannot be accurately determined from two of its silhouettes as viewed at right angles, these "shadows" do not allow inference of the true multidimensional utilization. The question of the degree of dependence or independence of dimensions becomes critical. Provided that niche dimensions are truly independent, with prey of any size being equally likely to be captured at any height, over-all multidimensional utilization is simply the product of the separate unidimensional utilization functions (May, 1975). Under perfect indepen-

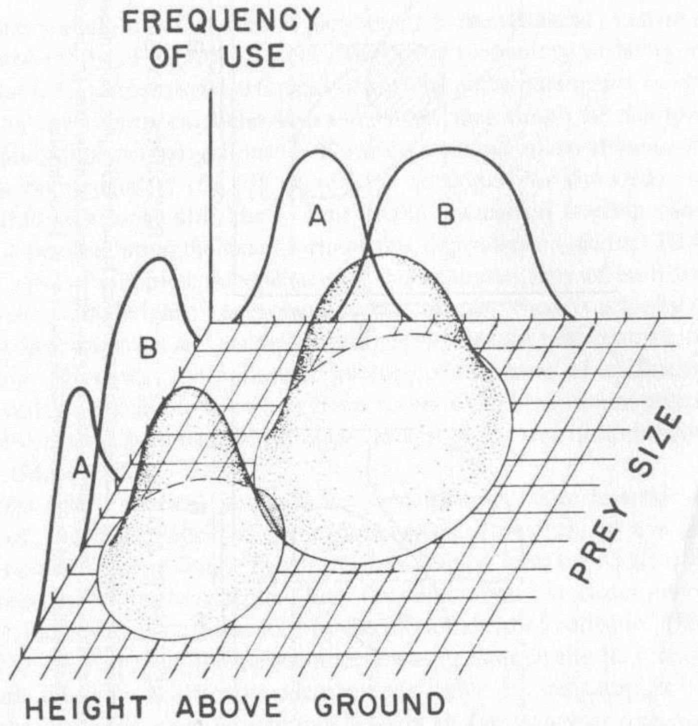

Fig. 2. Resource utilization surfaces for two hypothetical species, A and B, along two different niche dimensions. Silhouettes of these peaks on either resource axis alone overlap, but true multidimensional overlap is slight (see text).

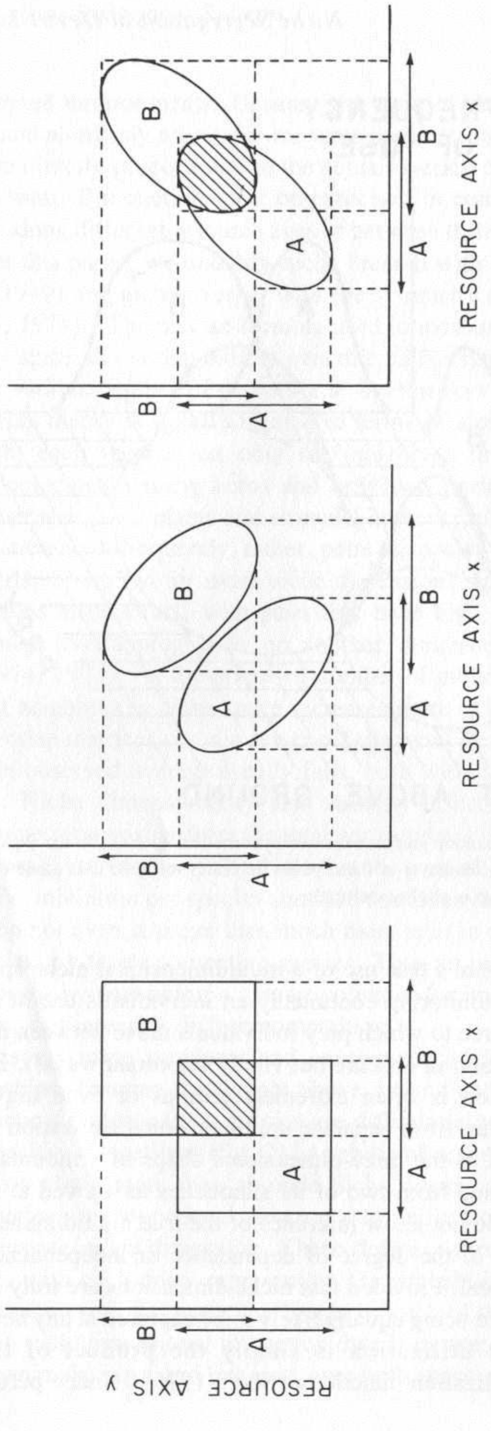

Fig. 3. Three different cases of niche overlap on two resource dimensions with identical unidimensional projections. In the leftmost plot, niche dimensions do not interact and unidimensional projections indicate multidimensional conditions accurately (dimensions are truly independent and niche axes are orthogonal). In the center and right plots, however, niche dimensions are partially interdependent and their unidimensional shadows can be misleading.

dence, the probability of capture of prey item *i* in microhabitat *j* is then equal to the probability of capture of item *i* times the probability of being in microhabitat *j*. Unidimensional estimates of various niche parameters (including overlap) along component niche dimensions may then simply be multiplied to obtain multidimensional estimates. However, should niche dimensions be partially interdependent (fig. 3), there is no substitute for knowledge of the true multidimensional utilization. True multidimensional overlap can vary greatly depending upon the exact form of this dependence (see fig. 3). In the extreme case of complete dependence (if, for example, prey of each size are found only at one height), appearances to the contrary, there is actually only a single niche dimension and a simple average provides the best estimate of true utilization. Moreover, the arithmetic average of estimates of undimensional niche overlap obtained from two or more separate unidimensional patterns of resource use actually constitutes an *upper bound* on the true multidimensional overlap (May, 1975).

In most lizard species, it would be virtually impossible to evaluate the degree of interdependence of niche dimensions. However, in a relatively sedentary subterranean skink (*Typhlosaurus lineatus*) from the Kalahari desert that specializes on fairly sedentary prey (termites), one can assess the degree to which foods eaten are influenced by the microhabitat of collection (Huey et al., 1974). Most species and castes of termites are eaten in similar proportions by lizards taken from different microhabitats (table 1), indicating that these two niche dimensions are largely independent in *Typhlosaurus lineatus*.

In reviewing major factors leading to ecological isolation among birds, Lack (1971) concluded that the most important were differences in geographic range, habitat, and foods eaten. Schoener (1974) recently reviewed patterns of resource-partitioning in some eighty-odd natural communities ranging from simple organisms such as slime molds through various mollusks, crustaceans,

TABLE 1

PERCENT AND TOTAL NUMBER OF PREY ITEMS EATEN BY TYPHLOSAURUS LINEATUS UNDER SPECIFIC MICROHABITATS

	LOGS		LEAF LITTER		CROTALARIA		GRASS
	Sandplain Areas	Sandridge Areas	Sandplain Areas	Sandridge Areas	Sandplain Areas	Sandridge Areas	Sandridge Areas
Allodontermes (schultzei?)							
Minor workers	32.3	34.2	34.4	21.9	29.2	30.2	40.7
Major workers	24.5	52.7	48.0	74.1	42.3	64.5	54.8
Psammotermes allocerus							
Workers	36.5	7.1	7.3	1.8	24.6	1.9	1.6
Soldiers	1.0	3.9	3.0	1.4	3.2	1.4	1.8
Hodotermes mossambicus	5.5	1.8	6.0	0.6	0.7	1.1	0.7
Other termites	0.3	0.3	1.4	0.1	---	0.9	0.4
Total number of termites	2,385	4,214	2,500	4,746	1,037	3,386	2,620

insects, and other arthropods to various members of the five classes of vertebrates including lizards. He identified and attempted to rank five resource dimensions by their degree of importance in niche segregation: macrohabitat, microhabitat, food type, time of day, and seasonality of activity. As will be seen below, desert lizards use all five of these dimensions in niche segregation.

Schoener concluded that habitat dimensions are generally more important in separating niches than food-type dimensions, which in turn tend to be important more often than temporal dimensions. Moreover, he concludes that terrestrial poikilotherms partition food by being active at different times of day relatively often compared with other animals.[1] He also suggests that predators partition resources by diurnal differences in time of activity more than other groups and that vertebrates segregate less by seasonal activity differences than do lower animals. Lastly, Schoener asserts that segregation by food type is more important for animals feeding on large foods relative to their own size than it is among animals that feed on relatively small items. We examine how well Schoener's first generalization (above) holds up among desert lizards below.

THE NULL HYPOTHESIS: RANDOM PARTITIONING OF RESOURCES

Observed estimates of niche overlap are often compared with values of limiting similarity predicted from theoretical arguments, such as those of MacArthur and Levins (1967; see, e.g., Orians and Horn, 1969) or May and MacArthur (1972; see May, 1974). Because such "magic" numbers depend strongly upon specific assumptions of models concerned (Abrams, 1975), we follow a somewhat different approach here.

How much would niches overlap if resources were simply allocated randomly among members of a community? Such "randomized" communities are useful for comparison with real communities to detect nonrandom patterns of niche segregation and community structure (Lawlor and Pianka, in prep.).[2] Various such randomized communities can be constructed with differing degrees of semblance to observed communities to elucidate the structure of the latter. Perhaps the most random way to construct an artificial community is to assign the utilization coefficients in the resource matrix with a random number generator. Lawlor and Pianka do this by sampling m values from a uniform random distribution over the interval zero to one for each "species." Dividing these values by their sum gives each of n species its utilization rate for resource j. Overlap matrices computed from such randomized resource matrices (randomization treatment 1) have remarkably similar distributions of niche overlap for a wide variety of artificial communities (table 2 and fig. 4).

TABLE 2

Overlap Statistics Computed from 100 Randomly Constructed Communities with Different Numbers of Equally Abundant Resources and Species As Indicated

Number of Species	Number of Resource States	Average Overlap	Average Maximal Overlap	Mean Variance in Overlap
5	5	.778	.940	.016
5	15	.756	.863	.005
5	25	.755	.843	.003
10	5	.774	.975	.018
10	15	.755	.903	.006
10	25	.755	.872	.004
15	5	.771	.985	.019
15	15	.759	.918	.006
15	25	.756	.885	.004
40	5	.774	.994	.019
40	15	.753	.943	.006
40	25	.752	.914	.004

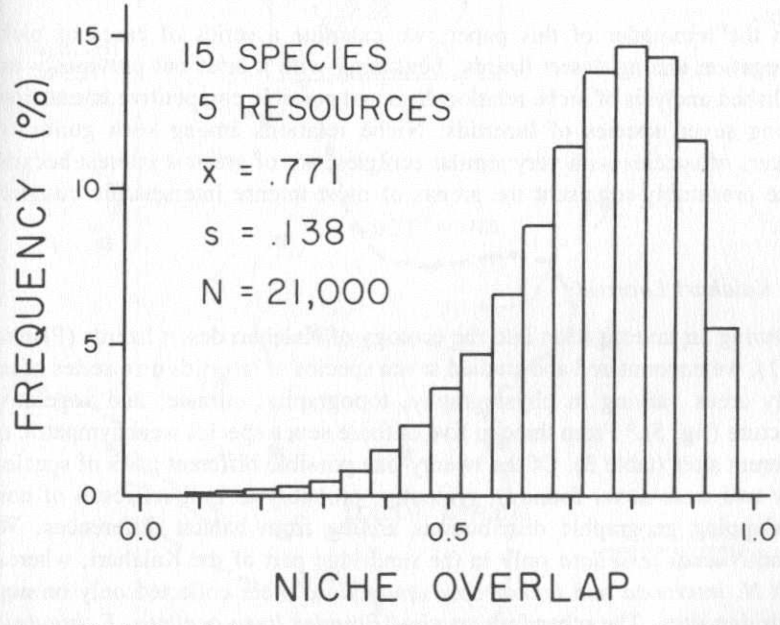

Fig. 4. Distribution of niche overlaps in 100 randomly constructed communities with 15 species and 5 equally abundant resource states. Five numbers were drawn from a uniform random distribution for each species and used to assign utilization coefficients in the resource matrix. Communities with different numbers of species and resource states have very similar distributions of overlap (see table 2).

Using a computer, 100 such randomized communities were constructed for all combinations of 5, 10, 15, and 40 species and 5, 15, and 25 resource states. Average overlap in these communities varied only from .752 to .778, increasing slightly with both increased number of species and with decreased number of resource states (table 2). Variance in overlap is quite low in these randomized communities, increasing slightly with increased number of species and with a reduced number of resource states (table 2). In a more realistic randomization routine (treatment 2), Lawlor and Pianka incorporate some of the structure of the real community by retaining zero utilization coefficients for resources that are not used by observed species and simply repartitioning randomly those that are actually used among each consumer. Still another randomization process is to interchange observed utilization rates among the actual resource states used by each species. Comparisons of the distributions of overlap in such randomly constructed communities with observed overlap reveal intriguing patterns in the structure of real communities (below).

NICHE RELATIONSHIPS AMONG SELECTED LIZARD GUILDS

In the remainder of this paper, we examine a series of cases of niche segregation among desert lizards, beginning with a brief but previously unpublished analysis of niche relationships and possible competitive interactions among seven species of lacertids. Niche relations among such guilds, or clusters of species with very similar ecolgies, are of greatest interest because these presumbly represent the arenas of most intense interspecific competition.

Kalahari Lacertids

During an investigation into the ecology of Kalahari desert lizards (Pianka, 1971), we encountered and studied seven species of lacertids on a series of ten study areas varying in physiography, topography, climate, and vegetative structure (fig. 5).[3] From three to five of these seven species were sympatric on different sites (table 3). Of the twenty-one possible different pairs of species, only two were never found in sympatry, probably as a direct result of nonoverlapping geographic distributions arising from habitat differences. We found *Nucras tessellata* only in the sandridge part of the Kalahari, whereas both *N. intertexta* and *Ichnotropis squamulosa* were collected only on nonsandridge sites. The other four species (*Eremias lineo-ocellata, E. lugubris, E. namaquensis*, and *Meroles suborbitalis*) are found on both sandridge and non-sandridge areas (table 3) and are usually sympatric.

