A MORPHOLOGICAL ANALYSIS OF THE STRUCTURE OF COMMUNITIES OF LIZARDS IN DESERT HABITATS[1]

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Abstract. Using nine measurements of the head, body, and appendages we characterize the morphological relationships among lizards in deserts of western Australia, southern Africa, and western North America. Each species was placed in a morphological space whose dimensions were the logarithms of the original measurements. We calculated the dispersion of the species in each region along principal components to assess the number of dimensions and volume of morphological space occupied. Euclidean distances between all pairs of species were calculated to assess the density of species packing within the morphological space. We also generated random subsets of the species pool within each region and calculated matrices of Euclidean distances for them.

In the combined sample of 83 species, the first three principal components accounted for 86, 8, and 3%, respectively, of the total variance in the dispersion of species in morphological space. Pairwise discriminant analysis revealed significant differences between the morphological distributions of the lizards in the three regions. When analyzed separately, the 54 Australian lizards occupied the largest volume, followed by the 11 North American species, and, lastly, the 18 southern African species. We used the average distance to the nearest neighbor (*NND*) as a measure of species packing. *NND*'s in Australian localities (18–36 species) and in North American localities (4–10 species) were considerably greater than those in southern African localities (10–15 species). When assemblages were adjusted for number of species, the Australian lizards were more widely spaced morphologically than those in either the North American or African localities.

Attributes of randomly generated assemblages did not differ morphologically from the subsamples of species found in each locality. Furthermore, the standard deviations of *NND*'s, a measure of the regularity of species packing, were similar in natural and randomly generated communities. Hence the present analysis provides little indication of interaction between species according to morphological attributes. Our morphological analysis confirmed some patterns revealed by studies of ecological relationships in the same localities.

Key words: African lizards; Australian lizards; community structure; desert lizards; discriminant analysis; Kalahari Desert; lizards; morphology; nearest neighbor; principal components; random communities; species diversity.

INTRODUCTION

Pianka (1967, 1969*a*, 1971) characterized the ecological relationships of lizards in desert habitats in Australia, southern Africa, and North America. From these he calculated niche breadths of each species separately, and of all species in each locality combined, along dimensions of time of activity, microhabitat, and type of prey (Pianka 1973). He also calculated the degree of overlap among all pairs of species along each of these dimensions. Although the average number of species per locality varied from eight in North America to 15 in the Kalahari Desert and 28 in Australia, niche breadths of species from the three regions were similar. Furthermore, niche overlap decreased with increasing numbers of species. Lastly, the combined

niche breadth of the species in each region increased in constant proportion to the average number of species per locality (Pianka 1975). Pianka's analyses thus indicated that variation in the number of species in a region is accommodated by change in the variety of resources utilized by the entire assemblage of lizards rather than by change in the average size of the niche of individual species along the axes measured.

In this paper, we take a multivariate approach to describe the structure of the communities of lizards studied by Pianka. We characterize each of the species of lizards morphologically and place it in a geometrically defined space whose dimensions are the logarithms of the several measurements. We then calculate the volume of morphological space occupied by each assemblage of lizards and an index to the density of species packing within it. Our analysis was inspired in part by those of Karr and James (1975) on birds and

Findley (1973, 1976) on bats, and follows very closely the methods of Ricklefs and Travis (1980), outlined below. Gatz (1979) has performed similar analyses on fish communities.

Although morphological analyses may be an alternative to ecological analyses, provided that the morphological adaptations of species reflect their ecological relationships, weaknesses of the morphological approach are that morphology usually does not respond to varying conditions over the life-span of the individual, as do behavior and physiology, and that each measurement may contain a very different amount of information about the ecological relationships of the species. Balancing these disadvantages are the relative ease and objectivity of obtaining measurements, greatly reduced sampling problems, and independence of the measurements from habitat structure. Some sets of anatomical measurements may provide a fairly complete ecological characterization of the species (Karr and James 1975, Bierregaard 1978, Cody and Mooney 1979, Gatz 1979, Ricklefs and Travis 1980). In lizards, relative leg lengths are strongly correlated with the use of space, just as head lengths are correlated with prey size (Pianka 1969b, Pianka and Parker 1972, Pianka and Pianka 1976).

