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CONVEXITY, DESERT LIZARDS, AND SPATIAL HETEROGENEITY

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Abstract. The number of lizard species in the flatland desert habitat is correlated with several different structural attributes of the vegetation. It is shown that both the horizontal and vertical components of spatial heterogeneity are correlated with the number of lizard species. The habits of the twelve component species are considered briefly as they relate to the partitioning of the biotope space. Three species are food specialists, eight display various substrate specificities, and only one species appears to be truly "convex." Two tests of the present interpretation of these results are proposed, and some speculations concerning Australian flatland desert lizards are made.

Using Shannon's (1948) measure of information as a diversity index, MacArthur and MacArthur (1961) demonstrated that bird species diversity is strongly positively correlated with foliage height diversity, and in later studies have elucidated the probable causal chain between these two variates (MacArthur, MacArthur and Preer 1962, MacArthur 1964). Briefly, the argument is that habitat exploitation patterns must be a compromise between extreme "specialization" and extreme "generalization." The way in which birds exploit the food habitat is seen as a compromise between restricted diet and very broad diet, resulting in maximum efficiency. MacArthur and MacArthur (1961) and MacArthur (1964, 1965) reason that three-dimensional exploitation of a complex environment (by birds) may take two different forms: a species can either be restricted in the food it takes (due to active preference or circumstance) or it can utilize a restricted foraging behavior, eating most of the food objects encountered. Only in cases of extreme food concentration (such as fruit trees) does the advantage of food specialization outweigh the disadvantages, and most birds have instead restricted their method of foraging. The theory of such compromises between specialization and generalization has been developed further by MacArthur and Levins (1964), MacArthur (1965), and MacArthur and Pianka (in press).

MacArthur and Levins (1964) point out that although the continuum from specialists to generalists has theoretical meaning, in practice the differences between particular species must be considered. In addition, the resource items must be specified, since a generalized feeder might be specialized with respect to substrate or other resources. Given competitive exclusion, all species must be specialized (on different resources) to some extent in order to coexist. On which resources do most of the species in a given taxon specialize, or how do the species of a particular taxon partition the environmental mosaic? And are there underlying trends which relate different taxa? In MacArthur and Levin's terms this becomes a question of the average shape of the "species pools." Is the bird species pool convex or concave in most habitats, and are the species pools of other taxa in other habitats generally similar or does the shape of these pools vary widely?

Ecologists have built a strong case for the importance of food as the primary resource for many species (Hairston, Smith and Slobodkin 1961, Lack 1954), and one worker has even suggested that "niche" be operationally defined as "the nutritional role of the animal in its ecosystem, that is, its relations to all the foods available to it" (Weatherly, 1963). Substrate preferences (which may be considered micro-habitat segregation) are often important determinants of the foods eaten by a species. Differences in foraging behavior are also closely related with both the substrates and foods exploited (MacArthur 1958). The substrates exploited and food species taken are resources on which many species have become specialized, and are usually closely interrelated. However, there are always species which have narrow requirements with respect to some resources, and broad requirements with respect to others. Since a multi-dimensional approach to the compromise reached by a particular species (i.e. its "convexity") has not been developed, the practical worker has to consider each of the resources separately.

Studies on flatland desert lizard diversity (Pianka 1965) show striking parallels with some of the previous work and suggest that similar considerations are appropriate for this group. The present investigation is based on data from 10 flatland desert study areas in a latitudinal gradient from southern Idaho to southern Arizona. Else-

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TABLE I. Lizard and plant data corrected to a 231 m^2 quadrat size

Number of Lizard Species	Plant Species Diversity	Plant Volume Diversity	Quadrat Variance in Standing Crop (m^3)	Quadrat Variance in % Coverage	Number of Plants	Quadrat Size (m^2)	Number of Quadrats
4	high	low	low	low	349	230.7	1
5	0.80	0.08	25.9	1.4	4,907	115.4	40
5	1.46	0.13	70.8	4.0	1,707	57.7	32
6	1.24	0.36	88.7	4.8	4,798	230.7	32
7	0.91	0.41	78.1	4.4	2,333	230.7	32
6	1.24	0.25	205.1	11.6	5,148	230.7	32
8	1.73	0.44	191.3	10.9	2,785	230.7	32
9	1.14	0.82	224.8	12.9	740	230.7	32
9	1.23	0.62	579.1	32.5	2,252	230.7	48
10	1.36	0.52	1447.6	81.0	2,328	230.7	40

where I have contrasted some of the current indices of diversity (Pianka in press) and concluded that in situations with many rare but regular species, a good index of diversity is simply the total number of species occurring on the area. Flatland desert lizards fit this case and, because they also undergo pronounced seasonal and annual fluctuations in population size, are not well measured by diversity indices which weight each species by its abundance. Species are seldom exterminated during these population fluctuations, as all the species expected to occur on an area (based on range maps) were generally found there, although they were often quite rare. The number of lizard species on the 10 sites varies from 4 to 10, generally increasing from north to south.

