

## CLIMATE, COMPETITION, AND THE STRUCTURE OF TEMPERATE ZONE LIZARD COMMUNITIES<sup>1</sup>

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**Abstract.** The roles of climate and competition in relation to the structure of temperate zone lizard communities were investigated. Lizard species richness was positively related to mean January temperature, but negatively related to warm-season precipitation and mean July temperature. Generic groups showed little overlap in morphological factor space but considerable overlap in habitat use. Species that were similar in either morphology or habitat use were dissimilar in the alternative factor space. A canonical correlation analysis revealed a significant relationship between lizard morphology and habitat use. In general, large bulky lizards were associated with extensive vegetative cover while smaller slender-bodied lizards were found in open desert or grassland conditions. No significant relationship was found between community size and measures of niche overlap or species packing in either morphological or ecological space. A comparison of species packing between the field communities and randomly generated null communities revealed no significant overdispersion of the natural communities in either habitat use or morphology, thus providing no evidence to support the limiting-similarity hypothesis.

**Key words:** *climate; community structure; habitat use; limiting similarity; lizards; morphology; null communities; species richness.*

### INTRODUCTION

Patterns of species richness and community structure have been investigated by ecologists in an effort to discern the basic principles of community ecology. Studies on communities of fishes (Gatz 1979, Findley and Findley 1985), amphibians and reptiles (Inger and Colwell 1977), and mammals and birds (Findley 1973, 1976, Brown 1975, Ricklefs and Travis 1980, Findley and Black 1983, Brown and Bowers 1984, 1985) have improved our understanding of the relationship between the biotic and abiotic environments and of the coevolution of organisms. Reviews of the literature by Pianka (1966*b*, 1967), MacArthur (1965, 1972), and Schall and Pianka (1978) have formalized eight major hypotheses of species diversity. These hypotheses include evolutionary time, ecological time, habitat structure, productivity and stability of primary production, climatic stability, predation, and competition. In this project, I used temperate zone lizard communities to test a few of these community structure hypotheses. Specifically, three questions were addressed. (1) Can patterns of lizard species richness be explained by environmental parameters? (2) Is lizard morphology a good predictor of habitat use? (3) Is there any evidence to suggest that lizard species within communities exhibit limiting similarities in habitat-use space and/or morphology.

The climatic stability and production hypotheses

have been evaluated for some temperate systems. For example, Rotenberry (1978) found bird species diversity, especially the evenness component, to decrease along a gradient of increasing climatic severity. Similarly, Weins (1974) has suggested that the number of grassland bird species in an area may be limited by periodically severe climatic conditions, and Hutson (1979) has demonstrated that the occurrence of habitat disruptions, whether in the form of climatic conditions or changes in productivity can influence the species diversity of model ecosystems. Increased production should increase species diversity (Connell and Orias 1964, Pianka 1966*b*) through decreased niche breadth. Over a sufficiently long time, species may become specialists and thus permit the invasion of additional species into the system. But, the unequal effects of increased productivity may result in competitive conditions that decrease diversity (Rosenzweig 1971, Riebesell 1974).

Attempts to evaluate the importance of competition in natural communities have proceeded either via species introduction/removal experiments (Holbrook 1979, Dunham 1980, Tinkle 1982), the artificial enrichment or depletion of some resource (Steimwascher 1979, Wilbur 1982), analysis of character shifts for groups of species in allopatry and sympatry (Soulé 1966, Grant 1968, Huey et al. 1974, Huey and Pianka 1974, 1977, Diamond 1978), or the construction of null communities (Gatz 1979, Ricklefs and Travis 1980, Ricklefs et al. 1981, Brown and Bowers 1984, 1985, Findley and Findley 1985). The experimental approach has several drawbacks relative to lizard communities. It yields information only slowly on portions of each

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community and does not reveal the mechanism of competition (Schoener 1974). Analyses of character shifts in sympatry and allopatry have been only marginally successful in detecting competitive effects (Grant 1972, Dunham et al. 1978). The null community approach (Connor and Simberloff 1984, Gilpin and Diamond 1984) has provided mixed results, but in some cases enables the evaluation of community-wide competitive effects.

Studies on lizard communities have been conducted primarily on tropical or subtropical systems (Rand 1964, Rand and Humphrey 1968, Schoener 1968, 1969, 1970a, b, 1976, Schoener and Gorman 1968, Roughgarden 1974, Inger and Colwell 1977) or on desert lizard systems (Pianka 1966a, b, 1967, 1969, 1971, 1973, 1981, 1986, Pianka and Pianka 1976, Pianka et al. 1979, Dunham 1980, 1983, Smith 1981). These studies suggest that the diversity and structure of lizard communities is related to productivity, spatial heterogeneity, and competition. However, only in the studies of Ricklefs et al. (1981) and Pianka have rigorous attempts been made to test hypotheses about community structure within extensive lizard communities. Furthermore, there have been no studies on the role of competition or habitat and environmental parameters in determining the structure of lizard communities across a diversity of temperate habitats. Likewise, our knowledge of the relationship between lizard morphology and habitat selection is confined primarily to observations made by Pianka during his extensive studies of desert lizard systems.

I used a multiple regression analysis to study the relationship between southwestern United States lizard species richness and various environmental parameters. I used factor analysis techniques to characterize the ecological (habitat use) and morphological characteristics of some temperate zone lizard species. The morphological factors of the species were then correlated through a canonical correlation analysis with habitat-use factors. Finally, regression models and null community analyses were used to determine if limiting similarity and diffuse competition can explain patterns of species packing and interspecific overlap in both habitat use and morphology.