On our sandridge study areas, *E. lineo-ocellata* and *E. lugubris* frequent habitats with red sands and large shrubs such as *Acacia mellifera*, often on the slopes or crests of sandridges. In contrast, *E. namaquensis* and *Meroles*

TABLE 3

LACERTIDS FOUND ON TEN KALAHARI DESERT STUDY SITES VARYING IN CLIMATE, VEGETATION, AND TOPOGRAPHY

	SANDRIDGE AREAS						NON-SANDRIDGE AREAS					
LIZARD SPECIES	L	K	M	B	A	X	G	D	R	T_s*	T_f*	T
Eremias lineo-ocellata	x	x	x	x	x	x	x	x	x	x	x	x
Eremias namaquensis	x	x		x		x	x		x		x	x
Eremias lugubris	x	x	x		x	x	x	x	x	x	x	x
Ichnotropis squamulosa							x			x		x
Meroles suborbitalis	x	x	x	x	x	x	x	x	x			
Nucras tessellata	x			x	x							
Nucras intertexta										x	x	x
Total number of lacertid species	5	4	3	4	4	4	5	3	4	4	4	5
Total number of lizard species	16	15	14	17	15	16	13	13	11	14	13	16

*T_s and T_f are sub-areas of T.

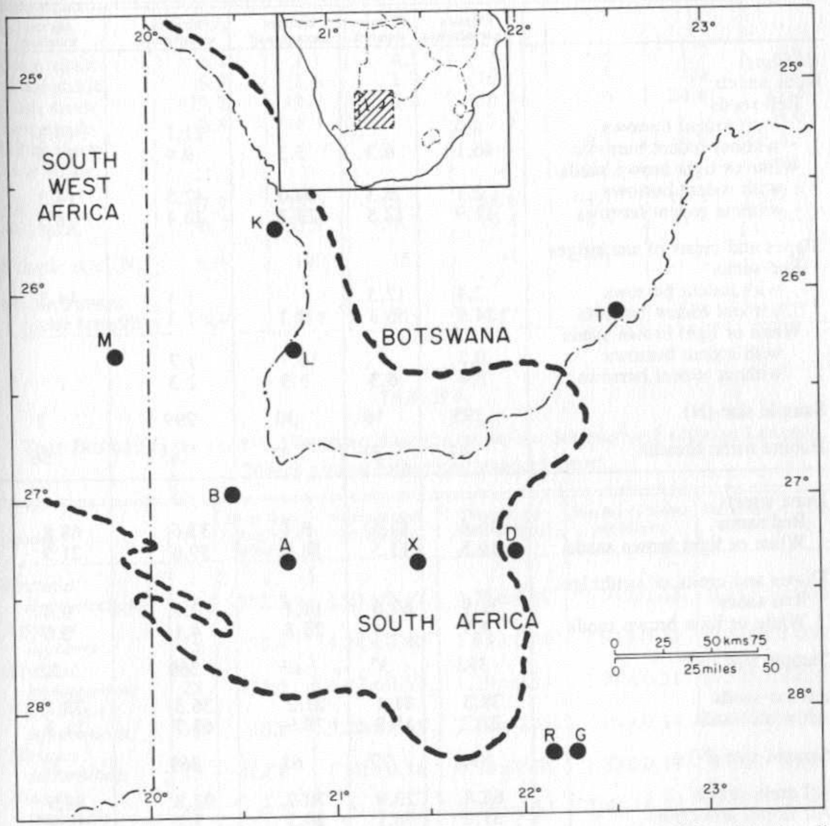

Fig. 5. Positions of ten study areas in the Kalahari desert of southern Africa. Six sites lie within the sandridge area, the approximate boundary of which is delineated by the dashed line following Leistner (1967).

suborbitalis are usually found in interdunal flats with either white or light-brown sands, generally with smaller shrubs such as *Rhigozum trichotomum* and often near rodent burrows (table 4). Although this habitat separation is certainly not complete, differences between the two red-sand species and the two white-sand species are fairly striking (tables 4 and 15). The fifth sandridge study area species, *N. tessellata*, occurs largely on red sandy flats but tends to be active somewhat later in the day than the preceding species (below). Habitat niche breadth is low in *E. lugubris* and *E. namaquensis*, intermediate in *E. lineo-ocellata* and *Meroles suborbitalis*, and high in *Nucras tessellata*. Overlaps in habitat among these species are given in table 15 (below).

TABLE 4

Habitat Relationships of Five Species of Lacertids in the Sandridge Region of the Southern Kalahari (Percentages)

	Eremias lineo-ocellata	Eremias lugubris	Eremias namaquensis	Meroles suborbitalis	Nucras tessellata
Habitats					
Dune streets					
Red sands					
with rodent burrows	8.9			21.1	14.3
without rodent burrows	46.1	6.3	3.3	9.4	28.5
White or light brown sands					
with rodent burrows	2.1	6.3	50.0	42.5	14.3
without rodent burrows	11.9	12.5	23.3	20.4	28.5
Slopes and crests of sandridges					
Red sands					
with rodent burrows	2.4	12.5		1.3	14.3
without rodent burrows	24.9	56.3	3.3	1.3	
White or light brown sands					
with rodent burrows	0.3		16.7	1.7	
without rodent burrows	3.4	6.3	3.3	2.3	
Sample size (N)	293	16	30	299	7
Habitat niche breadth	.42	.35	.37	.45	.56
Dune streets					
Red sands	46.4	13.5	6.4	33.6	68.8
White or light brown sands	16.8	13.5	58.7	59.6	21.9
Slopes and crests of sandridges					
Red sands	31.9	67.6	11.1	2.7	9.4
White or light brown sands	4.9	5.4	23.8	4.1	0.0
Sample size (N)	392	37	63	369	32
All red sands	78.3	81.1	21.2	36.3	78.1
All white sands	21.7	18.9	78.9	63.7	21.9
Sample size (N)	392	37	63	369	32
All dune streets	62.8	23.9	70.7	92.8	88.9
All slopes and crests	37.2	76.1	29.3	7.2	11.1
Sample size (N)	468	71	116	416	54

Microhabitats used by the various species also differ, with *Meroles* and *E. namaquensis* occurring in the open sun more often than other species; as a

TABLE 5

Percentages of Occurrence, Sample Sizes, and Microhabitat Niche Breadths of Seven Species of Lacertid Lizards.

	Eremias lineo-ocellata	Eremias lugubris	Eremias namaquensis	Ichnotropis squamulosa	Meroles suborbitalis	Nucras tessellata	Nucras intertexta
Michrohabitat							
Open sun	29.3	32.1	54.8	18.3	56.7	25.4	4.6
Grass sun	11.7	7.9	1.2	17.2	3.4	4.2	4.6
Bush sun	25.5	33.7	24.9	22.0	24.1	34.8	40.9
Tree sun	0.5	1.6	0.6	1.1			4.6
Other sun					0.1	0.9	4.6
Low sun	0.6				0.3		
Open shade	1.4	1.1	4.5	1.1	1.8	1.7	4.6
Grass shade	6.9	2.6	1.2	16.1	1.8	7.6	4.6
Bush shade	23.7	19.7	12.9	16.7	11.6	24.6	27.3
Tree shade	0.3	1.3		7.5			4.6
Other shade					0.1	0.9	
Low shade					0.1		
All sun	67.7	75.3	81.3	58.6	84.7	65.2	59.3
All open	30.7	33.2	59.3	19.4	58.5	27.1	9.2
Sample size (N)	635	190	167	93	482	59	11
Michrohabitat niche breadth	.369	.317	.219	.487	.211	.328	.325

TABLE 6

Time Budget Data on the Foraging Tactics of Seven Species of Lacertid Lizards (Means plus or minus one standard error)

Species	N	Total Time Observed (Minutes)	Meters Moved per Minute	Distance per Move (Meters)	Number of Moves per Minute	Proportion of Time Spent Moving
Eremias lineo-ocellata	15	152.5	1.23±0.37	0.76±0.07	1.54±0.42	0.143±0.030
Eremias lugubris	15	72.1	5.24±0.40	1.93±0.19	2.97±0.28	0.574±0.038
Eremias namaquensis	25	131.3	4.67±0.52	1.79±0.11	2.78±0.31	0.535±0.052
Ichnotropis squamulosa	5	20.9	3.20±0.41	1.12±0.18	3.10±0.14	0.546±0.079
Meroles suborbitalis	15	122.8	1.02±0.14	0.58±0.06	1.83±0.19	0.135±0.016
Nucras tessellata	11	59.7	7.71±1.23	2.23±0.33	2.90±0.37	0.502±0.052
Nucras intertexta	3	8.9	8.93±2.46	2.53±0.87	3.69±0.27	0.649±0.039

result of this heavy usage of a single microhabitat category, these two white-sand species have relatively narrow microhabitat niche breadths (table 5).

Even within the genus *Eremias*, foraging tactics differ rather strikingly among these lacertids (table 6). Both *Meroles suborbitalis* and *Eremias lineo-ocellanta* are conspicuously sit-and-wait predators, whereas the remaining five species forage more widely, moving not only more frequently but also over greater distances and a greater percentage of the time. In the white-sand versus red-sand habitat separation documented above (table 4), note that a widely foraging species is paired with a sit-and-wait species in each habitat.

TABLE 7

OBSERVED DIETS OF SEVEN SPECIES OF LACERTIDS (PROPORTIONS BY VOLUME)

Prey Category	Eremias lineo-ocellata	Eremias namaquensis	Eremias lugubris	Nucras tesellata	Nucras intertexta	Meroles suborbitalis	Ichnotropis squamulosa
Centipedes	....	....	....	....	....	0.001	0.001
Spiders	0.086	0.078	0.008	0.095	0.010	0.045	0.040
Scorpions & Solpugids	0.018	0.018	0.009	0.532	0.010	0.026	0.007
Ants	0.023	0.039	0.005	0.002	0.004	0.050	0.001
Other Hymenoptera	0.020	0.007	0.001	....	....	0.014	....
Locustidae	0.112	0.046	0.009	0.171	0.360	0.066	0.116
Blattidae	0.003	0.001	0.003	....	0.022	....	0.002
Beetles	0.152	0.023	0.009	0.010	0.131	0.147	....
Termites							
Allondotermes (unidentified)	....	....	....	0.001	....	0.003	0.015
Allondotermes major workers	0.109	0.075	0.530	0.002	0.077	0.085	0.494
Allondotermes minor workers	0.018	0.007	0.071	....	....	0.022	0.047
Psammotermes allocerus soldiers	0.002	0.005	0.013	....	....	0.002	0.001
Psammotermes allocerus workers	0.001	0.003	0.021	....	....	0.003	....
Hodotermes mossambicus	0.142	0.190	0.139	0.031	0.076	0.180	0.175
Trinervitermes spp.	0.123	0.288	0.120	0.006	0.009	0.177	0.034
Termite species "M"	0.001	0.004	....	....	....	0.002	0.006
Termite species "N"	0.023	0.061	0.010	....	....	0.010	....
Termite species "O"	0.003	....	0.019	....	....	0.003	....
Other unidentified termites	0.013	0.033	0.005	0.007	0.004	0.028	0.019
Homoptera & Hemiptera	0.041	0.007	0.005	0.0	....	0.022	....
Diptera	0.014	0.002	0.001	0.001	....	0.018	....
Lepidoptera	0.003	....	0.002	0.009	0.144	0.003	....
Larvae							
Coleoptera	0.023	0.008	0.002	0.001	....	0.035	0.031
Lepidoptera	0.002	0.023	....	....	....	0.001	....
Neuroptera	0.002	0.001	0.001	0.064	....	0.007	....
Unidentified larvae	0.017	0.015	0.008	....	....	0.016	....
Vertebrates	0.005	0.008	....	....	....	0.002	....
Plant Material	0.004	0.002	....	....	....	0.003	....
Miscellaneous	0.038	0.054	0.007	0.068	0.153	0.024	0.009
Total volume (cc)	111.04	25.18	58.97	10.58	2.29	92.95	23.69
Number of stomachs	1,135	218	238	79	6	780	112
Food Niche Breadth	0.357	0.239	0.107	0.104	0.170	0.323	0.117

TABLE 8

PERCENTAGES OF TERMITES, BY VOLUME, IN THE STOMACHS OF VARIOUS SPECIES OF KALAHARI LACERTID LIZARDS.

Species	Percentage of Termites
Eremias lineo-ocellata	43.5
Eremias lugubris	92.8
Eremias namaquensis	66.6
Meroles suborbitalis	51.5
Ichnotropis squamulosa	79.1
Nucras tessellata	6.4*
Nucras intertexta	16.6†

*Eats 53% scorpions and 17% grasshoppers.
†Eats 36% grasshoppers.

Not unexpectedly, certain dietary differences are associated with this dichotomy in foraging tactics (tables 7 and 8). One would expect sit-and-wait predators to rely largely on moving prey and to take a fairly wide variety of prey types, whereas widely foraging predators should encounter and consume non-moving types of prey more frequently and might well be able to be somewhat more selective as to which prey items they choose to consume, leading to narrower food niche breaths. For the sit-and-wait tactic to pay off, prey must be relatively mobile and prey density must be high (or predator energy requirements low). One might predict, then, that the sit-and-wait tactic would be less prevalent during periods of prey scarcity. The success of the widely foraging tactic also depends upon prey mobility and prey density and predator's energetic requirements (which should usually be higher than those of sit-and-wait predators because the latter expend less energy in search), but the spatial distribution of the prey and the searching abilities of the predator now assume substantial importance.

