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CHAPTER 1

Reptilian Species Diversity

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I. Introduction

Although species diversity has recently been termed a "non concept" (Hurlbert, 1971), it is an extremely useful notion that can be defined as the *effective number of species present* (Hill, 1973), either in a community, a portion of a community, or over a broader geographic area. Diversity can be quantified in a wide variety of ways, but its basic components are simply the actual number of species and their relative importances, usually measured by relative abundances (see also next section "Components of Diversity"). Many different indices of diversity have been proposed and used, and an extensive literature on species diversity has accumulated (for a sampling, see Woodwell and Smith, 1969; Krebs, 1972; MacArthur, 1965, 1972; Whittaker, 1972; Ricklefs, 1973; Pianka, 1966a; Schoener, 1974).

The ways in which species within ecological communities partition available resources among themselves is a major determinant of the diversity of coexisting species (Schoener, 1974). Moreover, the niche relationships of the component species in a competitive community strongly influence many aspects of community structure and function.

Here I attempt to review the present status of knowledge on species diversity of reptiles and I briefly compare aspects of reptilian species diversity with those in some other taxa, especially birds and mammals. Species diversity has received considerably greater attention in lizards than it has in other groups of reptiles. Much of my review therefore concerns lizard communities. Indeed, as I am the only one who has undertaken detailed ecological investigations of *entire* saurofaunas (Pianka, 1967, 1969a, 1971, 1973, 1974b, 1975), I discuss largely my own work, which has been restricted to deserts. I do, however, treat other studies where appropriate. In what follows, I draw freely from this body of my own data on desert lizard "communities" ("assemblages" would probably be a preferable

term—Pianka, 1973). To provide the reader with a background, I therefore briefly describe these desert-lizard systems.

Over the past decade, I have gathered data on the diets, times of activity, and microhabitats of over 15 000 individual lizards of 91 species on some 28 different desert study sites at similar latitudes on three continents. These areas vary widely in total number of lizard species: ten areas in western North America support from four to ten species, another ten sites in the Kalahari desert of southern Africa support from 11 to 17 species, while eight Australian study areas support from 15 to 39 sympatric species of lizards. Microhabitat and time of activity were recorded for most active lizards, and stomach contents were analyzed for those that could be collected. Many of these data have been published (Pianka, 1966a, 1967, 1968, 1969a, 1969b, 1970, 1971, 1973, 1974b, 1975; Pianka and Huey 1971; Pianka and Pianka, 1970, 1976; Pianka and Parker, 1972, 1975; Parker and Pianka, 1973, 1974, 1975, 1976; Huey and Pianka, 1974; Huey, Pianka, Egan, and Coons, 1974), and a number of other papers are in preparation.

II. Components of Diversity

Analyses of species diversity typically proceed through recognition of various components of diversity. However, diversity can be broken down into its components in a large number of different ways, all of which can provide potent insights into the factors underlying patterns of diversity. To set a theoretical framework for the remainder of this review, I next outline briefly various such approaches to diversity.

A. Number of Species and Their Relative Importance

As indicated above, the two fundamental factors determining the *effective* number of species present are simply (1) the total number of species actually present and (2) their relative importance; the latter may be estimated by relative abundance, biomass, or productivity (Dickman, 1968; Whittaker, 1970, 1972). The former component, number of species, is variously referred to as "species richness" and/or "species density," whereas the latter component is usually termed "equitability" and/or "evenness." Thus, two communities with the same number of species can differ in species diversity if one community has fewer very rare species than the other. Various indices of diversity weight these two components rather differently (Hill, 1973), and some indices all but ignore one component or the other. This may be justified to some extent; however, in birds at least, relative abundance contributes relatively little to species diversity as estimated

with Shannon's information theoretic index (Tramer, 1969; Longuet-Higgins, 1971); thus the evenness component of diversity can be disregarded for all practical purposes. Throughout much of this review, I concern myself with the number of reptilian species rather than their relative importance because adequate data on the latter are virtually non-existent in reptiles (see, however, Klimstra, 1958; King, 1964; Degenhardt, 1966; Turner, 1961, and this volume. Species diversities and niche breadths can be calculated with Simpson's (1949) index of diversity, $1/\Sigma p_i^2$, where p_i represents the proportional abundance of the ith species or resource. Thus computed, lizard species diversity is strongly positively correlated ($r = 0{\cdot}84$, $P < 0{\cdot}001$) with the number of lizard species on my 28 desert study areas (see Pianka, 1973, 1975 for data and discussion).

B. Within-Habitat Versus Between-Habitat Diversity

Two areas of equal size can support differing numbers of species if one area is spatially more heterogeneous than the other. Such a difference in habitat diversity can arise in two ways. First, one area may simply be more heterogeneous than another by virtue of its topography or some other factor. Second, topographically comparable areas can still differ in the number of effective habitats within them if the organisms on one area have more specific habitat requirements than those on another area (see also section II.B.3). Although the diversity of species *within* any given habitat could be similar on such areas, those with a greater number of effective habitats support more species, provided a large enough area is sampled. In such a circumstance, turnover in species composition from region to region within an area is greater in those with more effective habitats. MacArthur (1965) termed this "between-habitat" diversity to distinguish it from the diversity of species found together within any given habitat, which he designated "within-habitat" diversity [Whittaker (1965) simultaneously termed these α diversity and β diversity, respectively]. The total diversity of species occurring in a heterogeneous area includes both the between-habitat and within-habitat components, which are often difficult to separate because habitats grade into one another and because replacement of species in space is inevitable even within fairly homogeneous habitats, since virtually all habitats are somewhat heterogeneous. Thus, species will partition space within habitats as well as between habitats and these two types of diversity actually grade into one another. They can theoretically be separated by use of "point diversities", which consist of the species diversity occurring at a point in space. In practice, such point diversities are extremely difficult to estimate, but should always be lower than any areal estimate.