A series of 32 to 48 quadrats, ranging in size from 58 m^2 to 231 m^2, was staked out on each study area, and the perennial plants within these quadrats identified, measured and counted. Linear measurements were made of the height and width of the larger shrubs and trees, and the enclosed volume computed from the formula for the volume of oblate spheroids ($V = 4/3\ \pi\ a\ b^2$, where a is the linear dimension of the major axis, and b the same for the minor axis). No allowance was made for foliage density differences between shrub species. Small shrubs were counted but not measured. Three volume categories were selected corresponding to three natural layers: (1) the small semi-shrubs under 0.7 m^3, (2) the large woody shrubs (mainly *Larrea divaricata*) between 0.7 and 22.0 m^3, and (3) the largest shrubs and trees over 22.0 m^3. The proportions of the number of shrubs and trees in each of these three volume categories were used to calculate plant volume diversities according to the formula $H = -\Sigma p_i \log_e p_i$ (Shannon, 1948). Table I gives the data and Figure 1 graphically illustrates the results of these computations. There is a strong positive correlation between the total number of lizard species and the volume diversity of the perennial vegetation. No relation exists with plant species diversity, calculated using the relative abundance of shrub species as p_i's in the same formula (see Table I). These results are essentially a duplication of those of MacArthur and MacArthur (1961), except that they are for a terrestrial, relatively immobile taxon. It might seem strange that vegetative structure could control the diversity of an essentially two dimensional animal, but knowledge of the autecologies of the lizard species involved is enlightening. The scope of the present report does not allow elaborate expansion of the frequent substrate specificities of flatland desert lizards, but brief indications may be restated here (see also Pianka, 1965).

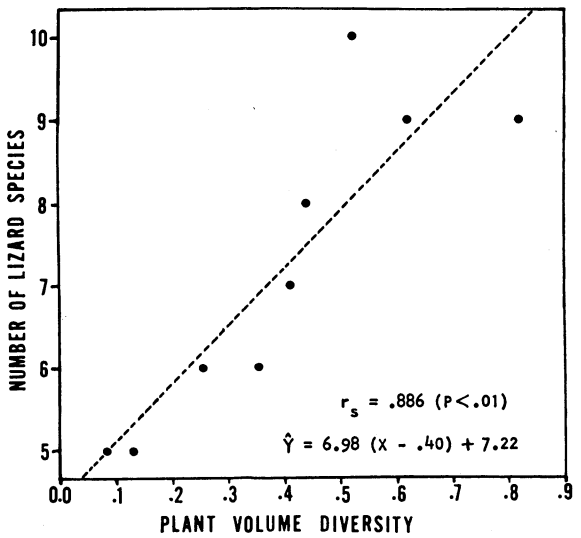

FIG. 1. Number of lizard species plotted against the diversity of plant volumes, irrespective of plant species. Spearman rank correlation coefficient (r_s) and linear regression equation are given in lower right hand corner.

Four species are found ubiquitously throughout the deserts (*Uta stansburiana, Crotaphytus wislizeni, Phrynosoma platyrhinos,* and *Cnemidophorus tigris*); and another 8 species (*Callisaurus draconoides, Sceloporus magister, Uma scoparia, Urosaurus graciosus, Dipsosaurus dorsalis, Coleonyx variegatus, Xantusia vigilis,* and *Heloderma suspectum*) are added variously in the southern deserts, never exceeding 10 species in any area. The 4 species which occur throughout the desert series exploit rather different habitats at the extremes of their ranges, but the manner of exploiting these differing habitats is similar.

Uta and *Crotaphytus* "sit-and-wait" under shrubs, usually moving only when a food item offers itself; *Uta* eats small insects and *Crotaphytus* the larger ones as well as various lizards. *Phrynosoma* also exploits the open spaces between shrubs by "sitting-and-waiting" while *Cnemidophorus* forages by constantly moving, walking from bush to bush, pausing occasionally to dig or climb for prey, but always progressing jerkily along. It is significant that the only teiid lizard in the system is this abundant species (*Cnemidophorus*), which exploits the

TABLE II. Summary of the ways in which the environment is partitioned by the twelve lizard species