METHODS

Lists of species were obtained for 10 localities in the Great Basin, Mohave, and Sonoran Deserts of western North America (Pianka 1965, 1967). Our community rosters are modified from Table 1 in Pianka (1967) in that localities U_1, U_2, and U_3 were treated as one, locality A was not included, *Coleonyx* was not included in locality E, and *Xantusia vigilis* was not measured and therefore could not be included in locality M. Between four and 10 species inhabited each of the localities which are described in more detail by Pianka (1965). Pianka (1971: Table 1) lists species of lizards at 10 localities plus two sublocalities in the Kalahari Desert of southern Africa (see also Pianka and Huey 1971). We include here only species that were collected. We do not include two species of fossorial, legless skinks of the genus *Typhlosaurus* because their measurements could not be compared to those of the other species. *Chameleo delepis* was omitted due to small sample size. Rosters for the Kalahari localities had between 10 and 15 species.

The lizards at eight localities in the Great Victoria Desert of Western Australia were tabulated by Pianka (1969: Table 1). Species are included in this analysis if they were collected in the locality, if their presence was indicated by tracks, or if they were highly expected owing to geographical range, habitat, autecology, and microhabitat. Two species, *Lerista* (formerly *Rhodona*) *macropisthopus* and *Tiliqua multifasciata*, were not measured, while four others (*Lerista bipes*, *Delma fraseri*, *Lialis burtoni*, and *Pygopus nigriceps*)

have no forelegs and only vestigial hindlegs, and therefore could not be included in our analysis. The remaining 54 Australian species were distributed among the localities in numbers ranging from 18 to 36.

Measurements, obtained from between 2 (most species were represented by considerably larger samples) and 1160 individuals of each species, included the snout–vent length, the length, width, and depth of the head, and the lengths of the jaw, forearm, forefoot, hindleg, and hindfoot. Sexes were not separated for the present analysis. The arithmetic average of each of the nine measurements for each species constituted the initial matrix of morphological data. We also calculated standard deviations and coefficients of variation for the measurements of species from North America and southern Africa.

All the analyses in this paper are based upon the distribution of species in morphological space defined by the original measurements. To normalize the data, we calculated the common logarithm (base 10) of each measurement. This transformation results in distributions of measurements that are approximately normal and have similar variances (see below). We calculated principal components based upon the covariance matrix obtained from the initial data set (Morrison 1967). The principal components, whose units are measured on the logarithmic scale, preserve the original spatial pattern of the species in morphological space. The new axes are orthogonal linear combinations of the original variables. That is, the projections of the positions of species onto any one of the principal components have zero correlation with the projections of those positions onto any other. Because the principal components are linear combinations of logarithmic values, they represent logarithms of the products and ratios of measurements and thereby portray the allometry of size and shape.

We applied a pairwise discriminant analysis to the logarithms of measurements of species in each of the three regions to determine whether the lizard faunas occupied different regions in the morphological space.

For each locality, we calculated a matrix of Euclidean distances between all pairs of species:

$$D_{ij} = \left[\sum_{k=1}^{9} (X_{ik} - X_{jk})^2 \right]^{\frac{1}{2}}.$$

where D_{ij} is the Euclidean distance between species i and j, and X_{ik} and X_{jk} are the logarithms of measurement k for species i and j. Note that distances based upon principal component scores would be identical. From the matrix of distances for each locality, we identified the closest and farthest other species in the morphological space and then calculated the averages and standard deviations of the nearest-neighbor distances (*NND* and *SDNND*) and farthest-neighbor distances (*FND* and *SDFND*) and the average

TABLE 1. Means and standard deviations of the logarithms (base 10) of nine measurements in the pooled sample of 83 species of lizards.

Measurement	$\bar{x}$	SD
Snout–vent length (SV)	1.79	0.185
Head length (HL)	1.11	0.173
Head width (HW)	0.97	0.207
Head depth (HD)	0.82	0.205
Jaw length (JL)	1.17	0.174
Forearm length (FA)	1.31	0.226
Hindleg length (HL)	1.48	0.216
Forefoot length (FF)	0.91	0.244
Hindfoot length (HF)	1.13	0.266

TABLE 2. Eigenvalues of a principal components analysis based on the covariance matrix.

	Principal component		
	1	2	3
Eigenvalue			
Pooled sample	0.3227	0.0305	0.0109
Australia	0.3597	0.0299	0.0138
Africa	0.1125	0.0333	0.0037
North America	0.3083	0.0287	0.0096
Square root of eigenvalue			
Pooled sample	0.5768	0.1746	0.1044
Australia	0.5997	0.1731	0.1173
Africa	0.3354	0.1824	0.0609
North America	0.5552	0.1693	0.0980
Cumulative proportion of variance			
Pooled sample	0.858	0.937	0.965
Australia	0.860	0.931	0.964
Africa	0.737	0.955	0.980
North America	0.881	0.963	0.990

neighbor distance ($\bar{D}$) among all pairs of species in each locality.