C. Diversity of Resources, Average Utilization, and Mean Overlap

Resource limited or "competitive" communities can differ in within-habitat diversity in only four different, logically possible ways (MacArthur, 1965, 1972; Pianka, 1974a), which are not mutually exclusive: (a) First, the diversity of resources available in a community determines the variety of opportunities for ecological diversification within it. All else being equal, communities with fewer different resources will support fewer species than those with a greater variety of available resources. (b) Second, the number of species that can coexist within a community decreases as the diversity of utilization of resources by an average species increases. [The former (a) corresponds roughly to "fewer niches" or to "a smaller overall niche space" and the latter (b) to "broader niches".] (c) Third, two communities with similar diversities of available resources (a, above) and average utilization patterns (b, above), can also support different numbers of species if they differ in the average extent to which resources are shared, or the amount of "niche overlap". Thus, all else being equal, a community with greater overlap will support more species than one with less overlap simply because more species use each resource (i.e., the exclusive part of the niche of each species is more restricted and there is "greater niche overlap"). (d) Fourth, communities similar with respect to all the above (a, b, and c) can still differ in species diversity by differing in the extent to which they actually support as many *different* species as possible, or to the degree to which they are truly "saturated" with species (i.e., with what might be called the number of "empty niches"). Under stable conditions, resources seldom go unused for very long; however, species present in a community generally expand their activities until all available resources are used, so that many communities presumably are effectively saturated with individuals (see Pianka, 1974a).

MacArthur (1972) summarized all but the fourth of the above factors in a very simple (indeed, tautological) equation for the species diversity of a community

$$D_S = \frac{D_R}{D_U}(1 + C\,\bar{\alpha})$$

where D_S is the diversity of species, D_R is the overall diversity of resources exploited by all species (diversity of available resources), D_U is the diversity of utilization by an average species (mean niche breadth), C measures the number of neighbors in niche space (a function that increases more or less geometrically with the number of niche dimensions—see next section), and $\bar{\alpha}$ is the average amount of niche overlap (MacArthur termed this the mean competition coefficient). Regardless of the validity of MacArthur's equation, it serves a useful purpose in focusing attention on the importance

of niche breadth and overlap in considerations of diversity. These various components of diversity are considered further below, in the context of some estimates from natural "communities" (assemblages) of lizards (Pianka, 1973, 1974b, 1975).

D. Temporal, Spatial, Trophic, and Taxonomic Components

A fruitful approach to understanding patterns of species diversity is through analysis of the ways in which the component species actually subdivide the environment or partition available resources among themselves. The actual number of different ways in which the ecologies of component species differ, or the number of *niche dimensions* (Levins, 1968; MacArthur, 1972; Pianka, 1974a, 1974b), is therefore an important determinant of species diversity. Effectively, a greater number of niche dimensions results in a larger overall niche space, which has the potential to support a more diverse community, all else being equal. Niche relationships are thus of considerable interest in any analysis of species diversity (see also Schoener, this volume). Indeed, studies of diversity are almost always accompanied by investigations of the resource utilization patterns of component species. Questions such as the following arise. How do species avoid or reduce interspecific competition? In what ways do niches actually differ? How much niche overlap can be tolerated? What is the contribution to species diversity of niche separation along various niche dimensions? Three very basic ways in which animals (including reptiles) avoid or reduce competition are (1) by being active at different times, (2) by differential use of space, such as microhabitat differences, and/or (3) by eating different foods. Reptilian niches differ in all three ways, and niche separation along each niche dimension contributes to species diversity. It is often convenient to partition within-habitat diversity into temporal, spatial, and trophic components (see Schoener, this volume).

Still another way in which diversity has occasionally been examined is in terms of its taxonomic components (Pielou, 1967; Lloyd, *et al.*, 1968; Heyer and Berven, 1973; Pianka, 1973). For example, diversity can be partitioned by taxonomic hierarchies to ascertain what fraction of total species diversity is attributable to various taxonomic levels, such as congeneric species living together in the same habitat.

III. Numbers of Reptilian Species

A. General

Table I gives an approximate breakdown of the numbers of families, genera, and species, both extant and extinct, in 17 orders of reptiles. Among extant

reptiles, only the lizards and snakes, and, to a lesser extent, the turtles, are represented by enough living species to generate ecologically interesting patterns of species diversity, though the low diversity of some groups may be of some interest in itself. Table II list the approximate numbers of living species in various families of lizards, snakes, and turtles. However, diversity has been studied most thoroughly in lizards; as a result, lizard diversity is emphasized below.

B. Temporal Patterns

1. *Geological Past and the Age of Reptiles*

Relatively little can be said about the diversity of fossil reptiles, of course, except that they certainly flourished during the Mesozoic era (indeed, the

Table I

Estimates of the number of families, genera, and species, both living and extinct, in various reptilian orders[a]

Order	Families Extinct	Families Living	Genera Extinct	Genera Living	Species Living
Cotylosauria	8	0	57	0	0
Mesosauria	1	0	1	0	0
Testudines	13	8	147	56	219
Eosuchia	2	0	14	0	0
Squamata					
Sauria	12	19	104	360	~2950
Amphisbaenia	2	4	3	16	130
Serpentes	2	9	37	416	~2005
Rhynchocephalia	4	1	26	1	1
Thecodontia	9	0	45	0	0
Crocodilia	14	2	124	8	21
Pterosauria	5	0	24	0	0
Saurischia	28	0	244	0	0
Ornithischia	13	0	111	0	0
Araeoscelidia	5	0	16	0	0
Sauropterygia	11	0	71	0	0
Placodontia	4	0	9	0	0
Ichthyosauria	5	0	20	0	0
Pelycosauria	8	0	45	0	0
Therapsida	55	0	298	0	0
Totals	201	43	1396	857	~5300