	Species	Family
A. Diurnal Species		
I. Widely foraging species	*Cnemidophorus*	TEIIDAE
II. Sit-and-wait species		
a. Under bushes	*Uta, Crotaphytus*	IGUANIDAE
b. Open spaces between shrubs	*Phrynosoma,* Callisaurus*	IGUANIDAE
c. Arboreal (trees, large bushes)	*Urosaurus, Sceloporus*	IGUANIDAE
d. Sand-dunes (open spaces)	*Uma*	IGUANIDAE
III. Herbivorous (IIa, b, c, and d)	*Dipsosaurus**	IGUANIDAE
B. Nocturnal Species		
I. Open foraging (?)	*Coleonyx*	EUBLEPHARIDAE
II. In Joshua tree rubble	*Xantusia*	XANTUSIDAE
III. Olfaction and digging	*Heloderma**	HELODERMATIDAE

Food "Specialists"	
Phrynosoma	Ants
Dipsosaurus	Floral and vegetative materials
Heloderma	Eggs and young of vertebrates

environment more like a bird than like a "typical" lizard; perhaps there is room for only one widely foraging species in this system. Although *Uta, Crotaphytus,* and *Cnemidophorus* have fairly diverse arthropod diets, *Phrynosoma* is a specialist on ants, which may be a rather concentrated food source somewhat like the fruit trees mentioned earlier (depending upon other factors, below). Other features of *Phrynosoma* fit into the often observed specialization on ants; the stomach-body volume ratio is high, suggesting that the abundant, but chitinous food supply is not overly nutritious. Accordingly, great numbers of ants are eaten and *Phrynosoma* has relaxed efforts at behavioral thermoregulation in order to maximally exploit this food supply (*Phrynosoma* has a significantly higher variance in body temperature than all other species). The large stomach to body volume ratio and relaxed thermoregulation are only possible because of the cryptic coloration and the spiny tank-like body form, which allow *Phrynosoma* a relative degree of immunity from predators, and which would appear to be important adaptations requisite to successful ant food specialization.[2]

Callisaurus is another lizard of the open spaces between bushes but, unlike *Phrynosoma,* feeds on a very wide variety of insects. This is accomplished by utilizing the "sit-and-wait" method of foraging; by standing up on its forelegs *Callisaurus* increases the area covered and maximizes the efficiency of utilization of the open spaces.

In the flatland desert both *Sceloporus* and *Urosaurus* are always found on or in association with very large shrubs and trees. *Urosaurus* exploits the outer branches of trees and seldom leaves the tree (Gates 1964), whereas *Sceloporus* uses the "sit-and-wait" strategym from the tree trunk, exploiting the ground immediately around the tree by facing head downwards on a perch on the tree trunk. Both of these arboreal species have broad diets, indicating that they must take a wide range of the available food species in order to exploit their rather restricted habitat space efficiently.

Uma, a diverse arthropodan feeder, has many morphological adaptations for its sand dune existence, and has never been found more than 50 m from typical sand dune habitat (Norris 1958). In this rather restricted habitat *Uma* is often the commonest lizard species.

Dipsosaurus, the only truly herbivorous flatland desert lizard, relies largely on *Larrea divaricata* flowers for its food (in the flatland desert) and falls into the food specialist category with *Phrynosoma.* The species is never very abundant and has a pronounced seasonal activity pattern which follows the flowering of desert plants. *Larrea* blooms in great profusion during the spring on the flatland desert, and during this period is a very concentrated food source.

Xantusia was found only underneath dead decomposing *Yucca* logs in the Mojave desert. Its diet is somewhat restricted, but this is likely due to its small size and extremely strict micro-habitat preference. This is a very secretive lizard, whose cryptic habits remind one of those of salamanders in more mesic areas.

Coleonyx and *Heloderma* are the only nocturnal lizards on the desert flats; the former has a broad diet and ranges widely, occurring throughout the Sonoran and Mojave deserts on many different substrates and in many plant associations, while the latter is a secondary carnivore with a fairly restricted diet (the eggs of lizards, snakes and birds, and the young of small mammals). *Heloderma* occurs only in the Sonoran desert, in which it survives from season to season by building up large fat reserves during the times of plenty to nourish it through the droughts and famine. The summer rains with their warm season production and breeding of prey species probably allow the continued existence of this species in the Sonoran desert. It is possible that *Coleonyx* can not expand its range northwards because the growing season is too short in the north, but this remains problematical. The preceding discussion is summarized in Table II.