#### METHODS

Twenty study sites were chosen in Arizona, California, and New Mexico to reflect a diversity of habitat types and lizard assemblages. The habitats studied ranged from flatland desert through sagebrush scrub to pinyon juniper woodland and ponderosa pine forests. The locations of the sites are listed in Appendix I. From two to eight lizard species were observed at each of the study sites.

Each study site was sampled for 3 d during the summer of 1979. Since lizard species are differentially cryptic, 3 d per site was probably not sufficient to reveal

all species. However, this sampling bias should be consistent throughout the study. Transects were performed by walking in a randomly chosen direction for 4 h each morning and 5 h each afternoon. For each lizard observed, perch height, perch temperature, and ambient air temperature were recorded. Also, a 9-m plant transect was performed in each of the four cardinal directions radiating from the point of initial sighting. The number of plants, and cover and height of each plant intersecting the transect were recorded at four levels: 0–0.5, 0.5–1, 1–2, and >2 m above the ground. Similar data derived from two 100-m plant transects performed at randomly chosen points at each study site were used to quantify the overall vegetation for comparisons among habitats.

Climatic data were derived from the National Oceanic and Atmospheric Administration publications for the weather stations located nearest each study site. These data were summarized from the 10 yr of weather information prior to the start of fieldwork (1968–1978). The weather parameters were chosen to reflect the environmental determinants of species diversity proposed by Pianka (1966b, 1967). Altitude, latitude, and thermal parameters were incorporated in the model because of the influence of the thermal environment on reptilian physiology.

Stepwise multiple regression was used to investigate the relationship between various environmental parameters and lizard species richness. The independent variables were (1) mean January temperature, (2) mean July temperature, (3) number of freeze-free days, (4) total warm-season precipitation (April–September), (5) total cold-season precipitation (October–March), (6) the coefficient of variation for the warm season precipitation computed on a year-to-year basis, (7) a seasonality of precipitation index calculated as the sum of the absolute values of the autocorrelations of monthly precipitation for lag times of 0–12 mo, (8) a measure of spatial heterogeneity calculated as the Shannon-Wiener diversity index for plant cover at 0–0.5 m (surface cover), 0.5–1 m (small shrub cover), 1–2 m (tall shrub cover), and >2 m (canopy cover), (9) latitude, and (10) approximate average altitude.

The stepwise regression model included an indicator variable for habitat type: open desert–sagebrush scrub habitats and woodland–forest habitats. This enabled the separation of potentially different alpha and beta diversity patterns. The value of this indicator variable was multiplied by the value of each of the above independent variables and then incorporated in the model as a potential interaction term. Thus, the regression model enables the detection of significantly different intercepts with respect to habitat type and significantly different slopes within habitat types. Therefore, the model is able to distinguish differing climatic patterns in desert–sagebrush scrub and woodland–forest habitats. Colinearity among the predictor variables was avoided by constructing the regression model using the

TABLE 1. The climate, habitat, and spatial diversity data for the 20 southwestern study sites.\*

Site	Habitat type†	Species richness	Jan $T_a$	Jul $T_a$	FFD	WSP	CSP	CVP	Seasonality	Spatial diversity‡	Lat.	Alt.
A	0	5	6.35	23.69	174.4	26.59	63.22	35.593	7.457	0.672	31.98	1520
B	1	6	12.12	34.90	317.2	5.77	9.28	49.382	0.680	0.707	32.98	380
C	1	6	12.09	32.80	340.4	11.15	10.96	34.683	1.740	0.780	32.62	460
D	1	8	11.13	32.36	281.4	3.58	5.83	134.212	0.770	0.524	33.62	460
E	1	3	11.84	35.58	358.9	4.19	9.23	81.196	0.909	0.668	34.05	310
F	1	5	2.48	24.51	165.7	14.99	8.67	35.595	3.129	0.696	33.92	1550
G	0	4	1.07	23.65	127.9	15.06	7.22	28.553	3.045	0.571	34.43	1980
H	1	4	1.79	25.34	175.1	14.78	8.01	38.478	2.438	0.621	34.57	1600
I	1	3	1.17	21.97	154.4	20.52	8.67	30.223	5.139	0.472	34.10	2130
J	0	3	0.69	24.32	160.6	16.46	10.66	16.540	1.913	0.695	35.30	1830
K	1	2	1.00	25.88	181.5	13.56	8.71	16.914	1.149	0.615	35.15	1680
L	0	2	0.14	21.99	158.8	26.34	15.36	27.936	4.722	0.825	35.75	1980
M	0	3	11.84	35.58	125.2	16.87	8.59	27.180	3.215	0.837	35.32	2290
N	0	4	6.18	26.77	197.4	16.28	8.06	36.920	2.971	0.749	32.38	1680
O	0	3	-1.73	24.67	169.8	12.09	11.87	32.001	1.223	0.608	36.45	1980
P	0	2	0.45	20.06	140.0	30.94	12.48	16.790	7.177	0.788	35.61	2290
Q	1	3	1.17	21.97	170.5	17.25	9.47	30.821	3.416	0.765	32.54	1220
R	0	2	6.42	24.91	221.4	30.91	14.85	44.056	10.115	0.863	32.25	1220
S	0	4	5.79	26.11	183.9	16.46	10.93	40.625	3.792	0.926	31.62	1830
T	0	4	8.13	29.52	245.0	16.94	14.14	25.628	3.075	0.858	33.29	1370

\*  $T_a$  = ambient temperature; FFD = number of freeze-free days; WSP = warm-season precipitation; CSP = cold-season precipitation; CVP = the coefficient of variation for the warm-season precipitation.