[a]After Porter (1972) modified.

numbers of species in various extinct groups cannot even be estimated with any degree of reliability). Reptiles appear to have been much more diverse at higher taxonomic levels during the geological past than they are now (Table I); thus, only 39 of 238 recognized families are still represented by living members. (These numbers could be biased by different criteria for classification in extant and extinct groups.) During the Mesozoic, reptiles radiated into a wide variety of ecological niches: for example, there were over 40 families of dinosaurs alone, including many large herbivorous and

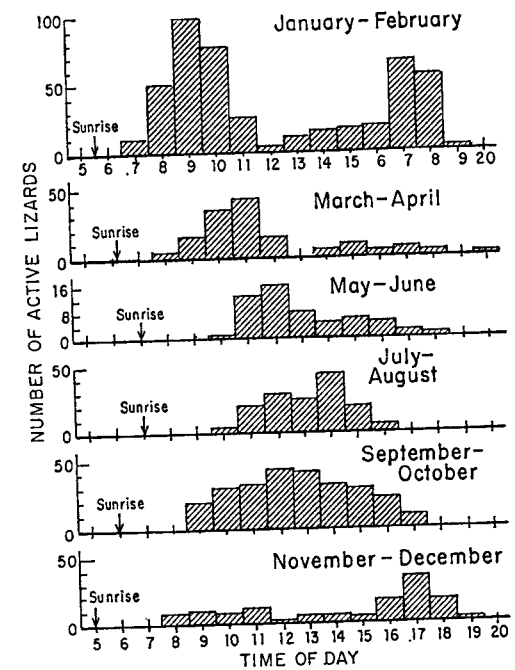

Fig. 1. Frequency distributions of times of activity of the lacertid, *Eremias lineo-ocellata*, in the Kalahari desert of southern Africa at bimonthly intervals. Average time of sunrise is shown with arrows. Time of activity changes seasonally, with a unimodal midday activity period during colder winter months and bimodal daily activity patterns during the warmer summer months. Converting to time since sunrise partially corrects for such seasonal shifts.

carnivorous genera, such as *Brontosaurus*, *Diplodocus*, *Stegosaurus*, *Allosaurus*, and *Tyrannosaurus*. Flying pterosaurs and gigantic aquatic mosasaurs, plesiosaurs, nothosaurs, and ichthyosaurs filled niches that presumably either no longer exist or are occupied by non-reptilian taxa today. Speculation over the causes of the extinctions of these giant reptiles abounds (Colbert *et al.*, 1946; Augusta, 1961; Colbert, 1947, 1961; Hotton, 1963;

Russell, 1965, 1967; Swinton, 1964, 1965; Axelrod and Bailey, 1968; Bakker, 1971, 1972; Spotila *et al.*, 1973; and others).

2. *Within-Habitat Differences in Time of Activity*

Times of activity of many reptiles are relatively consistent from day to day and change more or less regularly with the seasons (Fig. 1). Thus many species of diurnal lizards have a bimodal daily pattern of activity (early-late) during the warm summer months, but a single midday period of activity

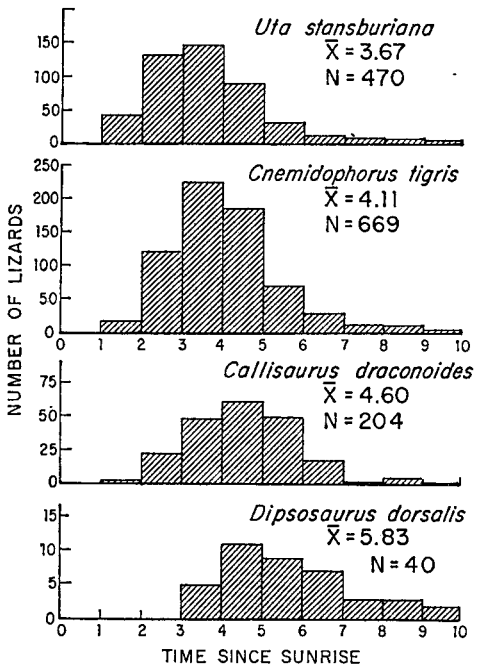

FIG. 2. Histograms of activity times of four species of lizards in the Sonoran desert, during the period when ambient temperatures are warming. Times of activity are expressed as time since sunrise to reduce variation due to seasonal shifts in activity times like those shown in Fig. 1. Differences between the mean times of activity of these four species are all statistically significant (t-tests, P's $< 0{\cdot}05$).

at cooler times of the year (Tinkle, 1967; Mayhew, 1968). Such seasonal shifts in time of activity presumably facilitate thermoregulation by allowing the animals to encounter a similar thermal environment at different times of year. Standardizing times of activity to "time since sunrise" (diurnal species) or "time since sunset" (nocturnal species) helps to correct for seasonal shifts in activity times and makes possible comparisons among species and between

communities (Pianka, 1973). Sympatric species often differ in their activity patterns, with some emerging later after others have become less active (Pianka, 1969b, 1973). Such a sequential replacement of species during the day is illustrated in Fig. 2 for four species of North American lizards in the Sonoran desert. Provided that prey species are rapidly renewed or that prey have temporal patterns of activity similar to those of lizards (which seems highly likely), such temporal separation of activity (either daily or seasonally) can result in exposure to different species of prey and permit coexistence of otherwise potentially incompatible competitors. Variation in times of activity within a resource-limited community could thus enhance community diversity by reducing competition among species.