Diets of these lacertids fit theoretical expectations reasonably well. The two sit-and-wait foragers have broader food niches than the widely foraging species (table 7). Two widely foraging species of *Nucras* specialize on relatively large generally nonmoving prey, whereas the other widely foraging species consume more termites (also relatively sedentary prey for diurnal lizards) than do the two sit-and-wait species (table 8). Prey size distributions are given in table 9.

Times of activity vary markedly among these lacertids, on both a daily and a seasonal basis. An instructive seasonal comparison can be made between the two sit-and-wait species, *Meroles suborbitalis* and *Eremias lineo-ocellata*, both of which are active throughout the entire year (*Nucras, E. lugubris*, and *E. namaquensis* are generally inactive during the winter). However, *Meroles* are adult (average snout-vent length nearly 66 mm) during winter (May-June) when mating occurs, whereas *E. lineo-ocellata* average only 30–40 mm during this same period (table 10). Ovigerous female *Meroles* were collected

TABLE 9

OBSERVED DISTRIBUTIONS OF PREY SIZE (IN CUBIC CENTIMETERS)

Prey Size Category	Eremias lineo-ocellata	Eremias namaquensis	Eremias lugubris	Nucras tesellata	Nucras intertexta	Meroles suborbitalis	Ichnotropis squamulosa
Under .001	0.6	0.3	. . . .	. . . .	. . . .	12.4	0.4
.001–.005	66.0	58.9	91.8	13.4	69.3	49.5	92.6
.006–.014	14.6	23.4	2.9	26.1	5.3	18.6	. . . .
.015–.024	10.6	11.8	3.6	11.8	9.3	13.9	1.5
.025–.034	4.3	3.4	1.2	12.6	1.3	2.7	2.3
.035–.044	1.3	1.0	0.3	2.5	. . . .	0.9	0.3
.045–.054	1.2	0.5	0.2	10.1	1.3	1.0	0.3
.055–.064	0.1	0.0	0.001	2.5	5.3	0.1	0.2
.065–.074	0.1	0.3	0.001	0.8	. . . .	0.1	. . . .
.075–.084	0.3	0.1	. . . .	1.7	. . . .	0.3	0.1
.085–.094	0.02	. . . .	. . . .	1.7	1.3	0.01	. . . .
.095–.104	0.3	0.1	0.002	4.2	4.0	0.2	0.05
.105–.174	0.1	0.05	0.001	3.4	. . . .	0.1	0.02
.175–.224	0.2	0.1	. . . .	1.7	. . . .	0.04	0.02
.225–.274	0.04	. . . .	. . . .	. . . .	1.3	0.1	. . . .
.275–.324	0.05	0.05	. . . .	1.7	. . . .	0.01	0.02
.325–.374	0.01	. . . .	. . . .	. . . .	. . . .	. . . .	0.05
.375–.424	0.02	. . . .	. . . .	0.8	. . . .	. . . .	0.05
.425–.474	. . . .	. . . .	0.001	0.8	. . . .	. . . .	. . . .
Over .475	0.03	0.05	. . . .	4.1	1.3	. . . .	. . . .
N (lizards)	980	195	215	48	6	702	105
N (total number of prey items)	10,947	2,574	12,221	119	75	9,626	4,362
Mean head length	11.53	10.87	12.24	11.74	14.41	12.23	12.24
Mean prey volume	.009	.009	.005	.074	.026	.009	.005

over a near five-month period that includes winter, from 21 May through 13 October (with a single record on 12 December); in contrast, ovigerous female *E. lineo-ocellata* were found from 24 November to 12 March. Juvenile *Meroles* emerged earlier and at a larger size than *E. lineo-ocellata*, resulting in a clear separation by size of the juveniles of the two species as they grow (fig. 6 and table 10). This size difference could well serve to reduce interspecific competition between juveniles of the two species (see also Broadley, 1969 and Schoener, 1976).

Distinct temporal patterns of activity occur within the day as well. For example, like many diurnal desert lizards, both *Meroles suborbitalis* and *E. lineo-ocellata* typically have a unimodal daily period of activity during the cold winter months, but this gradually gives way to a bimodal daily activity pattern during warmer months (figs. 7 and 8). Still other species appear to have only a single peak of activity each day. Some species, notably the two species of *Nucras* under study here, emerge and are active considerably later than the other lacertid species (table 11). Differences in thermal relationships were correlated with, and doubtlessly causally related to, these observed differences in temporal patterns of activity. Thus, *Meroles* have relatively low mean air and body temperatures, whereas these same statistics for *Nucras* are

TABLE 10

STATISTICS ON SNOUT-VENT LENGTHS (IN MM) OF TWO SPECIES OF LACERTIDS BY MONTHS (SEE TEXT AND FIGURE 6)

	Jan	Feb	Mar	Apr	May	July	Aug	Sept	Oct	Nov	Dec
Eremias lineo-ocellata											
Juveniles											
$\overline{X}$	24.89	33.72	21.50	42.95	36.35	36.42	40.16	45.06	48.61	. . . .	. . . .
S	3.18	6.19	2.12	13.48	10.26	5.16	4.94	7.05	6.81	. . . .	. . . .
SE	0.52	0.91	1.50	1.29	1.38	0.70	0.52	0.63	0.59	. . . .	. . . .
N	38	46	2	109	55	55	91	126	131	. . . .	. . . .
Range	19–33	21–46	20–23	21–66	20–61	27–58	29–60	34–70	37–69	. . . .	. . . .
Adults											
$\overline{X}$	59.97	60.31	59.27	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	55.00	55.00
S	3.45	2.57	3.81	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	3.99	4.65
SE	0.27	0.21	0.57	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	0.94	0.43
N	160	153	45	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	18	115
Range	48–68	54–66	50–67	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	47–62	41–63
Meroles suborbitalis											
Juveniles											
$\overline{X}$	38.73	46.06	52.19	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	32.97
S	5.26	6.12	5.73	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	3.57
SE	0.62	0.87	0.76	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	0.46
N	71	49	57	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	61
Range	26–49	28–53	38–64	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	26–43
Adults											
$\overline{X}$	62.38	62.08	. . . .	56.22	57.03	58.41	58.30	58.49	58.73	57.20	58.74
S	3.38	2.75	. . . .	3.34	6.11	3.83	3.03	4.22	3.62	2.17	3.14
SE	0.85	0.76	. . . .	0.39	0.57	0.50	0.38	0.50	0.49	0.97	0.72
N	16	13	. . . .	72	115	58	63	70	55	5	19
Range	57–66	59–70	. . . .	46–64	30–71	48–63	50.68	42–69	48–67	55–60	54–64

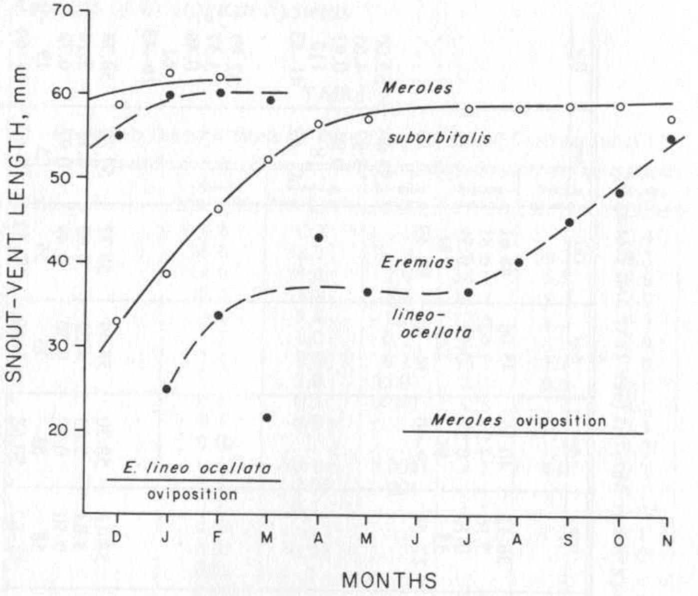

Fig. 6. Mean snout-vent lengths, by months, of two sit-and-wait lacertid species showing temporal separation by size. Statistics are given in table 10.

TABLE 11

NUMBERS OF LACERTID LIZARDS OBSERVED ACTIVE ABOVE GROUND DURING HOURLY INTERVALS AT VARIOUS SEASONS

SPECIES AND SEASON	TIME CATEGORIES 7	8	9	10	11	12	13	14	15	16	17	18
Eremias lineo-ocellata												
Spring	. .	. .	19	33	36	45	43	32	31	27	9	1
Summer	10	58	108	83	32	3	10	14	16	18	67	57
Fall	. .	3	16	37	56	31	5	11	14	6	8	4
Winter	. .	. .	. .	3	20	28	24	43	19	3	. .	. .
Eremias lugubris												
Spring	. .	. .	3	10		1	1	3	. .	. .	. .	. .
Summer	. .	25	58	32	15	1	12	6	6	4	2	1
Fall	. .	. .	12	19	14	7	2	4	. .	. .	1	. .
Winter	. .	. .	. .	. .	2	1	2	2	. .	. .	. .	. .
Eremias namaquensis												
Spring	. .	. .	3	10	5	5	3	3	5	5	0	3
Summer	. .	3	16	11	8	5	0	4	7	9	14	26
Fall	. .	. .	14	12	7	11	8	5	5	2	2	2
Winter	. .	. .	. .	. .	1	1	1	2	. .	. .	. .	. .
Meroles suborbitalis												
Spring	. .	. .	9	12	21	20	18	14	12	16	6	0
Summer	4	28	35	37	18	1	3	3	11	9	31	44
Fall	. .	1	6	30	41	27	45	32	19	14	5	4
Winter	. .	. .	. .	. .	15	27	28	46	16	2	. .	. .
Nucras tessellata												
Spring	. .	. .	. .	. .	. .	3	1		1	. .	1	. .
Summer	1	4	20	27	11	2	1	3	3	2	1	1
Fall	. .	. .	. .	. .	4	2	. .	1	. .	. .	1	. .

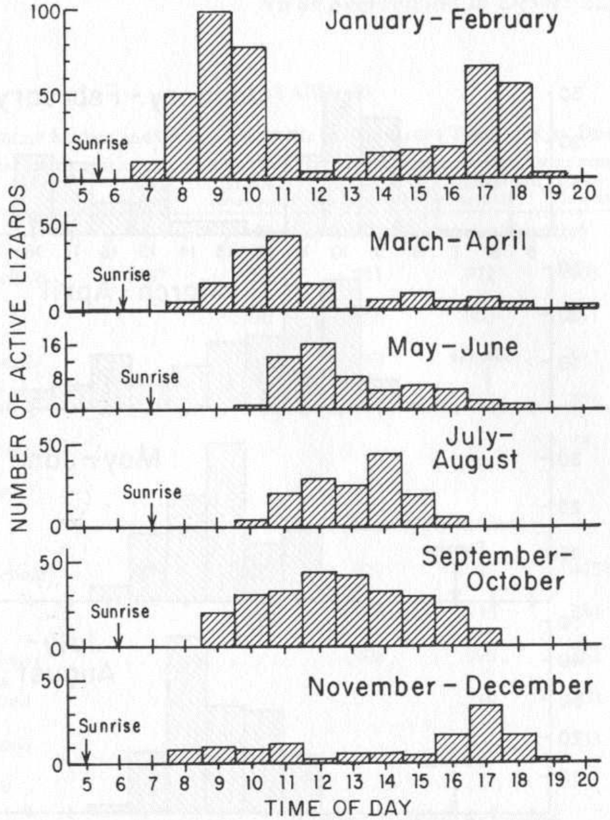

Fig. 7. Histograms of time of activity of *Eremias lineo-ocellata* at bimonthly intervals. Activity is bimodal during hot summer months but unimodal during midday in cooler winter months.