† 1 = open grassland or desert; 0 = woodland or forest.

‡ Shannon-Weiner  $H'$  for plant cover at 4 different heights.

reduction sums of squares criterion (Neter and Wasserman 1974).

Morphological data were derived from animals collected at the study sites, specimens deposited at the Los Angeles County Museum of Natural History, and the Museum of Southwestern Biology at the University of New Mexico. Only 4 specimens of *Sauromalus obesus* were measured; all other species were represented by a total of 19 or 20 specimens. Because of the seasonal changes in body sizes for lizards, and since each site was visited only once, no attempt was made to investigate intraspecific variation among study sites. The variables measured included snout-vent length, jaw length and width, head height, upper and lower appendage lengths for both the front and rear legs, front and rear foot length, length of digit 4 on the front and rear foot, and body width.

A principal axis factor analysis (Morrison 1976) was performed on the ecological and morphological species means in an effort to reduce the dimensionality of the data sets. The data were first normalized using the log transformation. Nonparametric schematic plots of the transformed data revealed no significant deviations from normality. A varimax rotation of the axes was used to simplify the interpretation of the results. The morphological and ecological factor scores were subjected to a canonical correlation analysis to reveal the relationships between the ecological and morphological spaces.

To investigate the potential effects of interspecific competition, interspecific distances and overlaps in ecological and morphological space were computed.

Morphological and ecological overlaps were computed using the technique of Harner and Whitmore (1977) and Whitmore and Harner (1980). Briefly, this technique uses discriminant function analysis to determine a linear combination of variables that provided maximal separation among the species. The overlap formula of MacArthur and Levins (1967) was then used with the discriminant scores to produce overlap values for each species pair in ecological and morphological space.

Interspecific distances in ecological and morphological space were calculated as Euclidean distances. The shortest distance between one species and all other species occurring in the same community was designated the "nearest neighbor distance" for that species in that community.

A stepwise multiple regression analysis was used to construct models of the relationships between the mean nearest neighbor distance and overlap variables and the community-size and habitat-type variables. Habitat type, classified as open (sagebrush scrub, flatland desert, or grassland) or woodland-forest was included in the regression model as an indicator variable.

The distribution of the mean nearest neighbor distances of the observed communities was compared with the distributions derived from artificially constructed null communities. The null communities were formed by selecting species at random and without replacement from the species pool consisting of all species observed during the course of the study. Communities with a given number of species were replicated 100 times each. The mean nearest neighbor distance and

TABLE 2. Regression results for the analysis of the lizard species richness data. The stepwise selection method was used; the significance level for entry into the model was .50, the significance level for staying in the model was .10.  $R^2 = 0.766$ .

Parameter	df	ss	ms	F	P
Regression	3	36.1692	12.0564	17.49	.0001
Error	16	11.0308	0.6894		
Total	19	47.2000			

	$\beta$	SE	Type 2 ss	F	P
Intercept	28.8451				
January $T_a$	0.3831	0.0755	17.7430	25.74	.0001
July $T_a$	-0.4497	0.1084	11.8549	17.20	.0008
Precipitation	-0.7209	0.1465	16.6968	24.22	.0002

mean overlap values for each community were then compared with the median of the computer-generated null distribution via nonparametric schematic plots (Tukey 1977).

RESULTS

Twenty-nine lizard species were observed at the 20 study sites (Appendix II). The climate and habitat data characterizing the sites can be found in Table 1.

Stepwise regression of lizard species richness on the climate and habitat variables accounted for 76.6% of the variation in lizard species richness and was composed of mean January temperature, mean July temperature, and warm-season precipitation (Table 2). The relationship between January temperature and species richness was positive, while both July temperature and precipitation were negatively related to species richness. Mean January temperature and mean July temperature are significantly correlated ( $r = 0.892, P < .001$ ). However, use of the type 2 sums of squares in the stepwise regression analysis insures against biases resulting from colinearities. Also, the negative relationship between richness and mean July temperature depends on the prior presence of the mean January temperature variable in the regression model (Neter and Wasserman 1974). The complete model as well as

the individual components explained a significant ( $P < .001$ ) amount of the variation in species richness.

Results of the factor analysis for the ecological data are presented in Table 3. Seven factors accounted for 97% of the variance in ecological space among lizard species. Plant cover and plant frequency (or "complexity") variables exhibited the most variation from species to species and were incorporated in factor axes that explained the most overall variation. However, the last three factors explained only 10.85, 9.47, and 5.44% of the variance, respectively. Variables such as perch temperature, perch height, and ambient temperature did not vary significantly from species to species; therefore these variables loaded most heavily on relatively minor factors. Thus, lizard species appear to select similar thermal aspects of the environment, but are more plastic in their use of vegetative components of the habitat.

Factor loadings for the analysis of morphological space are presented in Table 4. Here, only three factors were necessary to account for 95% of the variance in morphological space. The major components of the first factor were body width, front upper (humerus) and front lower (radius and ulna) appendage lengths, head height, and jaw width. Factor 2 was composed of rear foot and digit length while factor 3 consisted of jaw length. Morphologically, species were separated primarily on the basis of head and body shape and secondarily on the basis of the rear foot dimensions.