To test the hypothesis that the communities of lizards at different localities were morphologically random subsets of the pool of species within each region, we generated randomly assembled communities by drawing at random, from the species list, 20 communities of each of several sizes. In our algorithm, no species could be included in any one randomly generated assemblage more than once. We then calculated the community attributes (*NND, SDNND, FND, SDFND, $\bar{D}$*) for each of the random communities.

We emphasize that neither our analysis of natural communities nor our generation of random communities takes into account differences in the relative abundances of species or variation in their measurements either within localities or within regions.

RESULTS

Morphological space: all species combined

The initial data set contained nine measurements for each of 83 species of lizards. Means and standard deviations of the logarithms of these measurements are presented in Table 1. The largest variance, that for the length of the forefoot (0.060), was two times the smallest variance, that of the length of the head (0.030). According to Bartlett's test (Sokal and Rohlf 1969) the difference between these extremes is significant ($\chi^2_8 = 17.6$, $P < .05$).

The results of a principal components analysis based on the covariance matrix are presented in Tables 2 and 3. The eigenvalues of the covariance matrix are the variances of points in morphological space projected onto the principal components. The first principal component (PC1) is associated with the greatest amount of total variance in the distribution of species in the morphological space. The square roots of the eigenvalues are the standard deviations of the projections of the species onto the principal components, hence a measure of the dimension of morphological space along each component. The eigenvectors of the covariance matrix are the coefficients for each of the original variables in the linear combination that defines

each principal component. The projection of species *i* onto component *p* is defined by the expression

$$Y_{ip} = c_{1p}X_{i1} + c_{2p}X_{i2} + \ldots + c_{9p}X_{i9},$$

where the c's are the coefficients for variables 1 through 9 associated with the expression for component *p* and the X's are the original measurements for variables 1 through 9 for species *i*. For convenience, we have normalized the X's to a mean value of 0 by subtracting the overall mean from each measurement.

In the combined sample of 83 species, 86% of the variance is associated with the first principal component and 97% with the first three. The last six PC's have little apparent statistical or biological significance. The dispersions of species projections along each of the first three components have standard deviations of 0.577, 0.175, and 0.104. The values may be compared directly to the standard deviations of the original variables (0.173–0.244).

As one would expect, differences between species in one measurement are highly correlated with differences in other measurements. The coefficients of the eigenvectors (Table 3) indicate that most of the variation among species is related to a general size gradient, because all the coefficients for PC1 are positive and have similar value (0.28–0.40). The coefficients for PC2 are positive for the snout–vent length and the four head measurements, but negative for the four limb measurements, particularly the two hind limb measurements and the length of the forefoot. Therefore, species having extreme positive values of PC2 have rather more elongate bodies, larger heads, and shorter limbs than species with extreme negative values. Extreme positive values of PC2 belong to Australian skinks of the genus *Lerista*, in which several other species are legless, and *Omolepida*, both of which are elongate, short-limbed species. Large neg-

TABLE 3. Coefficients of principal components 1, 2, and 3.

Region and principal component	Variable*								
	SV	HL	HW	HD	JL	FA	HL	FF	HF
Pooled sample									
PC1	0.28	0.29	0.33	0.33	0.28	0.37	0.35	0.40	0.34
PC2	0.36	0.24	0.36	0.30	0.26	−0.09	−0.32	−0.30	−0.57
PC3	0.44	0.04	−0.18	0.09	0.15	−0.61	0.16	−0.34	0.48
Australia									
PC1	0.29	0.29	0.33	0.33	0.29	0.38	0.34	0.41	0.32
PC2	0.44	0.21	0.33	0.34	0.26	−0.22	−0.27	−0.38	−0.46
PC3	0.31	−0.04	−0.20	0.10	0.04	−0.59	0.25	−0.28	0.60
Africa									
PC1	0.28	0.28	0.35	0.35	0.30	0.34	0.38	0.35	0.36
PC2	−0.17	−0.20	−0.45	−0.30	−0.16	−0.10	0.27	0.28	0.67
PC3	0.31	0.02	−0.06	−0.00	0.21	−0.26	−0.72	0.50	0.14
North America									
PC1	0.36	0.32	0.36	0.35	0.32	0.33	0.30	0.36	0.29
PC2	−0.30	−0.24	−0.30	−0.12	−0.22	0.03	0.46	0.17	0.67
PC3	0.09	0.36	−0.31	−0.37	0.65	−0.34	0.01	−0.19	0.23

* See Table 1 for key to abbreviations.

ative values are found in some species of the Australian genus *Amphibolurus,* the African *Eremias,* and the North American *Callisaurus.* The coefficients of PC3 reveal species at one extreme in which the body and hindleg are elongated and the forelimb is shortened relative to other measurements (e.g., the nearly legless *Lerista* [formerly *Ablepharus*] *timidus*). At the other extreme are species with relatively long forelimbs and short bodies (virtually all the geckos and, in North America, *Phrynosoma*). The distributions of species with respect to PC1 and PC2 and with respect to PC2 and PC3 are plotted in Fig. 1 to show the general shape of the morphological space.