TABLE 12

STATISTICS ON BODY AND AIR TEMPERATURES OF SEVEN SPECIES OF LACERTID LIZARDS

SPECIES	AIR TEMPERATURE $\bar{X}$	S	SE	N	BODY TEMPERATURE $\bar{X}$	S	SE	N	$r_{AT \times BT}$
Eremias lineo-ocellata	28.87	5.06	.171	875	36.84	2.33	.092	636	.579
Eremias lugubris	29.08	3.29	.221	222	37.69	2.54	.192	176	.453
Eremias namaquensis	29.83	3.52	.263	179	37.70	1.92	.167	133	.330
Ichnotropis squamulosa	31.22	2.43	.230	112	36.33	1.76	.184	92	.307
Meroles suborbitalis	26.44	5.60	.218	661	35.54	2.16	.098	485	.553
Nucras tessellata	31.55	3.55	.394	81	39.39	3.19	.481	44	.669
Nucras intertexta	34.03	0.53	.270	4	38.87	1.52	.878	3	.864

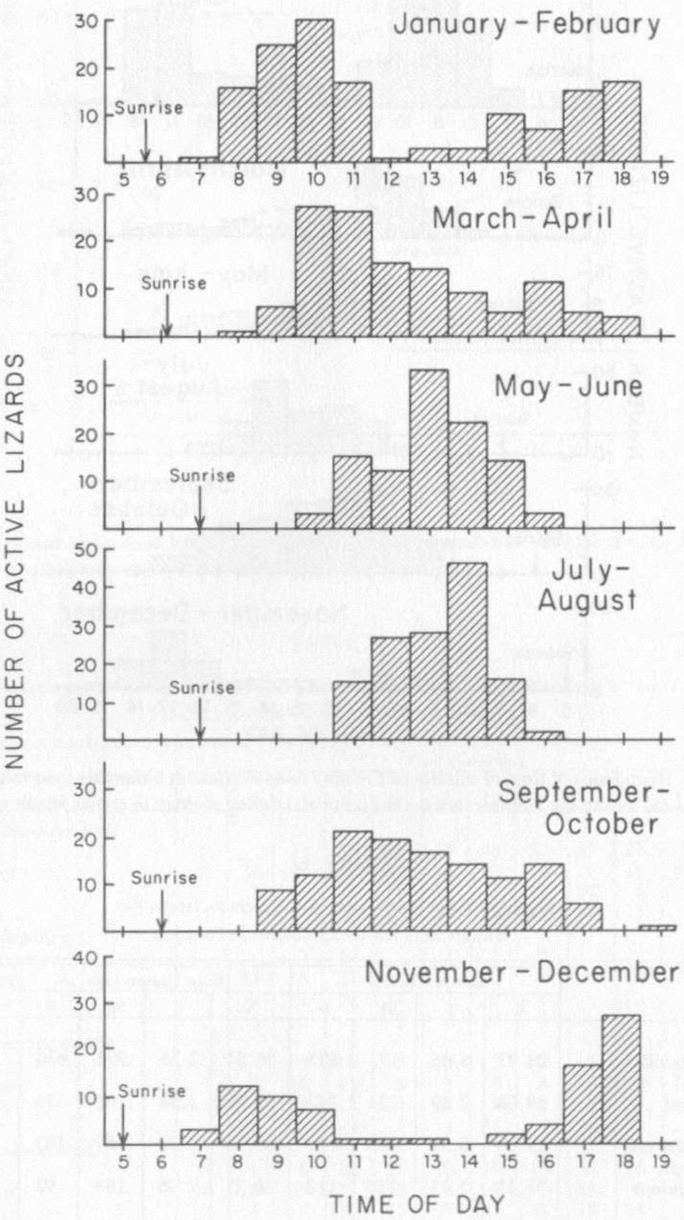

Fig. 8. Frequency distributions of time of activity of *Meroles suborbitalis* at bimonthly intervals.

TABLE 13

Overlap Matrices for the Lacertid Guild along Three Niche Dimensions

	Eremias lugubris	Eremias namaquensis	Ichnotropis squamulosa	Meroles suborbitalis	Nucras intertexta	Nucras tessellata
			Time of Activity (hours since sunrise)			
Eremias lineo-ocellata	.887	.954	.851	.972	.403	.903
Eremias lugubris	....	.790	.956	.803	.251	.905
Eremias namaquensis	....	....	.799	.933	.513	.859
Ichnotropis squamulosa	....	....	....	.754	.208	.863
Meroles suborbitalis	....	....	....	....	.431	.856
Nucras intertexta	....	....	....	....	....	.466
			15 Basic Microhabitats			
Eremias lineo-ocellata	.976	.902	.921	.901	.442	.967
Eremias lugubris	....	.945	.856	.935	.386	.977
Eremias namaquensis	....	....	.708	.996	.232	.895
Ichnotropis squamulosa	....	....	....	.710	.703	.886
Meroles suborbitalis	....	....	....	....	.233	.883
Nucras intertexta	....	....	....	....	....	.472
			19 Prey Categories by Volume			
Eremias lineo-ocellata	.899	.938	.926	.985	.532	.203
Eremias lugubris	....	.986	.990	.945	.271	.095
Eremias namaquensis	....	....	.990	.967	.346	.145
Ichnotropis squamulosa	....	....	....	.953	.374	.136
Meroles suborbitalis	....	....	....	....	.433	.151
Nucras intertexta	....	....	....	....	....	.331

comparatively high (table 12). Thermal relations of Kalahari lizards are considered in greater detail elsewhere (Huey and Pianka, 1977b).

Overlap matrices among these lacertides along various niche dimensions are presented in tables 13, 14, and 15. Table 14 gives multiplicative and summation estimates of over-all overlap, the latter representing an upper bound on the true multidimensional niche overlap (May, 1975) for the entire assemblage of seven species. Among the five species of lacertids in the

TABLE 14

Estimates of Over-all Niche Overlap among Seven Species of Lacertids along the Three Niche Dimensions of Table 13

	Eremias lineo-ocellata	Eremias lugubris	Eremias namaquensis	Ichnotropis squamulosa	Meroles suborbitalis	Nucras intertexta	Nucras tessellata
Eremias lineo-ocellata	. . . .	.779	.808	.726	.863	.095	.177
Eremias lugubris	.921	. . . .	.736	.810	.710	.026	.084
Eremias namaquensis	.931	.907	. . . .	.559	.899	.041	.112
Ichnotropis squamulosa	.899	.934	.832	. . . .	.511	.055	.104
Meroles suborbitalis	.953	.894	.965	.806	. . . .	.044	.114
Nucras intertexta	.459	.303	.364	.428	.366	. . . .	.073
Nucras tessellata	.691	.659	.633	.628	.630	.423	. . . .

Note: Product values above the diagonal and summation values below (the latter represent upper bounds on true multidimentional niche overlap [see May, 1975]).

TABLE 15

Overlap in Habitat among Five Species of Sandridge Desert Lacertids

	Eremias lugubris	Eremias namaquensis	Meroles suborbitalis	Nucras tessellata
Eremias lineo-ocellata	0.581	0.200	0.346	0.838
Eremias lugubris	. . . .	0.240	0.217	0.504
Eremias namaquensis	. . . .	. . . .	0.877	0.555
Meroles suborbitalis	. . . .	. . . .	. . . .	0.714

Note: Habitat categories are those of table 4.

sandridge area of the Kalahari, dietary overlap is essentially either all or none, whereas overlap in habitat varies more continuously, with values ranging from 0.2 to 0.88 (Table 15). Only two sandridge pairs overlap extensively in both diet and habitat (fig. 9). Interestingly enough, these two pairs with high over-all niche overlap (*Eremias lineo-ocellata* versus *E. lugubris* and *E. namaquensis* versus *Meroles suborbitalis*) both represent a pairing of a widely foraging with a sit-and-wait species.

Average overlap in microhabitat and time of activity in a 7-species lacertid guild randomized by treatment 2 (.70 and .65, respectively) did not differ significantly from the observed mean overlaps (.76 and .73). However, the observed overlap in diet among all seven species ($\bar{x} = .60$) *is* significantly

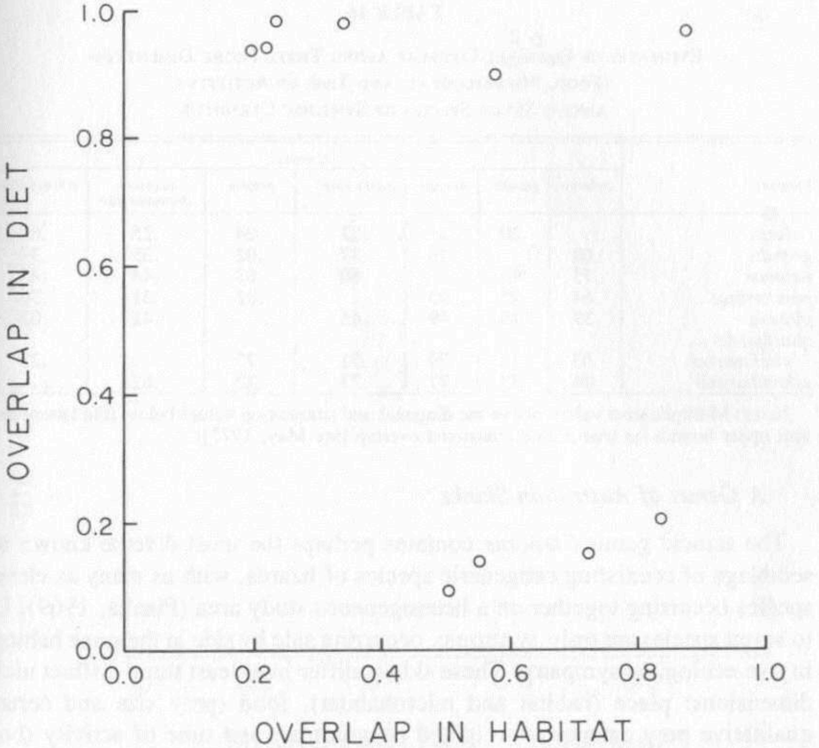

Fig. 9. Dietary overlap plotted against overlap in habitat among the five species of lacertids in sandridge areas. The two pairs with the highest over-all overlap include a sit-and-wait forager and a widely foraging species.

lower than that in communities randomized by treatment 2 ($\bar{x} = .84$, range .64 to .99 in 100 randomized communities). This nonrandomness is due to inclusion of the two species of *Nucras*, whose diets overlap relatively little with the remainder of the lacertid species (table 13): observed overlap in diet among the remaining five species averages .96, not significantly different from average overlaps under randomization treatment 2 ($\bar{x} = .85$, range .45 to .99). Among the five sandridge species, observed overlap in habitat based on the eight categories in table 4 (tables 15 and 20) is significantly lower than in guilds randomized by treatment 2 (observed $\bar{x} = .47$, randomized communities $\bar{x} = .73$ with a range of .49 to .89). Habitat separation may well be the primary factor allowing coexistence of the five lacertids in the sandridge area of the Kalahari.

TABLE 16

ESTIMATES OF OVER-ALL OVERLAP ALONG THREE NICHE DIMENSIONS
(FOOD, MICROHABITAT, AND TIME OF ACTIVITY)
AMONG SEVEN SPECIES OF SYNTOPIC CTENOTUS

Ctenotus	*Ctenotus* *calurus*	*grandis*	*helenae*	*pantherinus*	*piankai*	*quattuor-decimlineatus*	*schomburgkii*
calurus	. . .	.30	.37	.22	.04	.25	.60
grandis	.69	. . .	.79	.87	.02	.35	.37
helanae	.73	.93	. . .	.80	.03	.44	.43
pantherinus	.64	.95	.93	. . .	.02	.31	.36
piankai	.39	.49	.49	.45	. . .	.42	.02
quattuordecimlineatus	.63	.73	.79	.71	.77	. . .	.23
schomburgkii	.86	.73	.77	.73	.32	.62	. . .

NOTE: Multiplicative values above the diagonal and summation values below (the latter represent upper bounds on true multidimensional overlap [see May, 1975]).

A Genus of Australian Skinks

The scincid genus *Ctenotus* contains perhaps the most diverse known assemblage of coexisting congeneric species of lizards, with as many as eleven species occurring together on a heterogeneous study area (Pianka, 1969). Up to seven species are truly syntropic, occurring side by side in the same habitats in true ecological sympatry. These skinks differ in at least three distinct niche dimensions: place (habitat and microhabitat), food (prey size and certain qualitative prey categories weighted by volume), and time of activity (both daily and seasonal). Two species frequently forage in the open (*C. calurus* and *C. schomburgkii*), whereas the remaining five species are usually found either within or near spinifex grass tussocks, resulting in a bimodality in microhabitat overlaps. Among the five species of spinifex foragers, there are also two subguilds, one termite-eating group (*C. grandis, C. helenae,* and *C. pantherinus*) and another pair of species that consume considerably fewer termites (*C. piankai* and *C. quattuordecimlineatus*). Among the assemblage of seven species, dietary overlap varies from 0.06 to 0.99 (mean 0.64), whereas overlap in microhabitat is higher, varying only between 0.60 and 0.98 (mean 0.82). Over-all overlap is extremely high among several pairs of species of *Ctenotus* (table 16 and fig. 10). Somewhat surprisingly (and probably because of the subguild structure of the *Ctenotus* guild), mean observed overlap does not differ significantly from those generated by randomization treatment 2 for any of the three niche dimensions.

Australian Geckos

From four to nine species of nocturnal gekkonid lizards, including up to five congeneric *Diplodactylus*, occur in sympatry in the Great Victoria Desert of Western Australia (Pianka and Pianka, 1976). Differences in temporal patterns of activity are slight or nonexistent, but foods eaten as well as habitats and microhabitats exploited differ strikingly among these gekkonids. Larger species tend to eat larger prey than smaller species. Three species are food specialists, eating essentially nothing but termites. Three others are distinctly arboreal, with the majority of specimens first sighted off the ground. Two species are semiarboreal, one of which is apparently restricted almost entirely to *Triodia* grass tussocks. Due to clear-cut differences in habitat requirements, three large terrestrial species of *Nephurus* are always allopatric: one is restricted to sandridges, another to sandplain-*Triodia* habitats, and still another to shrub-*Acacia* habitats.

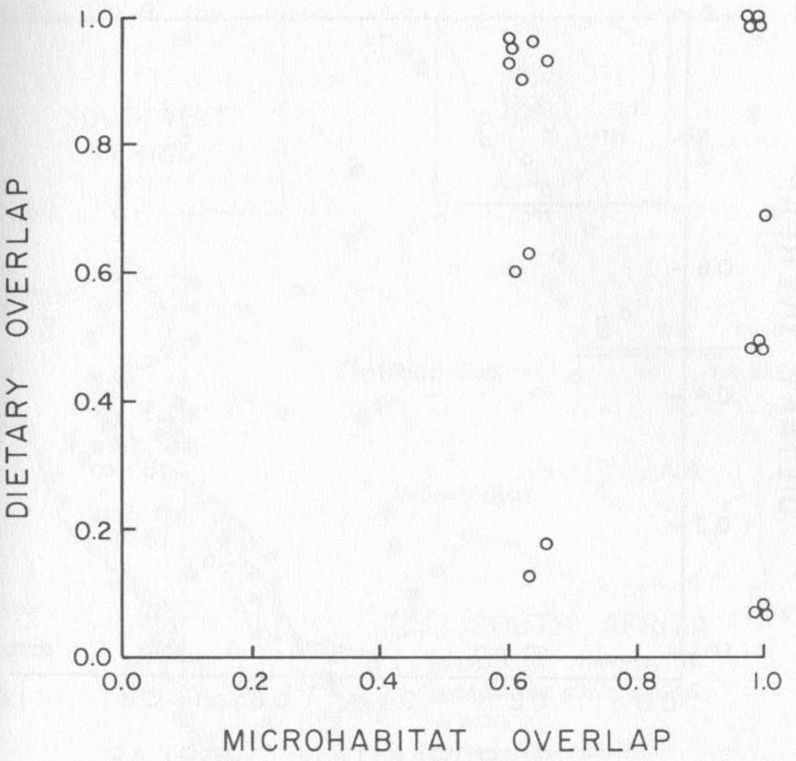

Fig. 10. Dietary overlap versus overlap in microhabitat among a guild of seven syntopic species of *Ctenotus* skinks consisting of three subguilds. Several pairs have exceedingly high over-all niche overlap.