The distribution of the species relative to the first three factors in ecological and morphological space is shown in Figs. 1 and 2. Generic groupings are indicated in the figures. Vegetative structure variables separated a continuum of arboreal and sit-and-wait foragers from widely foraging and ground-dwelling species. *Sceloporus* species and *Phrynosoma* species were separated along factor 1 whereas *Crotaphytus*, *Gambelia*, and *Cnemidophorus* species were separated along factor 2. In the space defined by the morphological factors, distinct generic groups existed. Wide-bodied, slow-moving, sit-and-wait foragers such as *Phrynosoma* species were separated from the slender-bodied and very fast,

TABLE 3. Factor loadings for the first seven factors (FACT1-FACT7) of the ecological data from 20 southwestern study sites. The factor axes were rotated using the varimax technique.

Variable	FACT1	FACT2	FACT3	FACT4	FACT5	FACT6	FACT7
Ambient temperature	-0.033	0.024	-0.133	-0.030	0.974	-0.046	0.101
Perch temperature	-0.402	-0.059	0.161	0.391	0.294	-0.304	0.675
Perch height	0.206	-0.093	-0.189	-0.204	-0.049	0.923	-0.122
Cover: 0 m-0.5 m height	-0.097	-0.115	0.873	-0.020	-0.367	-0.038	0.198
0.5 m-1 m height	-0.197	-0.098	0.000	0.912	-0.005	-0.121	0.202
1 m-2 m height	-0.009	0.967	-0.106	-0.095	0.006	-0.067	0.016
>2 m height	0.874	-0.135	-0.302	-0.252	0.076	0.151	-0.171
Frequency: 0 m-0.5 m height	0.975	0.107	0.053	-0.113	-0.085	0.108	-0.046
0.5 m-1 m height	-0.073	0.100	0.957	-0.028	0.081	-0.170	-0.061
1 m-2 m height	-0.114	-0.050	-0.047	0.963	-0.027	-0.101	-0.013
>2 m height	0.022	0.970	0.119	-0.040	0.027	-0.021	-0.048
% of variance	18.05	17.76	17.08	18.57	10.85	9.47	5.44

TABLE 4. Factor loadings of the first three factors (FACT1–FACT3) for the log-transformed morphological data from the 20 southwestern study sites.

Variable	FACT1	FACT2	FACT3
Snout-vent length	0.567	0.440	0.635
Jaw length	0.241	0.499	0.818
Jaw width	0.858	0.071	0.466
Head height	0.851	0.166	0.446
Front upper leg	0.940	0.259	0.068
Front lower leg	0.897	0.398	0.136
Front foot	0.690	0.672	0.205
Digit 4: front foot	0.439	0.796	0.257
Rear upper leg	0.778	0.551	0.233
Rear lower leg	0.652	0.714	0.055
Rear foot	0.129	0.956	0.213
Digit 4: rear foot	-0.086	0.950	0.256
Body width	0.946	-0.084	0.140
% of variance	47.28	34.02	13.9

widely foraging *Cnemidophorus* species. The differing foraging and thermoregulatory tactics of the species located on this continuum are clearly indicated. In the morphological space, the generic groups were less variable than in the ecological space and exhibited little intergeneric overlap. Since the position of each species within the morphological and ecological spaces was

based on means across all study sites, this trend suggests that habitat use by a particular species is more responsive to local conditions than is morphology.

The results of the canonical correlation analysis are presented in Table 5 and Fig. 3. The canonical correlation was significant ( $P < .005$ ) and explained 64.2% of the variance in the canonical space. Several general trends were apparent. For the ecological variable, ambient temperature and perch temperature increased, plant cover above 2 m decreased, whereas cover between 0.5 m and 1 m, and plant frequency between 1 m and 2 m increased from left to right. In general, the ecological variable proceeded from forest or woodland conditions to grassland or desert conditions. For the morphological variable, there was a general trend from wide-bodied large lizards to smaller, more slender lizards. Body width, jaw width, jaw length, head height, and front leg length decreased from negative values of the variable to positive values, whereas rear foot dimensions increased. Overall, the morphological trend was from large bulky lizards to smaller more slender species; the ecological trend proceeded from cooler, more densely vegetated conditions to hotter, more open situations.

Mean nearest neighbor distances in ecological space

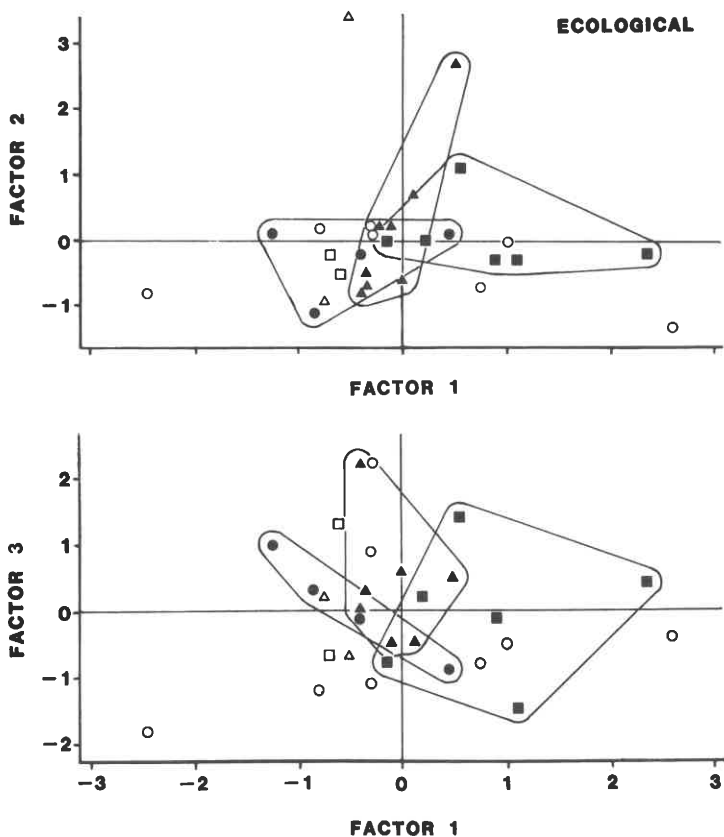


FIG. 1. The distribution of species in ecological space relative to the first three factor axes. *Cnemidophorus* ( $\blacktriangle$ ), *Crotaphytus* ( $\triangle$ ), *Holbrookia* ( $\square$ ), *Phrynosoma* ( $\bullet$ ), and *Sceloporus* ( $\blacksquare$ ). The remaining genera are indicated by  $\circ$ .