Morphological space: by region

The distributions of species in Fig. 1 suggest major differences between the regions in the morphological space occupied by lizards. This is confirmed by pairwise discriminant analyses (Table 4), results of which indicate that the lizard faunas of these regions, while overlapping extensively in morphological space, also are distinctive. The discriminant function itself is the single linear combination of original variables that maximizes the difference (among-groups sum of squares) between two sets of points projected onto itself. The coefficients of the discriminant function indicate that the lizard faunas of Australia and southern Africa are distinguished primarily by the ratio of head length to jaw length, African species tending to have the larger values. In comparing Australian and North American lizards, the largest coefficients implicate the ratio of jaw length to hind foot length, Australian species having the largest values, but the differences between these faunas are complicated by other variables with weaker coefficients. The comparison between North American and southern African species emphasizes the ratio of head length and head width to the length of the forearm. The discriminant functions contrasting North American lizards with those of the other two regions are allied to PC2, but the discriminant function separating Australian and African lizards does not correspond to any particular principal component.

The morphological distinctiveness of the lizards in each of the three regions is undoubtedly related to the different taxonomic compositions of each of the faunas. Species rosters used here include four families of lizards in each region: geckos, agamids, skinks, and varanids in Australia; geckos, one agamid, skinks, and lacertids in southern Africa; and iguanids and one each of the families Teiidae, Helodermatidae, and Eublepharidae (closely related to geckos above) in North America. The distributions of the largest six of these families on PC2 and PC3 of the combined principal component space are shown in Fig. 2. The lacertids, iguanids, and varanids are rather uniform in shape. The agamids, geckos, and especially the Australian skinks are much more diversified morphologically.

Principal components calculated for each region separately indicate the relative dimensions of the morphological space occupied by each of the regional faunas (Tables 2 and 3). According to the eigenvalues, PC1 and PC3 are greatly reduced in southern Africa compared to the other regions. In all three regions, the weightings of variables contributing to PC1 and PC2 are similar to those in the combined sample. PC3 represents different combinations of variables in each of the regions, but we did not test the significance of these differences and they represent only minor components of the total morphological variation among
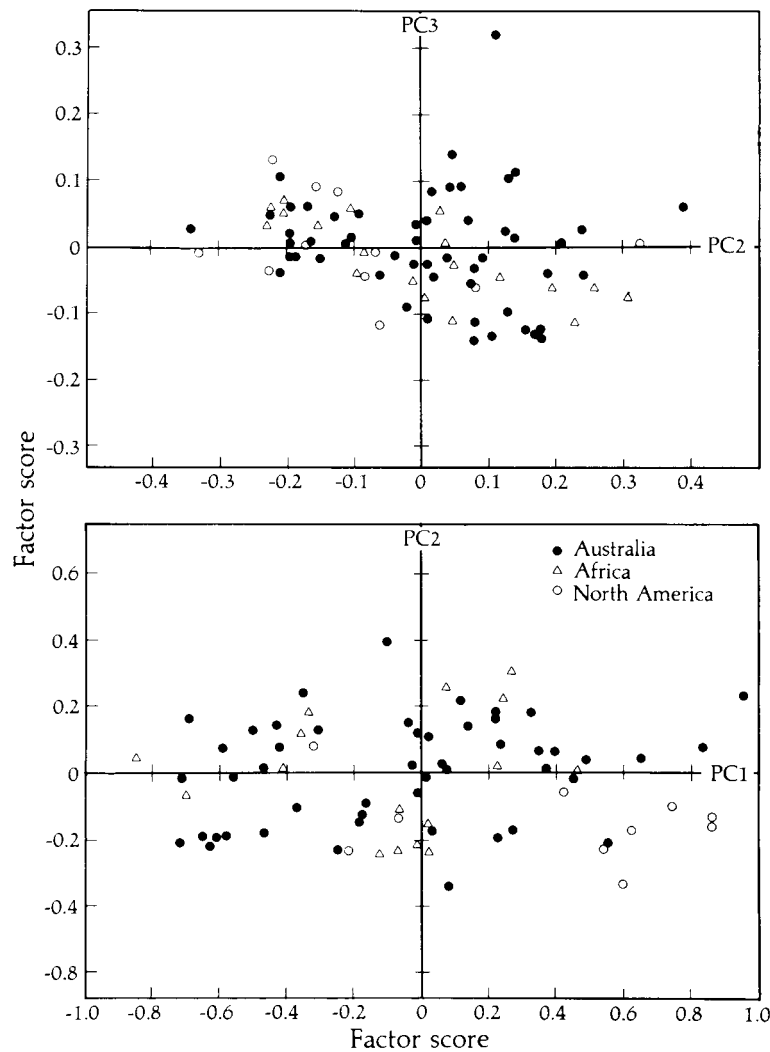
FIG. 1. Scores of lizard species on PC1 and PC2 (bottom) and on PC2 and PC3 (top) calculated from the covariance matrix of the pooled sample of 83 species.