Observed overlap in microhabitat and dietary overlap both vary greatly among these geckos, ranging respectively from 0.03 to 0.99 and from zero to 0.85 (plus two exceptionally high dietary overlaps of unity). Matrices of

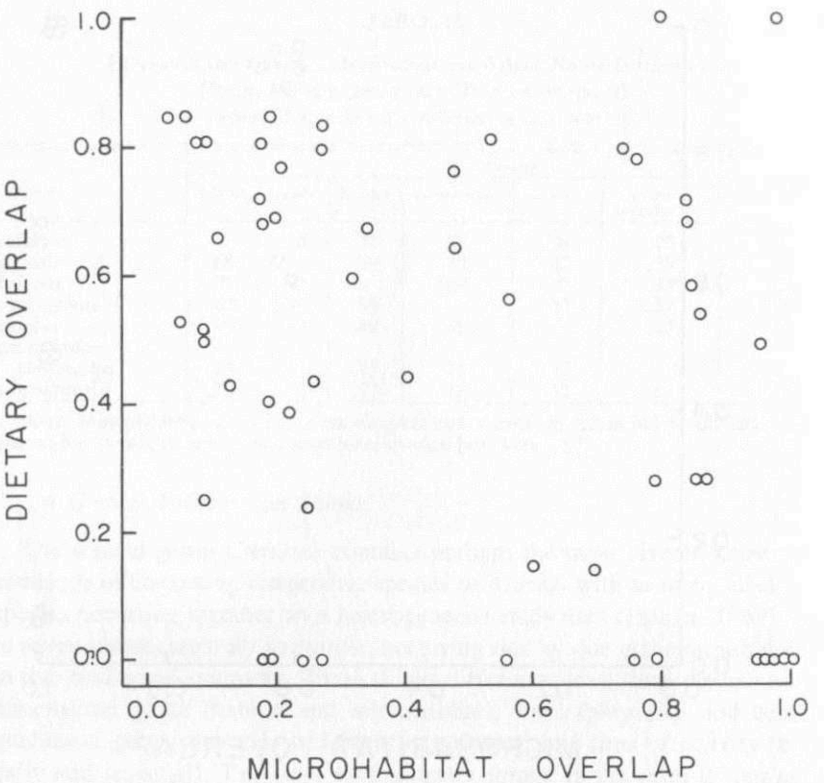

Fig. 11. Overlap in diet plotted against microhabitat overlap among sympatric species of Australian geckos. Some complementarity is suggested with relatively few pairs having high overlap along both niche dimensions.

estimates of overlap in diet and microhabitat are presented by Pianka and Pianka (1976). Exept for two pairs of termite specialists that overlap extensively in both diet and microhabitat, most sympatric species pairs with high dietary overlap tend to overlap relatively little in microhabitat and vice versa (fig. 11). Average overlaps actually observed in both diet and microhabitat among these geckos (means of .46 and .52, respectively) are significantly lower than those in guilds randomized by treatment 2 (respective means are .54 with a range of from .47 to .59 and .77 with a range of from .62 and .93 in 100 trials). Hence the observed differences in resource utilization promoting niche segregation are significantly nonrandom.

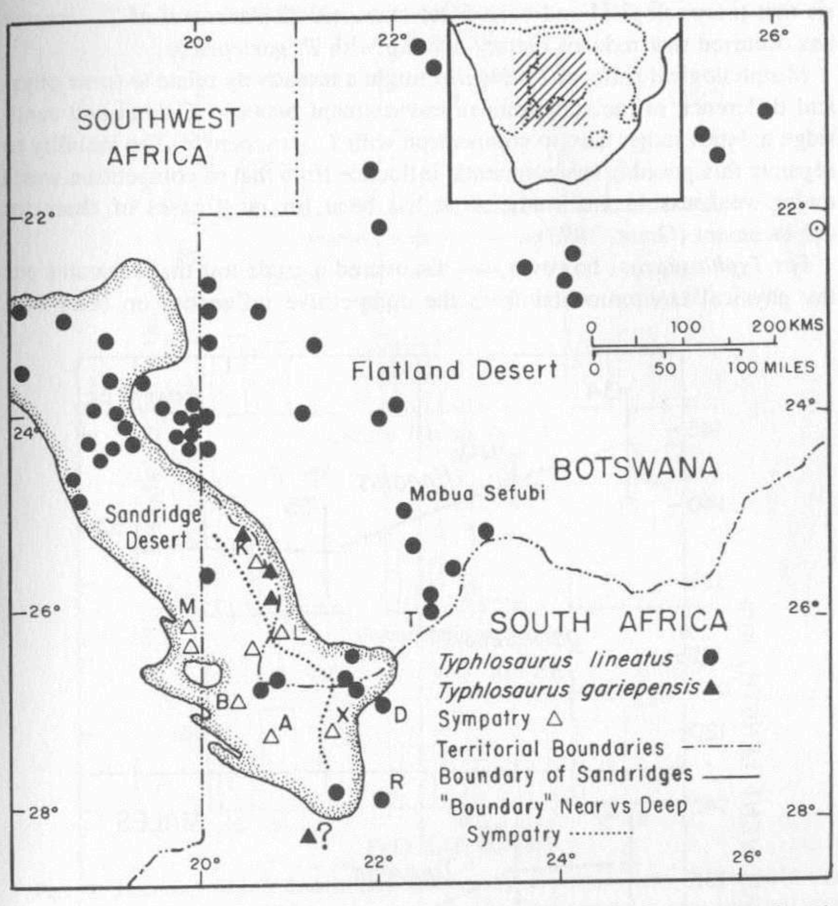

Fig. 12. Localities of collection of *Typhlosaurus lineatus* and *T. gariepensis* in central southern Africa.

Kalahari Fossorial Lizards: Character Displacement

Two species of legless, termite-eating, subterranean skinks are partially sympatric in the Kalahari sandveld. *Typhlosaurus lineatus*, the larger species, inhabits both flatland and sandridge provinces of the Kalahari (fig. 12) and *T. gariepensis* is restricted to southern sandridges. Snout-vent lengths (as a step function, not as a cline; fig. 13), head dimensions, proportional head lengths, and prey size (fig. 14) of *T. lineatus* are larger in sympatry than in allopatry (Huey et al., 1974; Huey and Pianka, 1974). These data support the hypothesis that morphological and behavioral character displacement of *T. lineatus* has occurred that reduces dietary overlap with *T. gariepensis*.

Morphological shifts of *T. lineatus* might alternatively relate to some physical difference in the subterranean environment between flatland and sandridge habitats rather than to competition with *T. gariepensis*. The inability to separate this possible environmental influence from that of competition was a major weakness in our study, as it has been for most cases of character displacement (Grant, 1972).

For *Typhlosaurus*, however, we discovered a crude test that separates out the physical environmental from the competitive influences on body size

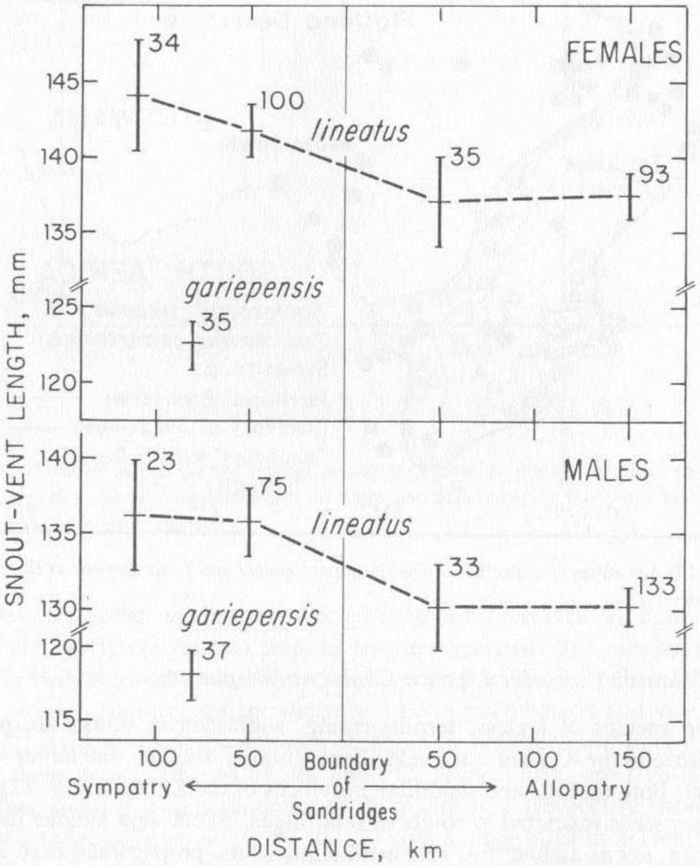

Fig. 13. Snout-vent lengths of female and male *Typhlosaurus* versus approximate distance from boundary of sandridges. Means shown as horizontal lines; two SE of the mean on either side by vertical lines. Numbers inside graph are number of lizards. (From Huey et al., 1974).

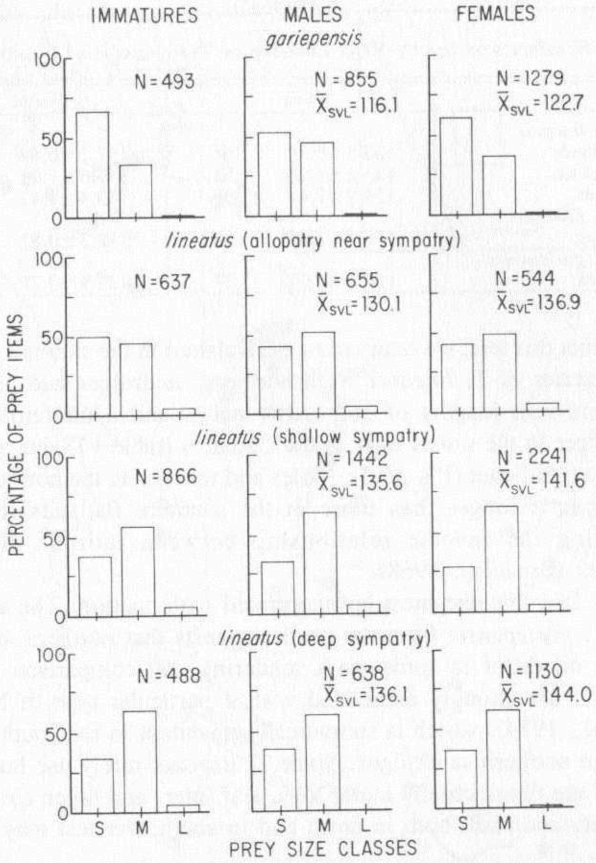

Fig. 14. Percentage of prey items in each of three prey volume categories (S = small [0–2.5 μl], M = medium [3–11 μl], L = large [over 11 μl]). Total number of prey items and mean snout-vent lengths included for adults. Sympatric *T. lineatus* eat more larger prey than allopatric *T. lineatus*. (From Huey et al., 1974)

(Huey and Pianka, 1974). Noting that *T. lineatus* is seemingly allopatric in the northern sandridge areas (fig. 12), we proposed comparing SVL's from a series from this region and from northern flatland localities. If *T. lineatus* from these two areas are similar in size, the hypothesis of character displacement is supported; if, however, *T. lineatus* are larger in nothern sandridges, the hypothesis of a response to the dune environment is favored. Alternatively, we could compare only northern and southern sandridge populations of *T. lineatus*. However, a possible inverse relationship between latitude and SVL in this species (Broadley, 1968) could complicate interpretations.

TABLE 17

STATISTICS ON SNOUT-VENT LENGTHS OF TYPHLOSAURUS LINEATUS

	Males		Females	
Allopatric *T. lineatus*				
South flatlands	130.5±0.59	166	137.2±0.68	128
North flatlands	133.2±1.25	51	141.6±1.03	56
North dunes	134.7±1.41	59	143.4±1.47	54
Sympatric *T. lineatus*				
South dunes	135.7±0.98	98	142.2±0.82	135
Sympatric *T. gariepensis*				
South dunes	116.1±0.78	37	122.9±0.77	35

To conduct this test, we returned to the Kalahari in the summer of 1976 and measured series of *T. lineatus* from northern sandridges and adjacent flatlands. Snout-vent lengths of both adult males and adult females average slightly larger in the dunes than in the flatlands (table 17), but these differences are insignificant (P's $> .2$). Males and females in the northern flatlands are significantly longer than those in the southern flatlands (P's $< .05$), documenting the inverse relationship between latitude and SVL in *Typhlosaurs* (Broadley, 1968).

"Tests" like this one must be interpreted with caution. The apparent absence of *T. gariepensis* from the north suggests that northern and southern sandridges do differ in some way, rendering any comparison suspect. *T. garienpensis* are strongly associated with a particular type of bunch grass (Huey et al., 1974), which is sporadically abundant in the south but rare or absent from northern sandridges. Since *T. lineatus* rarely use bunch grasses but instead are found chiefly under logs, leaf litter, and fallen *Crotalaria*, all of which are abundant both in north and in south, our test may have some validity.