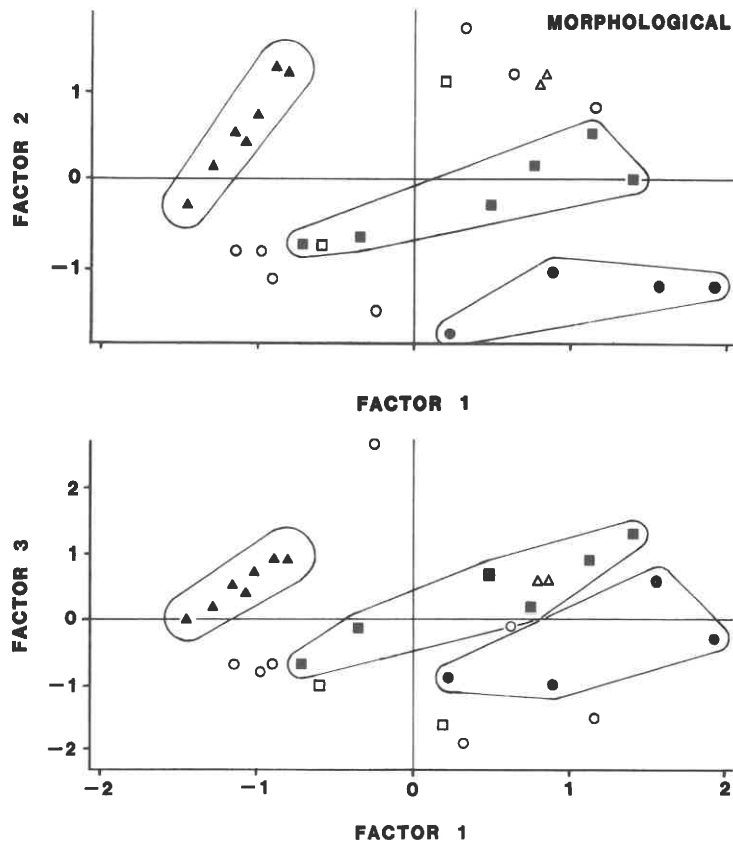


FIG. 2. The distribution of species in morphological space relative to the first three factor axes. Symbols for genera are as in Fig. 1.

(Table 6) showed no significant relationship to community size ( $P = .273$ ) or habitat type ( $P = .658$ ). These variables explained only 7% of the variance in the mean nearest neighbor distances (Table 6). Similarly, mean ecological overlaps were not related to community size ( $P = .847$ ) or habitat type ( $P = .404$ ). Community size and habitat type explained only 4.3% of the variance in the ecological overlap variable. In morphological space, mean nearest neighbor distance showed only a slight relationship with community size (slope =  $-0.1004$ ,  $P = .1012$ ) and none with habitat type ( $P = .828$ ). The overall model explained 19.1% of the variance and was not significant ( $P = .1642$ ). Also, mean morphological overlaps were not significantly related to community size ( $P = .3215$ ) or habitat type ( $P = .9113$ ). Thus, no significant trends were found relating community size and habitat type to measures of species packing and overlap in ecological and morphological space.

Five communities had mean ecological nearest neighbor distances above the null community medians, while 15 had mean nearest neighbor distances below the null median (Fig. 4). The probability of obtaining 15 samples below the median and 5 above is 0.014. Interspecific competition should result in nearest

neighbor distances greater than those of the null distributions. Thus, the ecological data exhibit significant clumping rather than the limiting similarity expected if the communities were structured by interspecific competition. In the morphological communities, 7 means were above the null medians while 13 were below. The probability of obtaining such a distribution of samples is 0.074. Again, most of the samples were below the null medians rather than above, exhibiting a tendency for clumping within morphological space rather than the limiting similarity predicted by the competition hypothesis. Thus, these morphological data provide no support for the competition hypothesis.

#### DISCUSSION

##### *Can patterns of lizard species richness be explained by environmental parameters?*

The stepwise regression model of lizard species richness included mean January temperature, mean July temperature, and warm-season precipitation. Spatial diversity was not included in the model. The results indicate that spatial diversity as measured in this study does not play a major role in determining the number of lizard species that can coexist in an area. This is

TABLE 5. The first two canonical variates for the 20 southwestern study sites. The canonical correlation was performed on the factor scores from the ecological and morphological data sets.