TABLE II

Approximate numbers of species in various families of lizards and snakes

Lizard family	Number of species	Snake family	Number of species
Scincidae	over 700	*Colubridae*	over 1400
Gekkonidae	about 600	*Viperidae*	about 150
Iguanidae	about 600	*Elapidae*	about 180
Agamidae	about 300	*Boidae*	about 58
Teiidae	about 200	*Hydrophidae*	about 60
Lacertidae	164	*Leptotyphlopidae*	about 50
Chamaeleontidae	109	*Uropeltidae*	about 44
Anguidae	88		
Cordylidae	47		
Varanidae	30		
Pygopodidae	25		
Total	about 3000	Total	about 2000

Among the more salient differences in time of activity of sympatric reptiles is the natural dichotomy of nocturnal versus diurnal activity. Many snakes and some lizards, especially gekkonids, are primarily or entirely nocturnal, whereas other snakes and most lizards and turtles are active strictly during daylight hours. Daytime activities of nocturnal reptiles could also be significant in that such species often may actively seek out warmer microhabitats than they encounter at night, thus hastening digestion. In any case, the thermal relations of nocturnal reptiles differ markedly from those of

diurnal ones. Only the latter can truly be said to thermoregulate while active (Parker and Pianka, 1974; Pianka and Pianka, 1976; Huey and Slatkin,

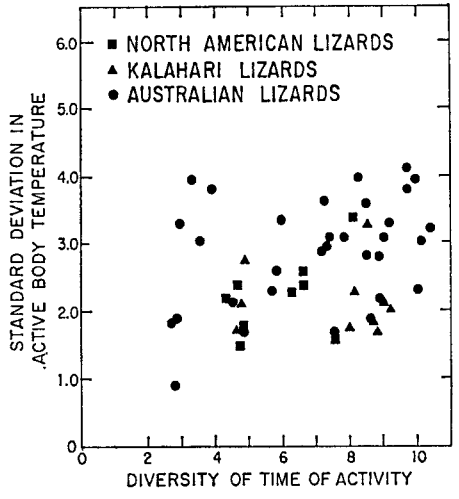

FIG. 3. Standard deviation of body temperatures of active lizards plotted against the diversity of times of activity, or the "time niche breadth" of Pianka (1973). Although scatter is great, species that are active over a broader time period tend to have more variable body temperatures than those which are active over a shorter period of time.

TABLE III

Means and 95% confidence limits (in parentheses) of times of activity expressed as time since sunrise, during the period when temperatures are rising, and active body temperatures of four species of lizards in the Sonoran desert*

Species	Time of activity	Body temperature
Uta stansburiana	3·67 (3·55–3·79)	35·3 (35·1–35·5)
Cnemidophorus tigris	4·11 (4·01–4·21)	39·5 (39·4–39·6)
Callisaurus draconoides	4·60 (4·42–4·78)	39·1 (38·8–39·4)
Dipsosaurus dorsalis	5·83 (5·29–6·37)	40·0 (39·4–40·6)

*In hundredths of an hour

1976). Thus body temperatures of nocturnal reptiles are typically low and strongly correlated with air and substrate temperatures, whereas body temperatures of diurnal reptiles are generally higher and less dependent

upon environmental temperatures. Diurnal species regulate their body temperatures through basking, thermal exchange with substrates, orientation to incident solar irradiation, and movements in and out of shade, as well as by the time at which they are active (Huey and Slatkin, 1976). Body temperatures of active diurnal reptiles often reflect their time of activity reasonably well (Pianka, 1969b and Table III), although microhabitats also affect body temperatures. Species emerging earlier in the day tend to have lower active

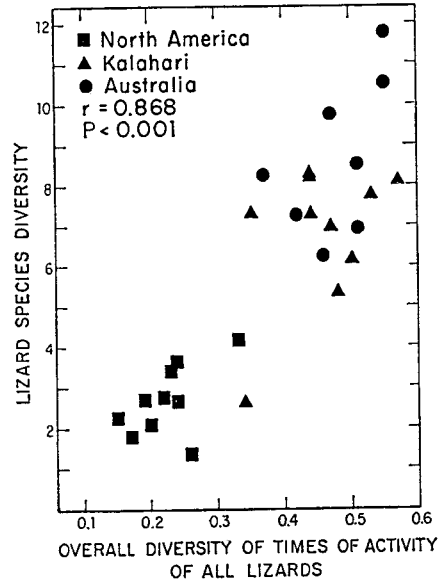

FIG. 4. Lizard species diversity plotted against the overall diversity of times of activity of all the lizards in 28 different saurofaunas. None of the correlations within continental desert-lizard systems are statistically significant, but when all 28 study sites are grouped, the correlation is highly significant.

body temperatures than those that emerge later; moreover, species active over longer periods of time often have more variable body temperatures than those with shorter periods of activity (Fig. 3), although there is considerable scatter. Thus, body temperatures of active reptiles often reflect their temporal patterns of activity and vice versa.

Lizard species diversity is strongly correlated with the overall diversity of times of activity of all the lizards within various desert saurofaunas (Pianka, 1975), which represents D_R in MacArthur's equation for the temporal dimension of the niche (Fig. 4).

C. Spatial Patterns

1. *Latitudinal Gradients*

Among the more conspicuous spatial patterns of species diversity are latitudinal gradients. The numbers of species of reptiles, and indeed those

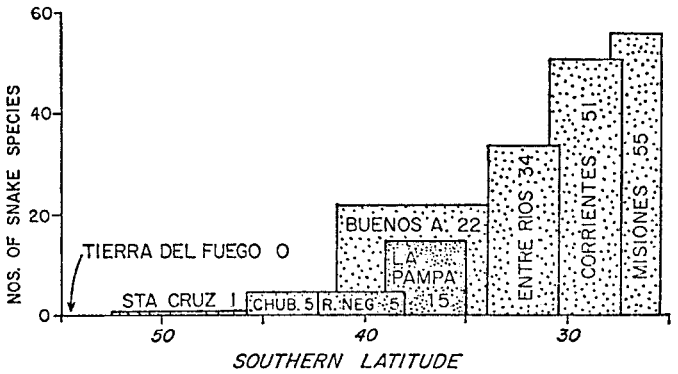

Fig. 5. Number of snake species from various provinces of Argentina at different latitudes, to show a latitudinal diversity gradient. From Fischer (1960), based on old data of Serie (1936).