These new data are consistent with the hypothesis that the larger size of *T. lineatus* where sympatric with *T. gariepensis* primarily reflects morphological character displacement, not interaction with the physical environment. The latter may have some influence, as suggested by the slightly larger size of males and females in the northern dunes than in the northern flatlands. However, the lack of significance for these differences suggests a minimal direct environmental influence.

Opportunities for natural experiments are invariably imperfect. Our assertions rest on the existence of an inverse relationship between latitude and SVL (Broadley, 1968; above) and on the assumption that the northern sandridges are effectively similar to the southern sandridges, despite the restriction of *T. gariepensis* to the south. We therefore argue only that our new data are apparently consistent with the hypothesis of character displacement. The strongest evidence in favor of this hypothesis remains the abrupt shift in SVL (fig. 13), the change in proportional head length, and the shift to larger termites (fig. 14).

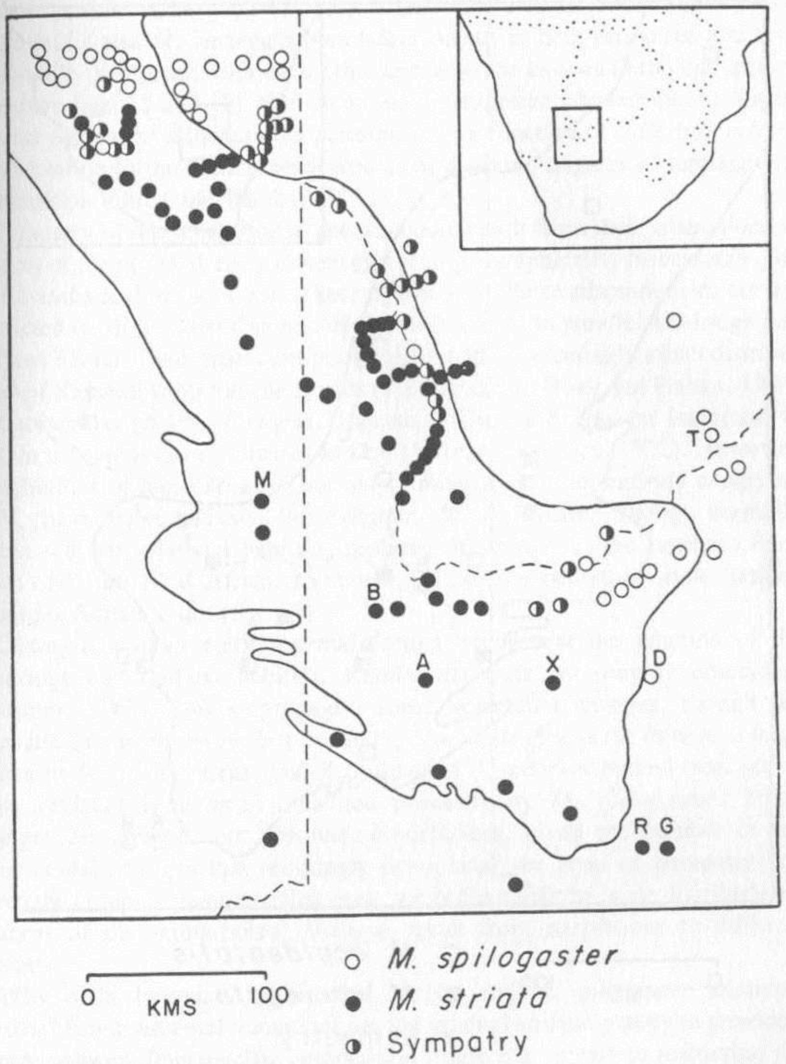

Fig. 15. Map showing known localities of collection of *Mabuya striata* and *M. spilogaster* in the southern Kalahari. The boundary of the sandridges is also shown as well as detailed distributions along several transects through the zone of parapatry. (From Huey and Pianka, 1977a).

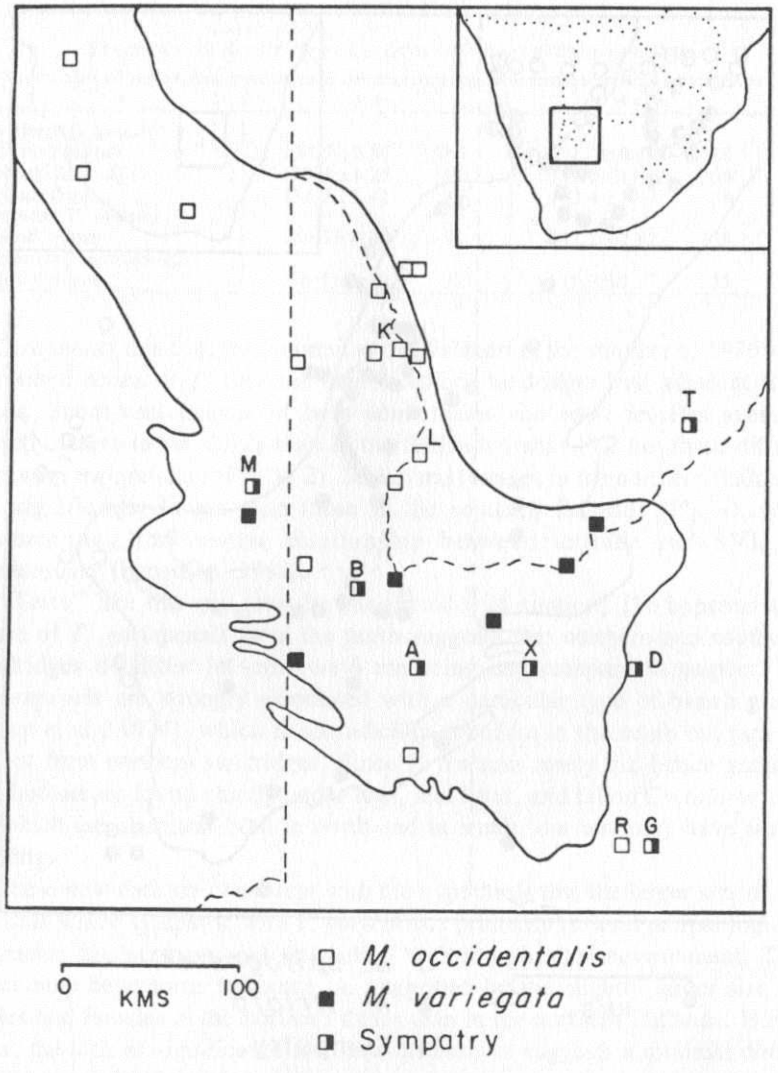

Fig. 16. Map showing localities of collection of two broadly sympatric species of terrestrial *Mabuya*, *M. occidentalis* and *M. variegata* in the southern Kalahari. Compare with figure 15.

Sympatry versus Parapatry among Kalahari Skinks

Four species of skinks of the genus *Mabuya* are common in the southern Kalahari. Distributions of the two semiarboreal species, *M. striata sparsa* and *M. spilogaster*, are parapatric and coincide crudely with the sandridge and flatland provinces, respectively (figs. 5 and 15). Two terrestrial species, *M. occidentalis* and *M. variegata punctulata*, occur in both provinces and thus are broadly sympatric with each other and with the two semiarboreal species (compare figs. 15 and 16). We attempted to determine whether these sympatric and parapatric distributional patterns were a function of differing degrees of adaptation to the habitat provinces or of differing degrees of interspecific competition (Huey and Pianka, 1977a).

Parapatry of the semiarboreal species could result from their adaptations to aspects of the physical environment that abut geographically. Necessarily, *M. occidentalis* and *M. variegata* either do not share these adaptations or are not restricted by them. Distributions of the former pair do parallel sandridge and flatland habitats; and these contiguous habitat zones seemingly affect distributions of Kalahari subterranean lizards (*Typhlosaurus*, Huey and Pianka, 1974) and terrestrial geckos (*Colopus*, Haacke, 1976), and may be important to certain terrestrial lacertid lizards as well (*Nucras*, Broadley, 1972). However, distributions of these *Mabuya* are only similar to, but not entirely congruent with, these major habitats. For example, *M. spilogaster*, though normally associated with flatland habitats, replaces *M. striata* in the northern dune areas of South West Africa. Moreover, *M. striata* occurs in some flatland localities further south (fig. 15).

Changes in other environmental factors occur near the junction of the sandridge and flatland habitats. Rainfall isohyets are roughly coincident (Leistner, 1967). Not surprisingly, some vegetation changes, though not dramatic can be observed. For example, *Acacia giraffee* is the dominant large acacia in *M. striata* areas, and *A. reficiens* (?), a darker-barked tree, seemingly replaces it in areas inhabited primarily by *M. spilogaster*. These changes are general, not absolute. Nonetheless, given the number of environmental changes that seemingly occur near the zone of parapatry and given the complex pattern of that zone, we believe that the basic distributional patterns of the semiarboreal *Mabuya* result from adaptations to different habitats.

Why is the boundary between *M. striata* and *M. spilogaster* relatively narrow? Environmental transitions are too gradual and too patchy to provide a simple answer. Interspecific competition might play a role in restricting the zone of sympatry. *M. occidentalis* and *M. variegata* overlap little with each other and with other species (tables 18 and 19). *M. striata* and *M. spilogaster* are, however, nearly identical in all niche parameters examined (position on sandridges, microhabitat associations, time of activity, body temperatures, and types and sizes of prey). Thus the parapatric species pair has high niche overlap, and broadly sympatric species pairs have much lower overlaps. This pattern is consistent with the hypothesis that competition between *M. striata*

TABLE 18

MATRIX OF OVERLAP VALUES BETWEEN PAIRS OF MABUYA IN THE KALAHARI

	spilogaster	occidentalis	variegata
striata	.990 .975 .970 .919 .915 .960	.994 .225 .529 .898 .542 .995	.982 .056 .833 .499 .575 .992
spilogaster		.983 .290 .809 .951 .760 .984	.977 .035 .936 .450 .404 .966
occidentalis			.952 .261 .941 .495 .643 .993

NOTE: From top to bottom, overlap values represent microgeography, microhabitat, season of activity, time of activity in summer, prey taxa, and prey size (from Huey and Pianka, 1977a).

TABLE 19

ESTIMATES OF OVER-ALL OVERLAP ALONG THE SIX NICHE DIMENSIONS OF TABLE 18

	striata	spilogaster	occidentalis	variegata
striata	1.000	0.755	0.065	0.013
spilogaster	0.955	1.000	0.164	0.006
occidentalis	0.702	0.796	1.000	0.074
variegata	0.656	0.628	0.715	1.000

NOTE: Multiplicative values above the diagonal and summation values below (the latter represent upper bounds on true multidimensional niche overlap [see May, 1975]). (From Huey and Pianka, 1977a.)

and *M. spilogaster* is relatively intense and might be sufficient to restrict the zone of sympatry.

Cody (1974) and Nevo et al. (1975) have noted that parapatric species are often interspecifically territorial or aggressive. Given a stable environment, selection would favor such aggression only if competition is potentially severe. However, several individuals of both semiarboreal species commonly occur on the same log or tree, and we noted little or no interspecific aggression between species in either indirect observations or tethering experiments.

The apparent lack of interspecific aggression does not necessarily invalidate the hypothesis that intense competition results in parapatry. These *Mabuya*, particularly *M. striata*, are social lizards and frequently occur in large numbers of the same log or tree. Evolution of interspecific aggressive behavior might be difficult or impossible in such gregarious species, even in the absence of gene flow with nearby allopatric populations.

Average overlaps in *Mabuya* communities randomized by treatment 2 do not differ from those actually observed in either diet or time of activity, but observed overlap in microhabitat ($\bar{x} = .30$) is significantly lower than in communities randomized by treatment 2 ($\bar{x} = .54$, range .38 to .67). However, this nonrandomness in microhabitat utilization stems from low overlaps with *M. occidentalis* and *M. variegata* since the observed overlap between *M. striata* and *M. spilogaster* is nearly complete (.98).

Conclusions: Comparisons among Guilds

Three guilds in addition to those discussed above were similarly analyzed. These include six species of nocturnal Kalahari geckos, five species of Australian *Varanus*, and seven species of Australian *Amphibolurus*. Patterns of niche overlap observed in seven guilds are summarized in table 20, which, for comparisons, also includes results of the treatment 2 randomization process. Note that, in all but one guild (*Ctenotus*), resource utilization is nonrandom along at least one or more niche dimensions, reducing overlap and promoting niche segregation. Overlap in time of activity is relatively high in most guilds ($\bar{x} = .78$; in all cases, observed mean overlaps either do not differ significantly from treatment 2 means or, if they do differ, observed overlap is significantly *greater* than in comparable randomized assemblages (that is, species are "packed in" on particular times of activity, which may simply reflect limited opportunities for ectotherms to exploit rapidly changing thermal conditions of desert environments). Hence differences in time of activity do not appear to contribute to niche segregation among these guilds of desert lizards. In contrast, many guilds show significantly nonrandom utilization of foods and microhabitats leading to reduced niche overlap. For example, dietary overlap among these guilds are usually lower ($\bar{x} = .67$) than overlap in time of activity ($\bar{x} = .78$); moreover, in 3 of the 7 guilds utilization of foods in significantly nonrandom *and* reduces overlap from that observed in treatment 2 randomized assemblages. Similarly, observed overlap in microhabitat ($\bar{x} = .59$) is low and resource utilization is significantly nonrandom (table 20).