Spatial heterogeneity in its broadest sense includes a horizontal, a vertical and a qualitative component. Plant volume diversity (the abscissa of Fig. 1) measures primarily the vertical component of spatial heterogeneity. However, only 2 of the 12 lizard species are directly dependent upon the vertical structure of the vegetation (the arboreal species *Urosaurus* and *Sceloporus*). It appears the horizonal and qualitative components of spatial heterogenity are more important to most of the lizard species, but these are difficult to quantify accurately. The horizontal component of vegetative spatial heterogenity

[2] It is interesting that an agamid lizard, *Moloch horridus,* has independently assumed this habitus in the Australian deserts, which have not been populated by iguanids. These observations on *Phrynosoma* suggest that the variance in body temperature of *Moloch* in nature should also be large. Indeed, Licht *et al* (1966) have recently reported that this is tentatively the case (their sample size of 5 is somewhat small).

may be estimated by calculating between quadrat variances in percentage cover and standing crop (Table I). The number of lizard species is positively correlated with both of these measures, though not as strongly as with plant volume diversity. I could derive no direct measure for the qualitative component of spatial heterogeneity except the plant species diversities mentioned earlier. It is apparent that an accurate index of qualitative spatial heterogeneity would have to include decomposing *Yucca*, blooming *Larrea divaricata* and sand dunes! Fortunately, plant volume diversity seems to be indirectly correlated with both the horizontal and qualitative components of spatial heterogeneity, and appears to have good predictive powers. Thus, 10 of the 12 species are dependent upon various spatial attributes of the environment, and only the 2 nocturnal species have to be explained by other means (*Coleonyx* and *Heloderma*). Flatland desert lizards partition the environment temporally, but the spatial subdivision of habitat space is a more important factor allowing the coexistence of many different species.

The preceding rather qualitative considerations do not allow quantification of the lizard "species pool," but they do suggest that convexity of iguanids is determined by the various possibilities for efficient micro-habitat utilization (given the "sit-and-wait" pattern of foraging). The single teiid (*Cnemidophorus*) is able to successfully exploit a wider range of environmental elements by foraging in a distinctly different manner from the various iguanid species. Thus, in the terms of MacArthur and Levins (1964) and MacArthur (1965), and considering the various substrates as the resources, *Cnemidophorus* is a "jack-of-all-trades," while all of the other species are variously specialized. However, stomach content analysis alone (using food species as the resources) would give a different picture, with many so-called "jacks-of-all-trades" and only 3 food specialists (*Phrynosoma, Heloderma,* and *Dipsosaurus*). The foods of these 3 species are usually (ants) or periodically (flowers and eggs) very abundant, which allows the evolution of food specialization because it is thereby possible to make particularly efficient use of a very selected diet. The 3 food specialists are thus least "convex," *Cnemidophorus* is most "convex," while the remaining 8 species are intermediate, being generalized in the foods they take and specialized in the substrates they utilize.

Although the post-facto explanation of community structure in terms of the number of possible ways the taxon can exploit the particular environment borders on being circular, such considerations allow some interesting predictions which can be used to test the ideas arrived at by this circular route. Thus we may argue that given the lizard body plan and the flatland desert habitat, there is a finite number of ways of dividing up the environment. Furthermore, there apparently are 4 or 5 ways of successfully coexisting in the structurally simple northern deserts, and at least 10 different ways in the spatially more complex southern deserts. Structurally simple flatland desert habitat occurs in small patches in the southern deserts, and preliminary observations indicate that two such habitats in the Mojave and Sonoran deserts support only 6 lizard species.

Another strong test of these statements consists of the examination of an independently evolved flatland-desert lizard system to see if a similar correlation holds. The Australian deserts form just such a system, being nearly as far south of the equator as the American deserts are north of the equator, and displaying a similar climatic pattern. These deserts have been populated by agamid lizards derived from iguanid ancestors, and have evolved independently of the American desert iguanids. The Australian agamids may be predicted to exploit the "sit-and-wait" type of foraging behavior by restricting themselves to specific micro-habitats, possibly the same ones used by the North American desert Iguanidae. There are no teiid lizards in Australia, but the skink family has radiated widely; most skinks forage in the same manner that *Cnemidophorus* forages. Superficially, some of these skinks anatomically resemble *Cnemidophorus* and it is possible that they will be found to fill the ecological role of widely foraging species in other areas. There are many species of geckos in Australia and it is probable that the ecological roles of *Coleonyx* and *Xantusia* will be filled by geckos in Australia. The Australian equivalents of *Heloderma* and *Crotaphytus* will probably be varanid lizards (monitor lizards), which are known to be large and voracious creatures. If the North American flatland deserts are saturated with lizard species, one would predict that the most complex flatland desert habitats in Australia should have only about 10 species of lizards. However, it is also possible that the Australian lizards may have been able to partition the environment more finely than their North American counterparts because of the regular summer rains, and that there will be more species at saturation in habitats of similar structural complexity. These alternatives could be distinguished by appropriate observations on the manners in which the component species exploit the environmental mosaic. It is also possible that there may be reciprocal relations with bird or mammal species' numbers, and this possibility could be approached by comparing the bird and mammal species in the two regions.

Although the present paper has dealt only with lizards in flatland desert habitats, similar conclusions have been reached for forest-dwelling lizards (Collette 1961, Rand 1964) and appear to be appropriate to rock-dwelling lizard faunas as well.

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