species. Evidently, however, the number of dimensions of the morphological space occupied by lizards does not vary markedly between continents.

Community characteristics

Various indices to the morphological distances between species within localities in each region are presented in Table 5. Consistent with the results of Pianka's (1973, 1975) ecological analyses, the average distance between pairs of species in morphological space ($\bar{D}$) was greater in Australia than in either North America or southern Africa. Not unexpectedly, the average farthest-neighbor distance (FND) was greatest in Australia and least in southern Africa. We believe that the nearest-neighbor distance (NND) is a more meaningful measure of community structure than either $\bar{D}$ or FND because it provides an index to

the density of species packing in morphological space. The relationship of nearest-neighbor distance to number of species in a locality is shown in Fig. 3. Average NND's were greater in Australian localities than in southern African localities, even though the former had more species. The morphological structure of communities in Australia is thus more open than it is in the Kalahari Desert, comparably so to the much less diverse communities in the North American deserts.

Average nearest-neighbor distances in communities generated at random from the pool of all the species in each region are indicated by dashed lines. In Africa and Australia, the average nearest-neighbor distances in natural communities did not differ greatly from a random sample of species within the region. For random communities with the same number of species,
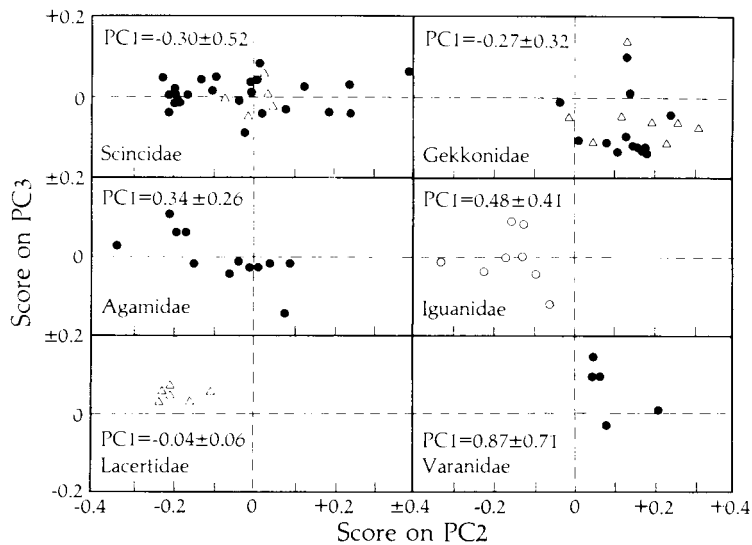
FIG. 2. Distribution of species of lizards in each of six families on PC2 and PC3 calculated from the covariance matrix of the pooled sample of 83 species. The mean and standard deviation of the distribution of species on PC1 are also indicated. Solid symbols = Australia; triangles = Africa; open circles = North America.

nearest-neighbor distances were considerably greater within the assemblages produced from the pool of Australian species. At North American localities, species found in the smaller communities were more widely spaced than the average random sample. We cannot make a statistical statement about the difference, however, because all North American communities we analyzed are built upon the same core of four species, *Cnemidophorus tigris, Uta stansburiana, Crotaphytus wislizeni,* and *Phrynosoma platyrhinos,* and thus are not independent samples. The large nearest-neighbor distance in the most diverse community is brought into line with the others when the aberrant *Heloderma suspectum* is excluded, as it was in the sampling of random communities.