SOME ANALYSES OF ENTIRE SAUROFAUNAS

Niche relationships and community structure of the complete lizard faunas on twenty-eight desert study sites were examined by Pianka (1973, 1974, 1975). Ten North American areas support from four to ten species of lizards, whereas ten southern African Kalahari sites had from eleven to seventeen species and eight areas in Western Australia supported from eighteen to forty

TABLE 20

Summary of Niche Overlap Statistics in Observed Guilds and in 100 Comparable Assemblages Randomized under Treatment 2 (See Text) along Three Niche Dimensions

Guild	Microhabitat				Food				Time of Activity			
	observed		Treatment 2		Observed		Treatment 2		Observed		Treatment 2	
	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.
Kalahari Lacertids (all 7 species)	.76	.06	.70^{NS}	.07	.60	.13	.84***	.03	.73	.06	.65^{NS}	.05
Kalahari Lacertids (5 sandridge species)	.94	.002	.81^{NS}	.02	.63	.16	.87**	.02	.87	.003	.78***	.01
Habitat overlap for above 5 lacertids	.47	.06	.73***	.02								
Australian *Ctenotus*	.81	.03	.85^{NS}	.03	.64	.12	.69^{NS}	.13	.59	.04	.67^{NS}	.03
Australian Geckos	.52	.11	.77***	.05	.46	.11	.54***	.09	.95	.002	.83***	.03
Australian *Varanus*	.30	.07	.80***	.03	.88	.005	.84^{NS}	.04	.53	.03	.56^{NS}	.04
Kalahari *Mabuya*	.30	.12	.54***	.06	.85	.007	.79^{NS}	.02	.84	.01	.77^{NS}	.01
Kalahari Geckos	.50	.12	.79***	.03	.76	.07	.82^{NS}	.03	.96	.001	.80***	.03
Australian *Amphibolurus*	.74	.02	.74^{NS}	.05	.57	.05	.75***	.02	.74	.03	.67*	.03

NS = not significantly different from observed
* = 5 or fewer out of 100 treatment means overlapped observed
** = only 1 out of 100 treatment means overlapped the observed mean
*** = none of 100 treatment means overlapped observed mean

species (Pianka, 1967, 1969, 1971). Two parallel analyses were performed on these entire saurofaunas. In the first (Pianka, 1973), to reduce the sampling error in characterizing resource utilization of component species, all lizards in each continental desert-lizard system were lumped into a single merged "community." An area-by-area analysis (Pianka, 1974, 1975) gave basically comparable results, outlined briefly below (for example, compare the niche overlap distributions in figure 2 of Pianka (1973) with those in figures 18, 19, and 20 of this paper). Details of methodology, and so forth, can be found in Pianka's papers.

Flatland Desert Lizards of North America

Partly because the number of lizard species coexisting on a given study area in the flatland deserts of western North America is low, guilds are not easily identifiable (indeed, they may not exist). Lizards are easily separated out as in the "ecological key" shown in table 21. Overlaps along the two niche dimensions that separate species in this merged North American lizard community are plotted in figure 17. Note that microhabitat overlap is low between many pairs and that only a few species pairs overlap extensively in both diet and microhabitat. Resource matrices for this assemblage of nine species[4] were randomized by treatment 2. Average observed overlap in time of activity ($\bar{x}$ = .58) did not differ significantly from the mean in 100 randomized com-

TABLE 21

Summary of the Ways in Which Resources Are Partitioned among Twelve Species of North American Flatland Desert Lizards

Habits	Species
I. *Diurnal species*	
A. Widely-foraging	*Cnemidophorus tigris*
B. Sit-and-wait foragers	
1. Underneath bushes	
a. Small prey items	*Uta stansburiana*
b. Large prey items	*Crotaphytus wislizeni*
2. Open spaces between shrubs	
a. Generalized diet of large insects	*Callisaurus draconoides*
b. Diet consists largely of ants	*Phrynosoma platyrhinos*
3. Arboreal (Trees, large bushes)	
a. Trunks and ground around base	*Sceloporus magister*
b. Primarily in outer smaller branches	*Urosaurus graciosus*
4. Sand Dunes (primarily open spaces)	*Uma scoparia*
C. Herbivorous (both floral & vegetative parts)	*Dipsosaurus dorsalis*
II. *Nocturnal Species*	
A. Open-foraging	*Coleonyx variegatus*
B. In Joshua Tree rubble	*Xantusia vigilis*
C. Capture prey by olfaction and digging (eats eggs and young of various vertebrates)	*Heloderma suspectum*

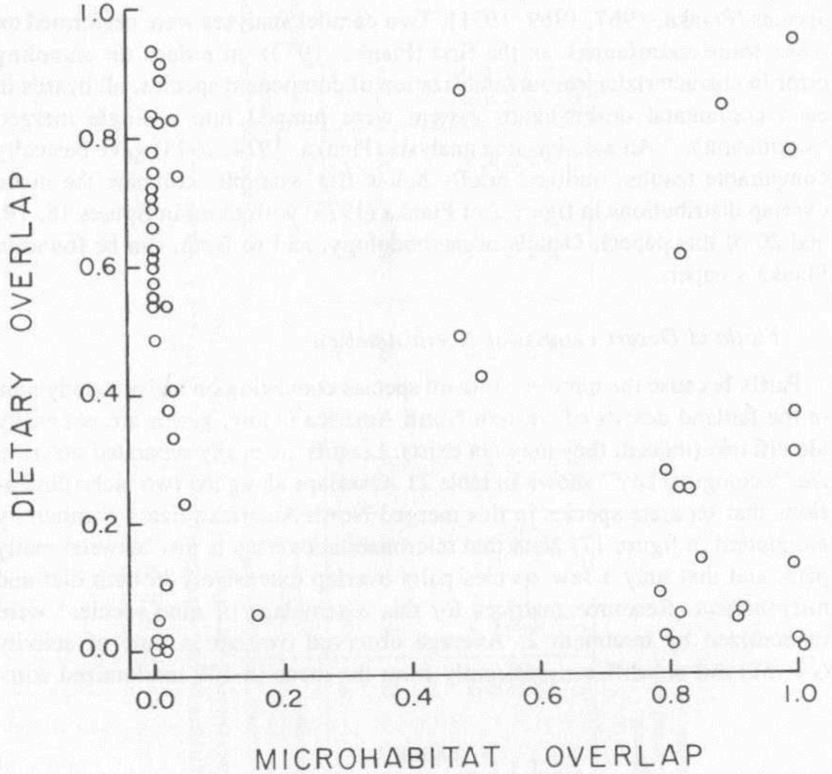

Fig. 17. Dietary overlap plotted against overlap in microhabitat among flatland desert lizards of western North America. Overlap in microhabitat tends to be either all or none, whereas dietary overlap values are distributed more evenly. Some complementarity of niche dimensions is suggested in that relatively few pairs of species overlap extensively along both axes. Compare with figure 11.

munities ($\bar{x} = .52$). Observed mean overlaps in diet (.43) and microhabitat (.34) were, however, significantly lower than in their respective randomized communities ($\bar{x} = .65$, range .55 to .75, and $\bar{x} = .47$, range .40 to .56), promoting niche segregation.

Niche Overlap Distributions: Evidence for Nonrandom Niche Segregation

Distributions of observed niche overlap along three dimensions were presented for the merged communities by Pianka (1973, figure 2). Figures 18, 19, and 20 show comparable distributions from an area-by-area analysis. Both the degree of overlap and the importance of various niche dimensions in separating species clearly differs between continents. For example, dietary overlap is quite high in the Kalahari ($\bar{x} = .65$) where termites comprise some 41 percent of the lizard diet by volume (in contrast, termites represent only about 16

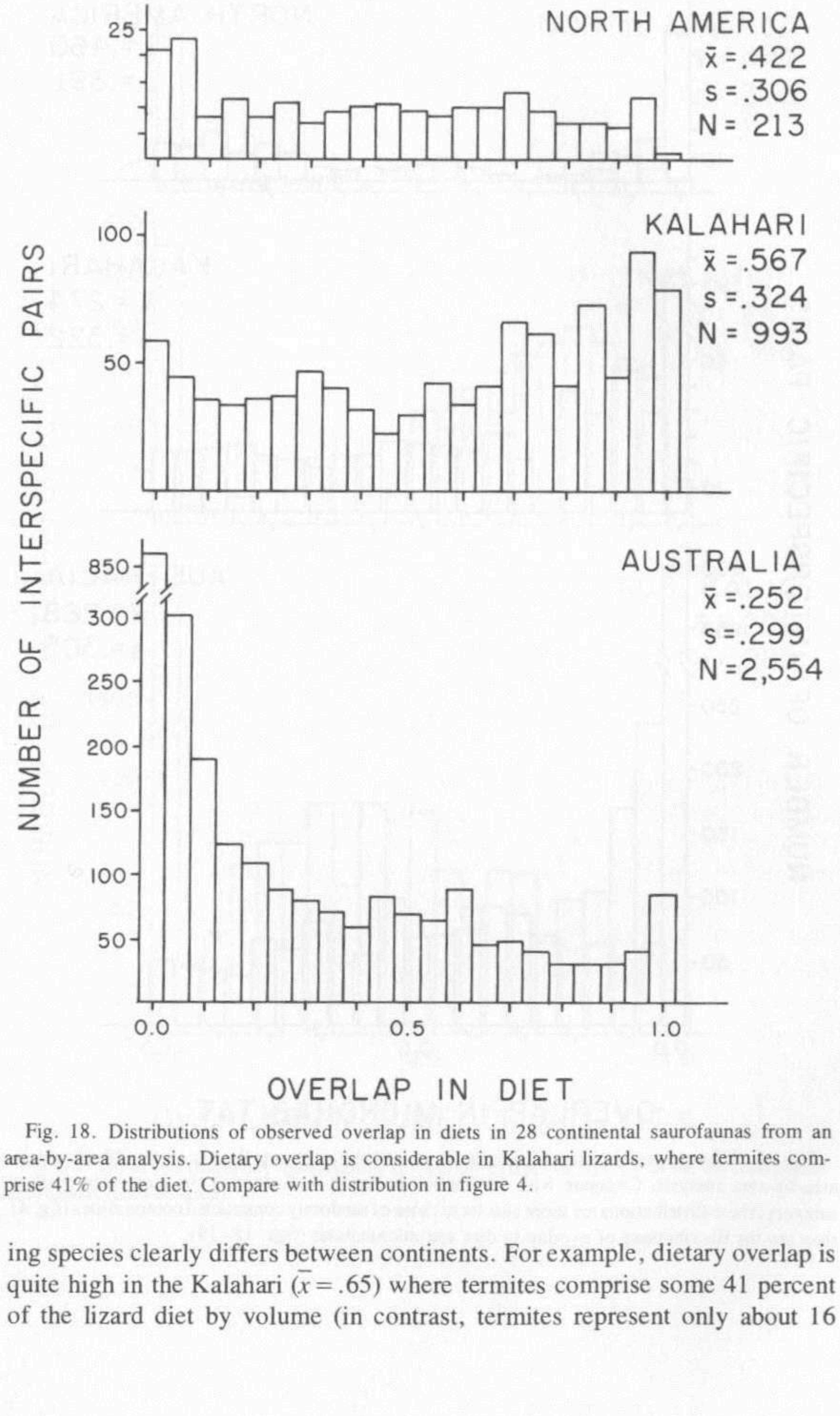

Fig. 18. Distributions of observed overlap in diets in 28 continental saurofaunas from an area-by-area analysis. Dietary overlap is considerable in Kalahari lizards, where termites comprise 41% of the diet. Compare with distribution in figure 4.

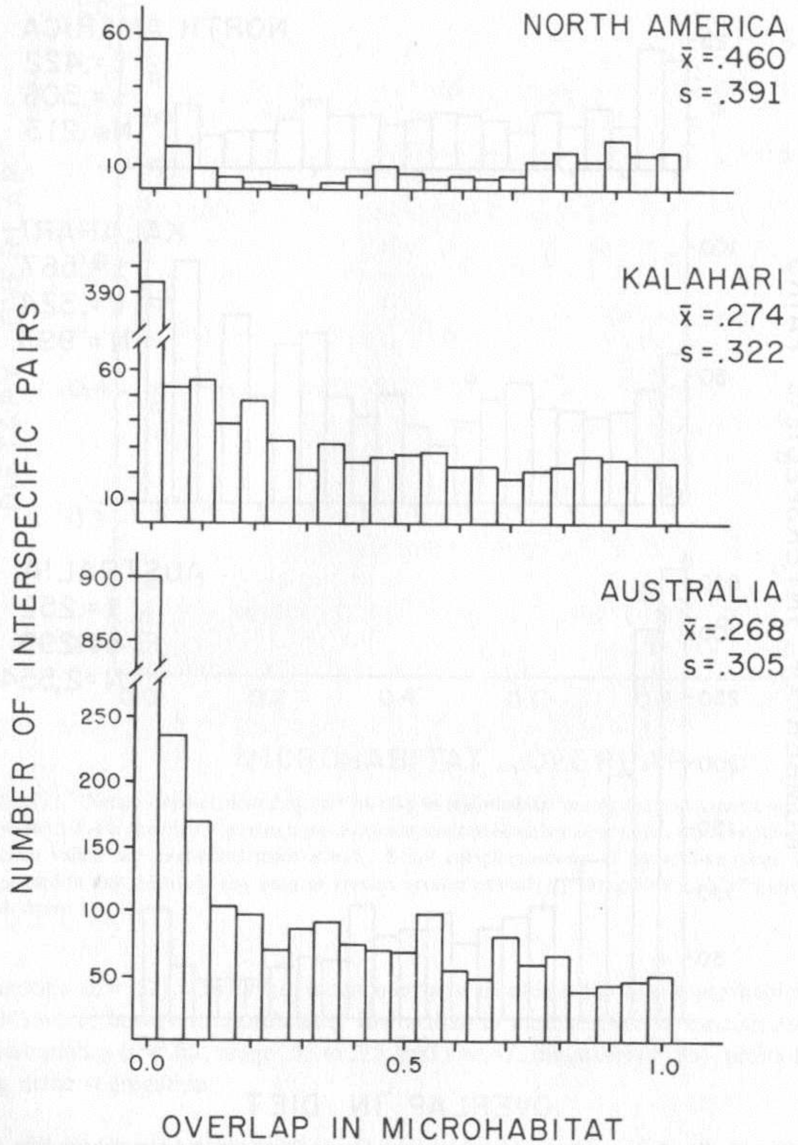

Fig. 19. Histograms of observed overlap in microhabitat among lizards on the 28 sites in an area-by-area analysis. Compare with distribution in figure 4. Excepting the large zero overlap category, these distributions are more similar to those of randomly constructed communities (fig. 4) than are the distributions of overlap in diet and microhabitat (figs. 18–19).