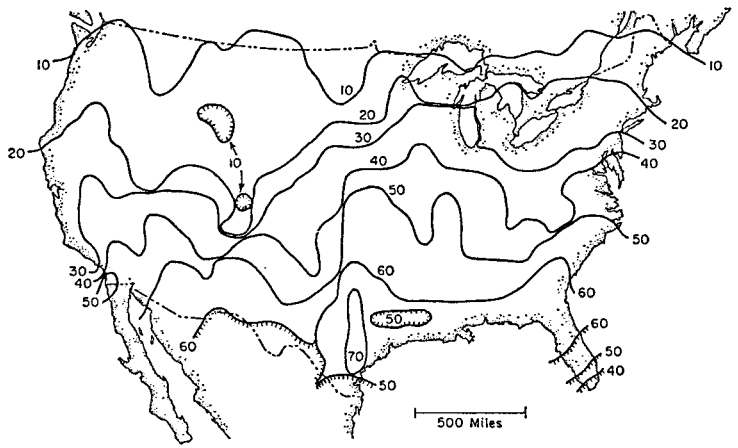

Fig. 6. Isopleths of equal number of species of reptiles in the continental United States. Note latitudinal increase in species density from north to south. From Kiester (1971).

of the vast majority of plant and animal taxa, increase more or less regularly from the temperate zones to the equator (Fischer, 1960; Terentev, 1963; Simpson, 1964; MacArthur, 1965; Cook, 1969; Kiester, 1971; Loman,

1976). Two such gradients in numbers of reptile species are shown in Figs. 5 and 6. Speculation abounds on possible reasons for these ubiquitous latitudinal patterns (for reviews see Pianka, 1966a; Whittaker, 1965, 1972; Uetz, 1974).

In a detailed ecological study of a latitudinal diversity gradient in desert lizards of western North America (Pianka, 1967), I concluded that increased spatial heterogeneity of the vegetation was a major factor allowing coexistence of more species in the south. Using path coefficients, Arnold (1972)

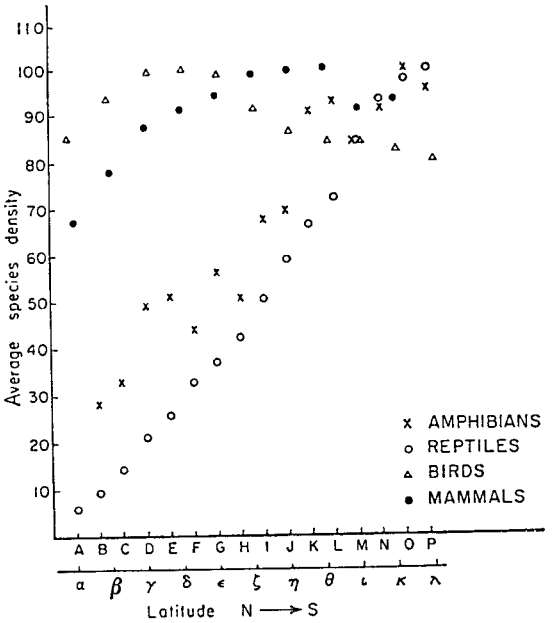

Fig. 7. Average species densities of amphibians, reptiles, birds, and mammals plotted against latitude in the continental United States. From Kiester (1971).

examined differences in snake species density and demonstrated that much of the variance in the number of sympatric snake species is related to species densities of their prey (see also "Trophic Relationships" and "Dependence on Other Taxa" below). Moreover, this effect was *not* due to a common correlation with latitude. Kiester (1971) analyzed species density of reptiles in North America north of Mexico and related the observed "astonishingly linear" latitudinal gradient (Fig. 7) both to topography and to complementarity with mammalian species density (see also "Interactions with Other Taxa" and "Reciprocal Relations" below).

2. *Species-Area Relationships*

With increases in the extent of an area sampled, the number of different species observed within an area typically first increases very rapidly and then increasingly more gradually until an apparent upper limit is reached, which reflects the species density and diversity of the overall area (Fig. 8). The notion of a "minimal sampling area" emerged from such species-area effects.

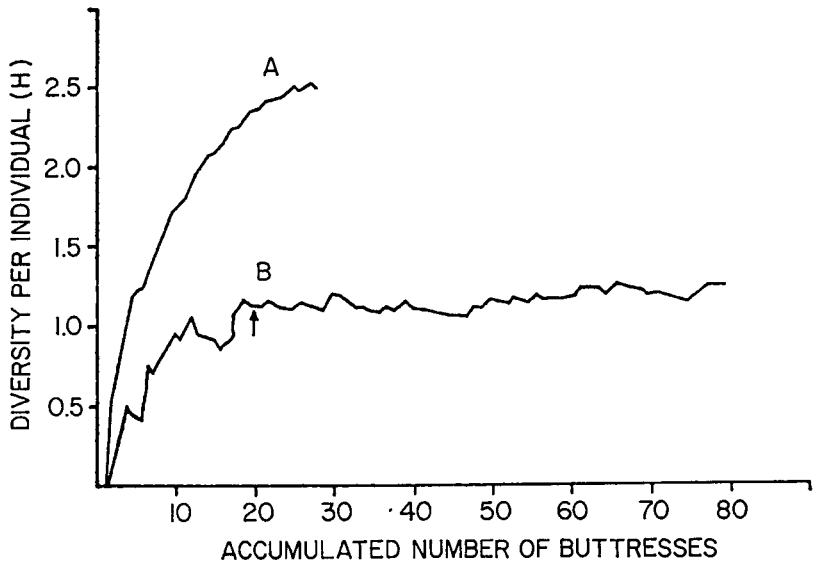

FIG. 8. Successive values of average diversity of lizards collected in tree buttresses from a moist tropical forest (A) and a dry evergreen forest (B). From Heyer and Berven (1973).