The standard deviation of the nearest-neighbor distances within a locality (*SDNND*) is an index to the regularity of spacing between species within the community. In Fig. 4, these values are compared to standard deviations of *NND*'s in the randomly assembled communities. No tendency is evident in the African and North American localities towards regular spacing of individuals in morphological space. In Australia, *SDNND*'s in five of the localities were substantially lower than those of the random communities, suggesting nonrandom spacing. In the two least diverse localities, a pure spinifex (*Triodia*) habitat and a pure shrub-*Acacia* habitat, and in the most diverse locality, *SDNND*'s exceeded those in randomly assembled communities. The five localities with low *SDNND*'s were similar in having a mixture of spinifex and eucalypts and therefore may not constitute independent samples. We did not attempt to test differences between natural and random communities statistically.

DISCUSSION

Aside from the obvious general relationship between morphology and the selection of microhabitats and foods (Pianka 1969b, Pianka and Parker 1972, Pianka and Pianka 1976), we cannot make a more precise statement concerning the ecological relevance of the measurements used in this study. Although our morphological space clearly corresponds in some way to the ecological space occupied by desert lizards, the resemblance could be only partial and quite distorted.

TABLE 4. Pairwise discriminant functions between lizard faunas of deserts of three regions.

	Comparison		
	Australia–Africa	Australia–North America	North America–Africa
Mahalanobis D^2	2.23	3.09	7.26
F ratio	2.96	2.74	3.87
df	9,62	9,55	9,19
Probability of H_0	≤.01	≤.01	≤.01
Coefficients*			
SV	0.189	−0.008	0.547
HL	−0.528	−0.164	−0.831
HW	−0.257	−0.119	−1.429
HD	0.005	−0.085	0.099
JL	0.463	0.401	0.208
FA	0.179	−0.183	2.445
HL	0.198	0.188	−0.066
FF	−0.067	0.186	−0.271
HF	−0.169	−0.302	−0.258

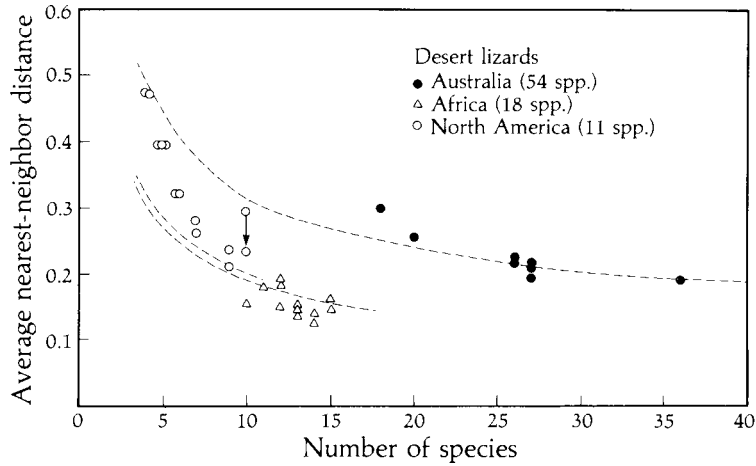* See Table 1 for key to abbreviations.

FIG. 3. Average nearest-neighbor distances plotted as a function of number of species for localities in Australia, Africa, and North America. The number of species in each region is included in parentheses. Dashed lines represent the trend of *NND*'s in randomly generated assemblages based on the species pool of each region. The arrow indicates the shift of position of community C (see Table 5) in North America when the aberrant large species *Heloderma suspectum* is removed.

At this point, it seems safest to proceed as if measurements of ecology and morphology provide different views of the structure of lizard communities which overlap to an unknown extent.

Our analysis is based on average measurements for each species. Yet each would more properly be represented by a cloud of points in morphological space. We attempted to assess the degree of variation within each species by calculating coefficients of variation CV = (standard deviation/mean) for each measurement and then averaging the CV's over the nine characters measured on each species. In North America,