Morphology		Ecology	
FACT1 (head, width, front leg)	-0.679	FACT1 (canopy)	-0.341
FACT2 (rear foot)	0.585	FACT2 (tall shrubs)	0.097
FACT3 (snout-vent + jaw length)	-0.443	FACT3 (surface)	-0.033
		FACT4 (low shrubs)	0.683
		FACT5 (ambient temp.)	0.349
		FACT6 (perch height)	0.033
		FACT7 (perch temp.)	0.475
Canonical correlation = 0.801		Canonical $R^2 = 0.642$	$F = 2.6792$
			$P < .005$

counterintuitive in light of MacArthur's (1972) approximate formula for species diversity and the results obtained by Pianka (1967) for desert lizards in North America. This result may be an artifact of scale. For example, four species co-occurred in each of Pianka's (1967) desert communities (*Phrynosoma platyrhinos*, *Cnemidophorus tigris*, *Uta stansburiana*, and *Gambelia wislizeni*). He also found the sand dune specialist *Uma scoparia* (Norris 1958), *Sceloporus magister* (an arboreal species), and the above species coexisting in the same community, suggesting that his study sites contained a greater diversity of habitat types (and thus greater variability in the spatial diversity measure) than those investigated in this study.

In my study, increased precipitation had a negative influence on lizard species richness in both desert-sagebrush scrub and woodland-forest habitats. Precipitation parameters have been used by Pianka (1975), Brown (1973), and others to indicate primary productivity. Whitford and Creusere (1977) studied a community of lizards in southern New Mexico for a period of 5 yr and found that lizard species richness increased following several years of above average rainfall, demonstrating that within a particular habitat, increased precipitation and consequently primary production can result in increased species diversity. When habitats with very different physiognomies are considered, increased

precipitation may correlate with greater standing biomass. But, for temperate zone lizards this may result in a reduction in the number of suitable thermal microhabitats and a concomitant decrease in species richness.

Given the documented relationship between lizards and the thermal environment (Brattstrom 1965, Huey and Slatkin 1976, Huey and Webster 1976, Huey and Pianka 1977, Hertz and Huey 1981, Porter and Tracy 1983, Waldschmidt and Tracy 1983), the presence of thermal components in the regression model involving lizard species richness is not surprising. The relationship between the thermal environment and lizard distributions has been explored to some extent by Porter and Tracy (1983). For example, they found the northern limit of *Dipsosaurus* to be determined by the soil moisture and temperature requirements of egg incubation. In this study, the positive relationship between mean January temperature and lizard species richness suggests that across southwestern habitats winter temperatures may limit the number of species that can coexist in a community, perhaps because the energy requirements for overwinter survival are less. Within this relationship, high July temperatures were negatively associated with species richness. This implies that habitats with cold winters and hot summers maintain fewer lizard species than those with cold winters

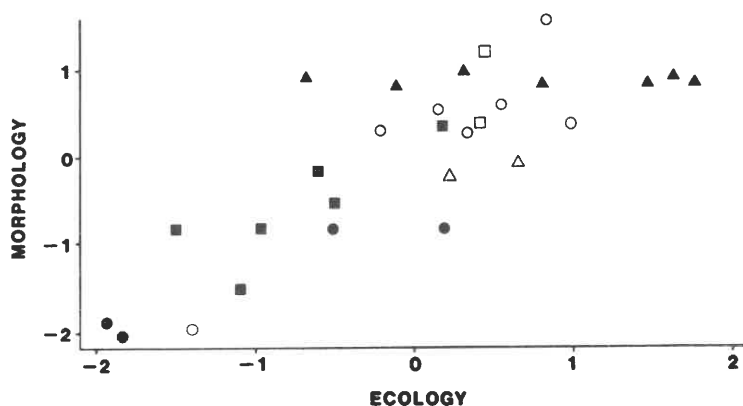


FIG. 3. Scatter diagram of the southwestern United States lizard species with respect to the first two canonical variates. Symbols for genera are as in Fig. 1.



TABLE 6. Regression results for the ecological and morphological nearest neighbor distances (NND) and overlaps ( $\alpha$ ).

	Ecological		Morphological	
	NND	$\alpha$	NND	$\alpha$
Intercept	0.8831	.2550	1.2566	.1050
Slope				
Community size	-0.0494	.0059	-0.1004	-.0184
Habitat type	-0.0607	.0800	0.0395	.0063
Overall $P$	.5383	.6897	.1642	.5161
$R^2$	0.070	0.043	0.191	0.075

and moderate summers. It is probable that cold winter temperatures require the accumulation of greater fat reserves for overwinter survival. However, cold winter temperatures are correlated with cooler summer temperatures, and thus, the accumulation of sufficient fat reserves may be impossible for many species. Habitats with moderate thermal regimes probably fit within the tolerance ranges of more lizard species than habitats with extreme temperature regimes.

Regulation of lizard species richness in the Southwest by the different ectothermic physiological tolerances of the species seems to be a reasonable hypothesis. Gorman and Hillman (1977) found the primarily allopatric species *Anolis gundlachi* and *A. cristatellus* were segregated on the basis of thermal physiology, and Pacala and Roughgarden (1985) have noted important thermal effects in their *Anolis* system. Similarly, Spellerberg (1972) has shown that distributions of some Australian lizards may be limited by thermal regimes.

*Is lizard morphology a good predictor of habitat use?*

Studies on organisms as diverse as fish (Gatz 1979), bats (Findley and Black 1983), and birds (Brown and Bowers 1985) have demonstrated the connection between morphology and diet or habitat use. For example, Brown and Bowers (1985) noted the relationship between bill morphology in hummingbirds and flower morphology of their diets and Findley and Black (1983) observed that bats that were similar in morphological space were also similar in diet. Some patterns for lizards (Pianka 1986) seem intuitive, for example: head proportions and jaw length are associated with prey size (Roughgarden 1974, Pacala and Roughgarden 1985), and leg length is associated with running speed and use of open spaces (Pianka 1969, Pianka and Parker 1972, Pianka and Pianka 1976). Body shape also plays a significant role with respect to foraging mode, predator escape, and reproductive effort (Vitt and Congdon 1978). That lizard morphology and ecology are related is perhaps best demonstrated by the profound morphological similarity of *Moloch horridus* (an agamid ant specialist in Australia) and *Phrynosoma platyrhinos* (an iguanid ant specialist in North America) noted by Pianka (1986).