Both the slopes and the upper asymptotes of species-area curves increase with diversity and are used in various indices of diversity.

A related observation is that small or topographically monotonous islands usually support fewer species than larger or topographically variable islands. Indeed, on a log-log plot (Fig. 9), the logarithm of species density increases approximately linearly with the log of island area. An equilibrium theory of island biogeography (MacArthur and Wilson, 1967) interprets such patterns as arising from a balance between rates of immigration and extinction. Immigration rate is considered to be little affected by island size or complexity but rather it decreases with distance from source areas, whereas extinction rate is unaffected by distance *per se*, but increases with both decreasing island size and increasing island homogeneity.

3. *Habitat Specificity and Between-Habitat Diversity*

Many Australian desert lizards have highly specific habitat requirements (Pianka, 1969a, 1972). At least eight species are found only on sandridges, another ten species are virtually restricted to sandplains with spinifex grass (*Triodia*), and still another 16 species appear to occur only in areas with a

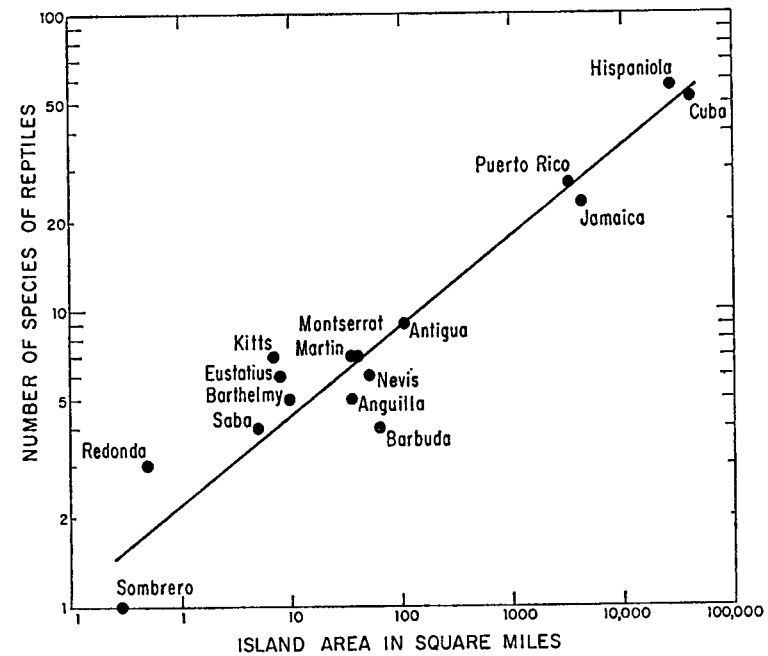

FIG. 9. Log-log plot of the number of species of reptiles (mostly lizards, but includes a few snakes) against island size for 16 islands of different sizes in the Lesser and the Greater Antilles (West Indies). These data, which are somewhat dated, are from Dunn (1934).

vegetation of shrubs and/or acacias. In the Australian sandy deserts, long stabilized sandridges typically alternate with interdunal areas composed of sandplain-*Triodia* habitat and/or shrub-*Acacia* habitats, so that many habitat-restricted species occur in close proximity. The exceedingly difficult problem of defining a "habitat" arises. Should sandridges be considered a different habitat than sandplains? They grade into each other and some species with more catholic habitat requirements occur on both. Answers to such questions are entirely arbitrary and justified only by ecological utility. Habitats should be defined by the organisms rather than by ecologists. Indeed I consider sandridges and sandplains distinct habitats in Australia

where several lizards have specialized to one or other* but not in the Kalahari desert of southern Africa where only a single lizard species is restricted to sandridges (Pianka, 1971; Huey and Pianka, 1974; Huey *et al.*, 1974). Thus, turnover in lizard species composition in horizontal space is more pronounced in Australia than in the Kalahari and the between-habitat component of diversity is greater in the former desert (see also Pianka, 1973).

4. *Within-Habitat Partitioning of Space*

Considerable variation exists among reptiles in the ways in which they use space. Some are entirely subterranean, both burrowing and fossorial, while others are aquatic (both fresh water and marine), terrestrial, and/or arboreal. Intermediates, including semi-aquatic, semi-arboreal, and semi-fossorial species also occur. Even among such natural groups, microhabitat differences may be pronounced. For example, some terrestrial lizards such as *Callisaurus draconoides* frequent the open spaces between plants, whereas others, such as *Uta stansburiana* and *Urosaurus graciosus*, spend most of their period of activity underneath or within plants of various sorts, sometimes of a particular life form (Pianka and Parker, 1972; Pianka, 1966b, 1969b, 1973). Arboreal *Anolis* partition vegetation among species through comparable differences in the perches they use, or their "structural niches" (Rand, 1964; Williams, 1969; Schoener, 1968, 1970; Andrews, 1971). Other climbing lizards are virtually restricted to rocks (saxicolous species such as *Sauromalus*). Differential use of space within a habitat presumably often leads to exploitation of different prey and reduces interspecific competition; hence a spatially heterogeneous habitat typically supports a great variety of space users and generally contains a diverse community.