the average CV ranged between 13% in *Callisaurus diaconoides* and 25% in *Sceloporus magister*. In southern Africa, average CV's ranged between 12% (*Pachydactylus rugosus*) and 32% (*Agama hispida*). We could detect no correlation between the variation within species and the distance to the nearest neighbor. Nor did values for the American and African species differ as a whole. Typical CV's of 15–20% in our sample correspond to distances of 0.06–0.09 on a scale of base-10 logarithms, which is much less than the average distance to a nearest neighbor. We presume, therefore, that the distances between species
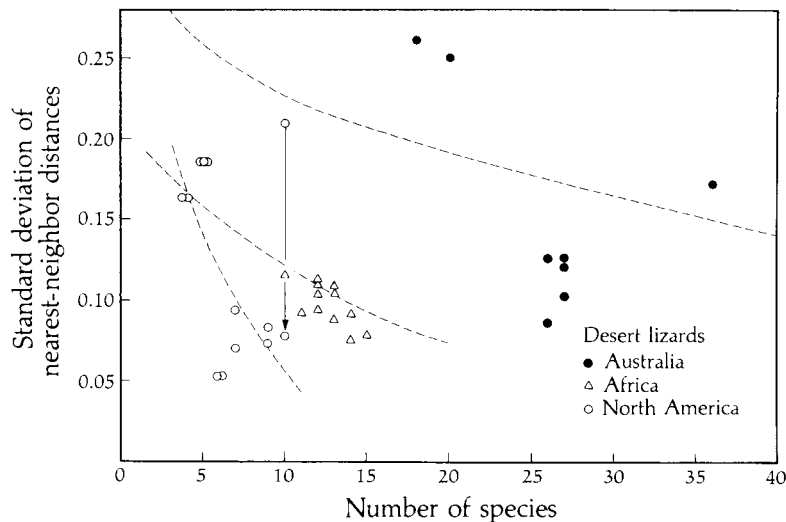

FIG. 4. Average standard deviations of nearest-neighbor distances plotted as a function of number of species for localities in Australia, Africa, and North America. See legend for Fig. 3.

TABLE 5. Morphological characteristics of communities.

Locality*	Number of species	Characteristics				
		NND	SDNND	FND	SDFND	$\bar{D}$
Australia						
A	26	0.224	0.087	2.215	0.460	0.907
M	27	0.213	0.103	2.167	0.487	0.881
D	27	0.195	0.127	2.123	0.436	0.830
E	36	0.193	0.173	2.136	0.421	0.792
L	26	0.219	0.126	2.165	0.435	0.881
G	27	0.211	0.212	2.148	0.434	0.840
N	20	0.257	0.251	2.118	0.461	0.793
Y	18	0.300	0.261	2.201	0.504	0.904
Africa						
L	14	0.126	0.076	0.713	0.116	0.438
K	13	0.151	0.088	0.701	0.118	0.439
M	12	0.149	0.110	0.894	0.173	0.509
B	15	0.145	0.079	0.988	0.192	0.530
A	13	0.148	0.105	0.875	0.180	0.489
X	14	0.140	0.092	0.878	0.167	0.492
G	13	0.139	0.109	0.877	0.176	0.477
D	12	0.187	0.113	0.876	0.181	0.503
R	10	0.155	0.116	0.722	0.114	0.445
T_s	12	0.188	0.105	0.868	0.190	0.485
T_f	11	0.179	0.092	0.722	0.129	0.466
T	15	0.162	0.095	0.845	0.177	0.456
North America						
U	4	0.474	0.165	0.931	0.209	0.668
I	4	0.474	0.165	0.931	0.209	0.668
L	5	0.397	0.186	0.912	0.186	0.588
G	5	0.397	0.186	0.912	0.186	0.588
V	6	0.322	0.053	1.057	0.169	0.491
S	6	0.322	0.053	1.057	0.169	0.491
E	5	0.397	0.186	0.912	0.186	0.588
P	7	0.264	0.094	1.079	0.165	0.660
M	7	0.281	0.070	1.061	0.154	0.643
T	9	0.211	0.073	1.054	0.152	0.610
W	9	0.235	0.083	1.066	0.149	0.625
C	10	0.296	0.210	1.459	0.349	0.763
C'	9	0.234	0.083	1.066	0.149	0.625

* Letters correspond to locality designations in Pianka 1967, 1969a, 1971.

are meaningful compared to the amount of variation within species, particularly the distances along dimensions of shape rather than size.

Accepting the limitations of the morphological approach, the principal conclusions of our analysis are as follows: (1) Most of the morphological variation among species of lizards is organized along a major size dimension and one or two shape dimensions. (2) The total morphological volume occupied by the lizards of each region is greatest in Australia, with the largest pool of species, slightly less in North America, with the smallest number of species, and by far the least in southern Africa, where many species are small. (3) The density of species packing in morphological space, judged by the average nearest-neighbor distance within localities, was greatest in southern Africa. The most diverse communities in North America and Australia had similar densities of species packing, but both were less than that found in the Kalahari desert communities. (4) The observed assemblages of

species in each region did not differ morphologically from assemblages having the same number of species drawn randomly from the region's pool of species.