In this study, the canonical correlation between the morphological and ecological data showed that large bulky lizards were associated primarily with cooler and more densely vegetated conditions, whereas smaller and slender species were found in warmer and more open conditions. Locations of the species within the canonical space indicate that this trend holds both within and between macrohabitats. This result is consistent with the work of Asplund (1974) on *Cnemidophorus*. He found that larger whiptail lizards spent more time in the shade than smaller whiptail lizards with the same thermal preferences, and attributed this pattern to the effect of size on the rate of heat exchange with the environment.

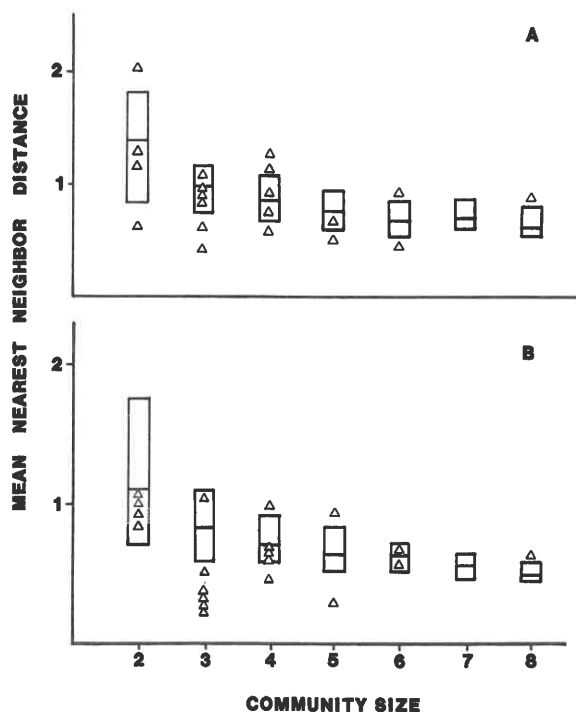


FIG. 4. Schematic plots for the distribution of the natural ( $\Delta$ ) and null (boxes) morphological (A) and ecological (B) communities. The top horizontal line in each box represents the upper quartile of the null distribution. The center and lower horizontal lines represent the median and lower quartiles, respectively.

*Do lizard species exhibit limiting similarities within communities?*

Evidence for the role of interspecific competition on microhabitat utilization, diets, and population dynamics of lizards has been presented by Pacala and Roughgarden (1982, 1985), Roughgarden et al. (1983), Schoener and Gorman (1968), Lister (1981), Huey et al. (1974), Huey and Pianka (1974), Pianka (1973, 1974, 1975), Case (1983), Smith (1981), and Dunham (1980, 1983). In this study, the null community tests and the regression analyses provided no evidence to support the hypothesis that a limiting similarity in morphology and habitat use exists within the wide variety of lizard communities investigated. The nearest neighbor distances and interspecific overlaps in ecological and morphological space showed no significant relationship with community size. Thus the predictions of the diffuse competition hypothesis were not met by these data. A null community analysis of desert lizards by Ricklefs et al. (1981) provided similar results. However, my own reanalysis of those data (J. S. Scheibe, *personal observation*) shows that whereas North American lizard communities exhibit significant clumping, seven out of eight Australian desert lizard communities have mean nearest neighbor distances that are greater than expected on the basis of a null community test. Also, Pianka (1986) simulated removal-introduction experiments based on diet for his lizard communities and found evidence for compensatory interactions among naturally coexisting species.

Results from null community analyses have been mixed. Fox (1981) and M'Closkey (1976, 1978) working on mammals, Dillon (1981) working on gastropods, and Brown and Bowers (1985) working on hummingbirds have detected significant nonrandom community patterns. Alternatively, Ricklefs and Travis (1980), Ricklefs et al. (1981), and Findley and Findley (1985) working with birds, lizards, and fish, respectively, have detected no significant nonrandomness. Clearly, the null model approach to community ecology has not been resolved (Connor and Simberloff 1984, 1986, Gilpin and Diamond 1982, 1984). The conflicting results may result from a lack of competition, null model design, the complex mechanics of competitive interactions (Rosenzweig and Abramsky 1986), and even the presence of competitive effects within and between communities.

My null community analysis revealed significant clumping of communities in both ecological and morphological space rather than the limiting similarity predicted by the competition hypothesis. Clumping of the natural communities may indicate convergence in resource utilization within communities even in the presence of interspecific competition. Brown and Bowers (1985) found temperate North American hummingbirds to be more similar in bill length, body weight, and wing length than predicted on the basis of several

null models. Thus, these data do not falsify the competition hypothesis. Also, there is some evidence that is consistent with the hypothesis. For example, the canonical correlation revealed a significant relationship between lizard morphology and habitat use. However, plots of the species within factor space showed lizards that were similar in morphological space such as *Crotaphytus* and *Gambelia* to be dissimilar in habitat-use space. At the same time, *Holbrookia maculata* and *Cophosaurus texana* were very different in morphological space but very similar in the ecological space. This indicates that within study sites, species that were similar morphologically differed significantly in their use of habitat, and species that were similar ecologically either differed morphologically within the canonical space or did not coexist in the same habitat.