Numerous anatomical correlates of the ways in which reptiles use space are apparent. For example, aquatic species, such as sea snakes and crocodilians, often have laterally compressed, dorsoventrally expanded bodies and/or tails, and non-ophidians usually possess webbed feet. Fossorial species have very reduced appendages or lack them. Arboreal species are typically long and slender, often with long and/or prehensile tails, and, if they are legged, possess claws or toe lamellae that are well suited for climbing. Among lizards, hindleg lengths, relative to their snout-vent lengths (SVL) are often reasonably good indicators of where an animal spends its time. Species that frequent open spaces typically have longer hindlegs (relative to SVL) than those that stay closer to cover (Pianka, 1969b; Pianka and Parker, 1972; Pianka and Pianka, 1976). There is probably a direct causal

* An avian ecologist probably would not consider Australian sandridges and sandplains distinct habitats because very few birds are restricted to either (Pianka, 1972).

relationship to these correlations since such longer-legged animals are presumably faster runners and are less dependent upon cover to escape from predators. Counterbalancing this, however, shorter leg length doubtlessly facilitates movements within dense vegetation (Pianka, 1969b).

Morphological correlates of reptilian niches, particularly relative hindleg length and head length (next section), should allow powerful analyses of species diversity and niche relations in terms of these anatomical correlates.

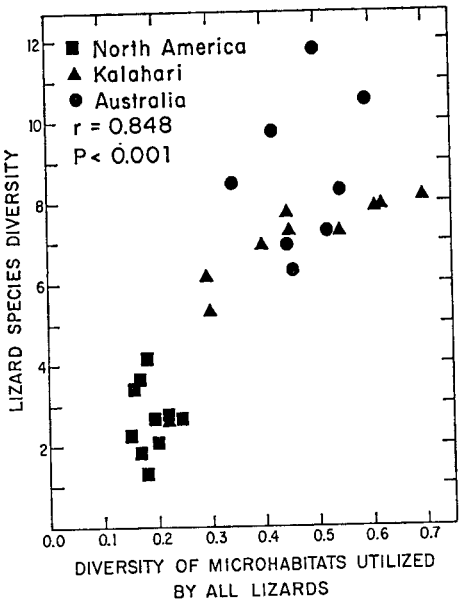

FIG. 10. Lizard species diversity plotted against the diversity of microhabitats actually exploited by all the lizards occurring together on 28 different desert study sites. The correlation for all 28 areas is highly significant statistically, but only one of the three correlations within continents is significant (Kalahari desert: $r = 0{\cdot}847$, $P < 0{\cdot}01$).

Indeed, in an attempt to demonstrate evolutionary convergence between the independently evolved chaparral habitats in central Chile and those of southern California, Sage (1973) used anatomy to map ecology. I have constructed a comparable but different "morphological niche space" for North American desert lizards and compared it with the same space as used by Australian species; this comparison demonstrates quantitatively where Australian lizards exploit new niches and where they partition more finely those that are used by North American species. Extension of this analysis to the Kalahari should be informative (Pianka, in preparation). Similar analyses of anatomical correlates of niche relationships have been published for rotifers (Hutchinson, 1968) and tyrannid flycatchers (Keast, 1972).

In Figure 10, estimates of lizard species diversities on my 28 desert study areas are plotted against the overall diversity of microhabitats actually exploited by the entire saurofauna of each site (see also Pianka, 1973, 1975). Only one of the correlations within the three continental desert-lizard systems is statistically significant (Kalahari desert, $r = 0{\cdot}847$, $P < 0{\cdot}01$). The Pearson product moment correlation coefficient for all 28 study areas is also highly significant ($r = 0{\cdot}848$, $P < 0{\cdot}001$). The latter result is probably *not* circular, as it might at first appear, because the correlation fails within two of the three desert systems.

D. Trophic Relationships

Differences in foods eaten by various sympatric reptiles can be important in considerations of diversity because such trophic diversity reduces interspecific competition for food and makes possible maintenance of a diversity of reptiles.

Reptiles consume a wide variety of foods, including leaves, flowers, However, because actual foraging techniques used by lizards (and snakes) fruits, eggs, insects and other arthropods, snails and other molluscs, as well as various vertebrates (fish, amphibians, other reptiles, birds and mammals). Some species have highly specific diets. Most turtles prey upon plants, arthropods, molluscs, and/or fish. Lizards tend to be fairly opportunistic feeders, generally eating a wide variety of arthropods, though a few are herbivorous and some prey almost exclusively upon vertebrates, especially other lizards. Snakes are generally carnivorous, but they prey upon almost every sort of animal food; moreover, many snakes are often somewhat restricted in their diets, with, for example, lizard-eaters, mammal-eaters, and those that feed on invertebrates. Grouping snakes into various such feeding "guilds," Arnold (1971) found that much of the variance in snake species densities was related to prey species densities (Fig. 11). His analysis demonstrated that both prey species densities and predator (snake) species densities were inversely correlated with latitude, but that, given knowledge of prey species density, latitude itself contributed very little to reducing residual variance in snake species density. Figure 12 plots lizard species diversity against the overall diversity of foods eaten by entire saurofaunas. Interestingly enough, in contrast to Arnold's result for snakes, little correlation is apparent among these saurofaunas (although lizard species diversity is not correlated with food diversity, the number of species of lizards is correlated with the diversity of foods eaten within North America—see below). Apparently niche separation along the trophic dimension is less important in lizards, which have relatively broad food niches, than in snakes, many of which possess narrow food niches (are stenophagous).