The three regions were originally chosen for study in part because they appeared to offer similar habitats for lizards. Pianka (1973, 1975) found, however, that the lizards used different resources in each region. As a whole, Australian and African lizards used a greater portion of the time and microhabitat dimensions available to them than did the North American species. The latter, however, were more catholic in their use of prey categories than their counterparts in the other two regions. In the Kalahari Desert, 41% of all prey taken were termites. In Australia, 25% were vertebrates. Hence, whether or not the physiognomy, vegetation, and climate of the three desert regions differ, lizards use resources in substantially different ways, which are reflected in their morphology. It is not surprising that the southern African species, which specialize strongly on termite-feeding, are the least di-

TABLE 6. Taxonomic diversity of lizards in three desert regions.

Region	Number of families	Family diversity*	Number of genera	Genus diversity*	Number of species
Australia	4	3.5	16	10.6	54
Africa	4	3.4	11	9.2	18
North America	4	2.4	11	11.0	11

* Diversity was calculated within each region by the expression $\exp(-\Sigma\ p_i \ln p_i)$, where p_i is the proportion of genera which are in the ith family or species in the ith genus.

verse morphologically, even though we have not established the particular connection between morphological measurements and termite prey.

Ecological and morphological analyses raise important questions concerning the organization of biological communities. First, is the total space, ecological or morphological, occupied by the fauna determined primarily by the opportunities provided by the environment (including the preemption of those opportunities by competitors), or does the space occupied reflect the historical development of the fauna? Secondly, is the level of species packing within the occupied space determined by interactions between the species, or do species join the community independently of those already present? To answer these questions is to resolve the relative roles of species production and dispersal vs. local environment and ecological interaction in organizing communities. Our analysis is a step toward characterizing community structure but discovering causal mechanisms will require additional approaches.

The differences in number of species in the three regions reside at the taxonomic level of the species (Table 6). All three areas have four families of lizards represented on the rosters used in this analysis, and except for the agamids, geckos, and skinks, which occur in both Africa and Australia, the families differ in each region. There are slightly more genera in the deserts of Australia than in those of Africa and North America, but when genera are weighted by number of species, the generic diversity in the three regions is similar.

Although the number of families and genera is similar in each of the three areas, the morphological diversity within each family varies considerably. Based on our choice of characters, Australian skinks occupy by far the largest morphological volume of the 11 families represented in our study. Overlapping but smaller spaces are occupied by families in Africa and North America. It would be instructive to determine whether Australian skinks are filling a space uniquely available in Australia or whether the family possesses greater powers of diversification than do others owing to unique adaptations it may possess (cf. Greer 1976).

The four species of *Mabuya* skinks in the Kalahari Desert are much less varied morphologically than their Australian counterparts.

In conclusion, our morphological study has revealed patterns of regional morphological diversity and species packing in morphological space that are consistent with ecological studies in the same localities. Morphological approaches offer the advantages of sampling large numbers of species assemblages unambiguously and measuring the evolutionary diversification that underlies community structure more precisely than does an ecological approach. If ecological and morphological measurements can be intercorrelated, they will offer a much more complete description of communities and provide a stronger phenomenological basis for the formation and testing of ecological theory.

LITERATURE CITED

Bierregaard, R. O., Jr. 1978. Morphological analyses of community structure in birds of prey. Dissertation. University of Pennsylvania, Philadelphia, Pennsylvania, USA.

Cody, M. L., and H. A. Mooney. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9:265–321.

Findley, J. S. 1973. Phenetic packing as a measure of faunal diversity. American Naturalist 107:580–584.

———. 1976. The structure of bat communities. American Naturalist 110:129–139.

Greer, A. E. 1976. A most successful invasion. The diversity of Australia's skinks. Australian Natural History 18:428–433.

Karr, J. R., and F. C. James. 1975. Ecomorphological configurations and convergent evolution in species and communities. Pages 258–291 in M. L. Cody and J. M. Diamond, editor. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Morrison, D. F. 1967. Multivariate statistical methods. McGraw-Hill, New York, New York, USA.

Pianka, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Dissertation. University of Washington, Seattle, Washington, USA.

———. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333–351.

———. 1969a. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology 50:498–502.

———. 1969b. Sympatry of desert lizards (Ctenotus) in western Australia. Ecology 50:1012–1030.

———. 1971. Lizard species density in the Kalahari desert. Ecology 52:1024–1029.

———. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

———. 1975. Niche relations of desert lizards. Pages 292–314 in M. Cody and J. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Pianka, E. R., and R. B. Huey. 1971. Bird species density in the Kalahari and the Australian deserts. Koedoe 14:123–130.

Pianka, E. R., and W. S. Parker. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. Copeia 1972:493–508.

Pianka, E. R., and H. D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. Copeia 1976:125–142.

Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. Auk 97:321–338.

Sokal, R. R., and J. F. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.