Aside from problems of statistical power associated with the null community analysis (Diamond and Gilpin 1982, but see also Connor and Simberloff 1984, 1986, Hopf and Brown 1986), and the fact that I was unable to evaluate potential competitive interactions within communities, several explanations can be proposed to account for the results. Perhaps lizard communities in the Southwest are not structured by competition, and the number of species existing within a habitat is strongly influenced by climate, physiological tolerance, and perhaps productivity variables. Although little is known about the effects of age structure and indeterminate growth on patterns of resource utilization in temperate zone lizards, such a hypothesis seems reasonable. Work on insect life histories by Taylor (1981) demonstrates the importance of physiological time for ectothermic organisms and reveals interesting ecological results. Inger and Colwell (1977) found the effect of environmental unpredictability on amphibians and reptiles may be the prevention of distinct guild formation. Also, as the studies of Dunham (1980, 1983), Smith (1981), Tinkle (1982), and Weins (1984) illustrate, interspecific competition may be important only during "crunch" years. During "good" years, species may be capable of expanding their local ranges and thus occupy communities within which there is no competition. If my study occurred after a series of good years, the lack of a limiting similarity and the clumped nature of the communities would be possible. This would certainly explain why these patterns are different from those observed by Pianka (1973, 1974, 1975). It is also possible that phylogenetic history is of overriding importance in determining the anatomy of these lizard species. Finally, competition may play a significant role in structuring southwestern lizard communities through interactions with nonsaurian organisms. Competition has been detected between rodents and ants (Brown et al. 1979), hummingbirds and insects (Brown et al. 1981), and perhaps even between lizards and birds (Schall and Pianka 1978, Pianka 1986). No effort was made in this study to detect nonsaurian interactions. Aside from the inverse relationship between

similarity in morphology and habitat use, as would be predicted if competition were the driving force of lizard community structure, I have little evidence to suggest that these lizard communities exhibit a significant limiting similarity.

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## APPENDIX I

TABLE A1. Locations of the 20 study sites. Site letter designations correspond to those used in Appendix II.

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Site A	South Western Research Station, 8 km north of Portal, Cochise County, Arizona.
B	3.8 km west and 3.2 km north of Gila Bend, Maricopa County, Arizona.
C	Jack's Well, Cabeza Prieta Wildlife Refuge, Pima County, Arizona.
D	Corn Springs, 16 km east and 12.8 km south of Desert Center, Riverside County, California.
E	Sand dunes just south of Rice on Rice road, Riverside County, California.
F	Abandoned ranch, 14.7 km east and 3.2 km north of San Antonio, Socorro County, New Mexico.
G	Ladrone Mountains, ≈ 16 km southwest of Bernardo, Socorro County, New Mexico.
H	Plains west of the Manzano Mountains, east of Highway 6 and south of Belen, Valencia County, New Mexico.
I	San Agustin Plains, 3.2 km east of Magdalena, Socorro County, New Mexico.
J	The northwest talus slope of the Sandia Mountains, west of Placitas, Bernalillo County, New Mexico.
K	The west mesa, 4.8 km west of Rio Rancho, Bernalillo County, New Mexico.
L	3.2 km south of Jemez Springs on Highway 4, Sandoval County, New Mexico.
M	3.2 km north of Bluewater Lake, McKinley County, New Mexico.
N	East slope of the Organ Mountains, Dona Ana County, New Mexico.
O	Angel Peak campground, southeast of the four corners area near Highway 44, San Juan County, New Mexico.
P	11.2 km west of Las Vegas, San Miguel County, New Mexico.
Q	Jornada Experimental Range, east of Las Cruces, Dona Ana County, New Mexico.
R	Dark Canyon, ≈ 13 km east of Highway 137, Guadalupe Mountains, Eddy County, New Mexico.
S	Indian Creek Canyon, Animas Mountains, Hidalgo County, New Mexico.
T	Blue River, Blue Mountains, 48 km north and 16 km east of Clifton, Graham County, Arizona.

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## APPENDIX II

TABLE A2. List of species, and sites at which the lizards were observed or captured.

Species	Sites																			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
<i>Callisaurus draconoides</i>		X	X	X																
<i>Cnemidophorus exsanguis</i>	X											X	X	X						X
<i>C. inornatus</i>									X											X
<i>C. neomexicanus</i>								X			X									
<i>C. tessellatus</i>						X	X			X								X		
<i>C. trigris</i>		X	X	X																
<i>C. uniparens</i>									X											
<i>C. velox</i>															X	X				
<i>Cophosaurus texana</i>							X										X			X
<i>Crotaphytus collaris</i>				X						X					X	X				
<i>Dipsosaurus dorsalis</i>		X	X	X																
<i>Eumeces obsoletus</i>															X					
<i>Gambelia wislizeni</i>					X	X		X				X								
<i>Holbrookia maculata</i>								X	X		X									
<i>Phrynosoma cornutum</i>								X												
<i>P. douglassi</i>	X												X							
<i>P. modestum</i>						X	X													
<i>P. platyrhinos</i>			X																	
<i>Sauromalus obesus</i>				X																
<i>Sceloporus clarki</i>																				X
<i>S. jarrovi</i>	X																		X	
<i>S. magister</i>		X	X	X		X														
<i>S. poinsetti</i>																			X	
<i>S. undulatus</i>										X			X		X	X		X	X	
<i>S. virgatus</i>	X																			
<i>Uma scoparia</i>					X															
<i>Urosaurus graciosus</i>		X		X	X															
<i>U. ornatus</i>	X								X			X							X	X
<i>Uta stansburiana</i>		X	X	X		X		X										X		