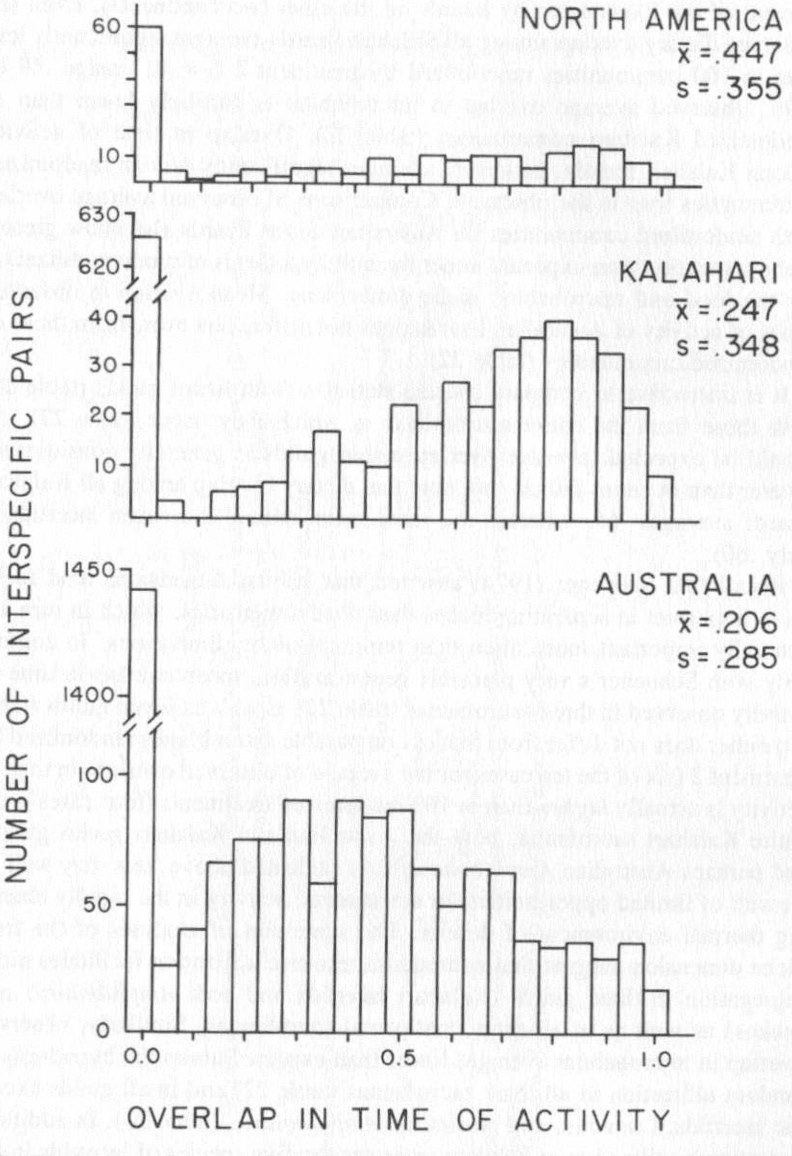

Fig. 20. Observed frequency distributions of overlap in time of activity in the 28 continental saurofaunas (area-by-area).

percent of the foods eaten by lizards on the other two continents). Even so, observed dietary overlap among all Kalahari lizards averages significantly less than in 100 communities randomized by treatment 2 ($\bar{x} = .81$, range .69 to .89). Observed average overlap in microhabitat is similarly lower than in randomized Kalahari communities (table 22). Overlap in time of activity among Kalahari lizards, however, averages significantly *less* in randomized communities than in the observed. Comparisons of observed average overlap with randomized communities for Australian desert lizards also show greater niche separation than expected under the null hypothesis of random utilization for the food and microhabitat niche dimensions. Mean overlap in observed times of activity of Australian lizards does not differ, however, from those of randomized communities (table 22).

It is instructive to compare overlap statistics from lizard guilds (table 20) with those from the entire saurofaunas in which they occur (table 22). As would be expected, average overlap within guilds is generally considerably greater than in entire faunas (but note that dietary overlap among all Kalahari lizards averages .65, whereas the same mean among the seven lacertids is only .60).

Recall that Schoener (1974) asserted that habitat dimensions tend to be more important in separating niches than food dimensions, which in turn are generally important more often than temporal niche dimensions. In conformity with Schoener's very plausible generalization, mean overlap in time of activity observed in three saurofaunas (table 22) as well as seven guilds (table 20) either does not differ from that of comparable assemblages randomized by treatment 2 (six of the ten cases) or the average of observed overlaps in time of activity is actually *higher* than in 100 randomized treatments (four cases—the entire Kalahari saurofauna, both the Australian and Kalahari gecko guilds, and perhaps Australian *Amphibolurus*). As indicated above, this may well be a result of limited opportunities for ectothermic activity in the rapidly changing thermal environment of deserts. The same sort of analyses of the food niche dimension suggest that nonrandom resource utilization facilitates niche segregation in three guilds (Kalahari lacertids and both *Amphibolurus* and geckos) as well as in all three continental saurofaunas. Similarly, observed overlap in microhabitat averages lower than expected under the hypothesis of random utilization in all three saurofaunas (table 22) and in all guilds except the lacertids, *Ctenotus*, and Australian *Amphibolurus* (table 20). In addition, nonrandom utilization of habitats separates the five species of lacertids in the sandridge region of the Kalahari. Thus these studies of niche segregation among desert lizards certainly support Schoener's generalization that habitat, microhabitat, and food niche dimensions are more important in niche segregation than temporal niche dimension, both in guilds and in entire saurofaunas.

TABLE 22

SUMMARY OF NICHE OVERLAP STATISTICS AMONG ENTIRE SAUROFAUNAS AND FOR 100 COMPARABLE ASSEMBLAGES RANDOMIZED UNDER TREATMENT 2 (SEE TEXT) ALONG THREE NICHE DIMENSIONS

(Compare with Table 20)

Saurofauna	MICROHABITAT				FOOD				TIME OF ACTIVITY			
	Observed		Treatment 2		Observed		Treatment 2		Observed		Treatment 2	
	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.	$\bar{x}$	var.
North America†	.34	.18	.47***	.15	.43	.11	.65***	.04	.58	.17	.52^{NS}	.15
Kalahari†	.29	.10	.45***	.11	.65	.08	.81***	.03	.35	.17	.32***	.14
Australia†	.29	.09	.43***	.10	.32	.09	.43***	.09	.30	.11	.30^{NS}	.11

†Saurofauna means may differ slightly from those presented by Pianka (1973) due to corrections and addition of new data for some species.
NS = not statistically significant.
*** = range of means observed in 100 trials did not overlap observed.

Niche Overlap and Diffuse Competition

Various estimates of over-all multidimensional niche overlap can be generated from unidimensional patterns of resource utilization. As indicated above, the product of several unidimensional estimates of niche overlap usually (though not always) underestimates true multidimensional overlap unless niche dimensions are independent (orthogonal). In contrast, a simple arithmetic average of several unidimensional estimates of overlap almost always[5] overestimates true overlap; indeed, such an average provides the *upper bound* on true multidimensional niche overlap (May, 1975). When averaged among all pairs within each of the twenty-eight saurofaunas, both these estimates of over-all overlap are strongly intercorrelated ($r = .97$, $P << .001$) so that statements to follow concerning upper bound estimates (summation overlap) also apply to multiplicative estimates. Both measures of over-all overlap vary inversely with number of lizard species (fig. 21) and with the standard deviation in annual precipitation (fig. 22), a measure of environmental variability (see also Pianka, 1974, 1975). The latter correlation vanishes when the number of lizard species is held constant by partial correlation, but the former remains significant ($r_{xy.z} = -.56$ $P < .01$), suggesting that the extent of tolerable overlap is not a function of environmental variation but rather that it is related to the number of competing species and the intensity of diffuse competition. Pianka (1974, 1975) interprets this pattern as indicating that competitor-species density influences tolerable-niche overlap, with a greater number of competing species (more intense diffuse competition) demanding greater average niche separation among coexisting species. Extensive niche overlap with fewer competitors could be roughly equivalent to lower overlaps between pairs of species but summed over more competitors.

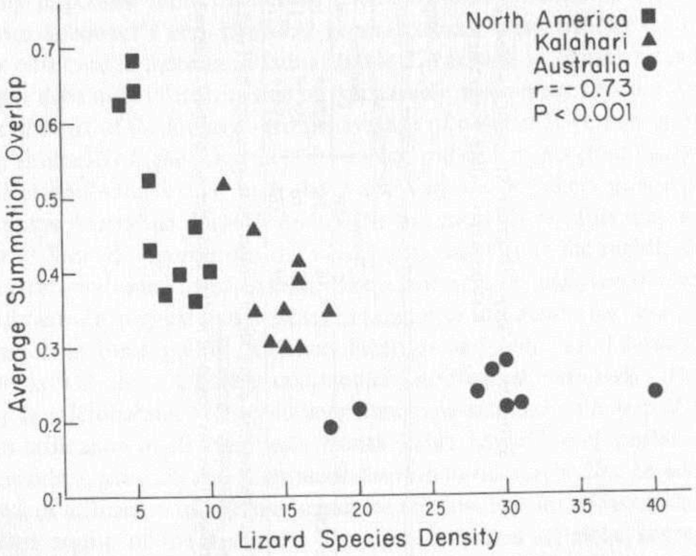

Fig. 21. Average niche overlap (over-all summation) plotted against estimated numbers of lizard species (continents coded by shape). Similar inverse correlations exist with multiplicative over-all overlap and with several estimates of maximal tolerable niche overlap.

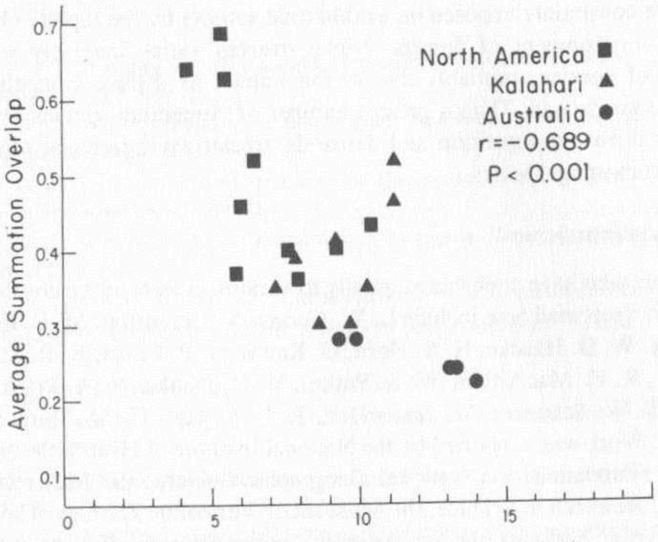

Fig. 22. Average over-all summation niche overlap plotted against the standard deviation in annual precipitation for 23 desert study areas (continents coded by shape). This correlation disappears when the number of lizard species is held constant by partial correlation.

SUMMARY

Nonrandom utilization of resources reduces overlap among desert lizards, thereby facilitating resource partitioning; in three continental saurofaunas and all but one of seven lizard guilds examined, niche segregation was demonstrated along at least one niche dimension. The relative importance of different niche dimensions in separating species differs among guilds and among continental saurofaunas. Spatial dimensions (habitat and microhabitat) separate lizard species more often than food dimensions, although both are important. No temporal niche segregation was discernible in this analysis; desert lizards examined are "packed" into short time periods, presumably because of severe constraints imposed on ectothermic activity by the rapidly changing thermal environment of deserts. Niche overlap varies inversely with the number of species, probably due to the impact of diffuse competition in diverse saurofaunas. Thus a greater number of competing species results in stronger diffuse competition and demands greater average niche separation among coexisting species.

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1. The use of time of activity as a niche dimension can be justified in several ways (MacArthur and Levins, 1967; Pianka, 1969, 1973, 1975; Schoener, 1974, 1975). If resources are rapidly renewed, exploitative competition cannot occur unless individuals are active a fairly short time of each other: otherwise, resources may be replenished during the interval separating species. Moreover, when microhabitat and food categories are crude and temporally changing, differences in time of activity may in fact be associated with differential use of space and food resources that would not be reflected without much greater precision in recognition of appropriate nontemporal resource states. Thus, the microhabitat "open sun" clearly changes with the daily march of temperature; similarly a given crude prey category such as "ants" may usually lump a series of prey species with temporal segregation. Hence it is often both appropriate and useful to treat time as a niche dimension.

2. We offer only a preliminary and abbreviated treatment of Lawlor and Pianka's analysis here.

3. For descriptions of these study areas and their funas, as well as details of our methods, see Pianka, 1971, and Pianka and Huey, 1971.

4. Three species with very restricted distributions, *Heloderma, Xantusia,* and *Uma,* were omitted.

5. If all niche dimensions are perfectly dependent upon one another (in which case there is really one a single niche dimension), the average of observed unidimensional values equals the true multidimensional value.

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