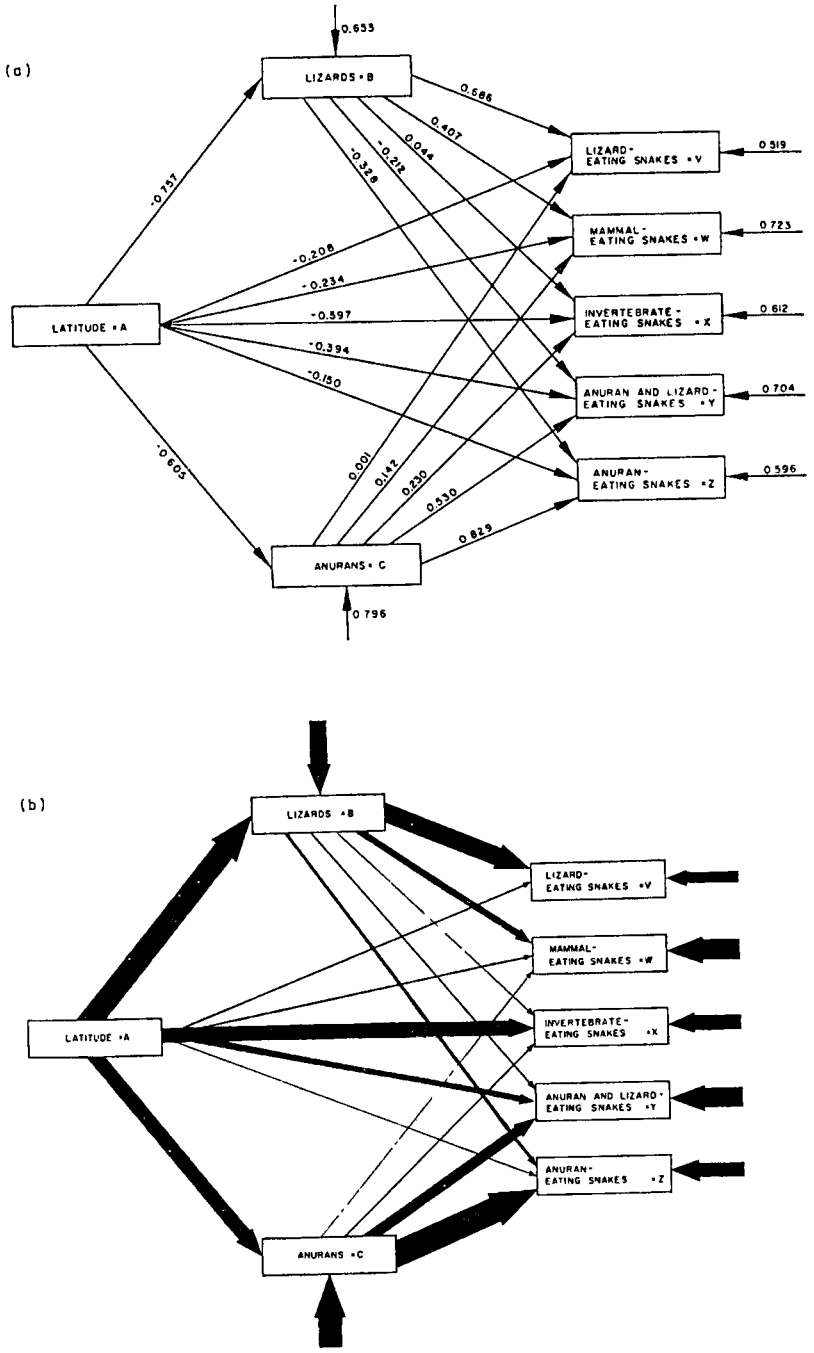

Fig. 11. (a, above) Path coefficients between species densities of snakes and their prey and latitude. (b, below) Coefficients of determination along various paths represented by widths of arrows. From Arnold (1971).

The majority of lizards are insectivorous, rather opportunistic feeders, taking with little apparent preference a wide range of types and sizes of arthropods encountered (Pianka, 1973; Parker and Pianka, 1975); however, smaller individuals (or species) tend to eat smaller prey than larger species or individuals (Fig. 13). Mean prey size changes with growth during ontogeny

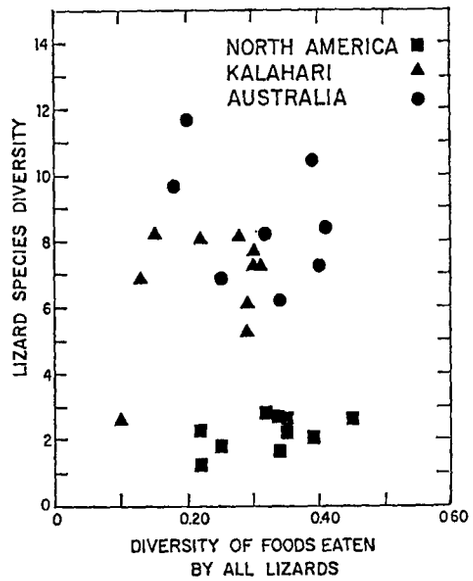

FIG. 12. Lizard species diversity plotted against the overall diversity of foods consumed by entire saurofaunas. None of the correlations, either within or among continental desert-lizard systems, are statistically significant.

as well. Thus, just as relative length of a lizard's hindleg reflects its microhabitat usage (above), head proportions and jaw length are often reasonably good indicators of the foods a lizard consumes. Correlations between the size of an animal's trophic apparatus and the size of its prey are widespread, both among lizards and numerous other animals, such as insects, birds, and mammals (Schoener, 1967, 1968; Pianka, 1969b; Pianka and Pianka, 1976). Lizard dentition may also reflect diet in useful ways (Hotton, 1955). Hence, as indicated above, such anatomical correlates of saurian ecology can be used very effectively in analyses of resource partitioning and species diversity.

Rather few species of lizards have evolved pronounced dietary restrictions. Among these are the ant specialists *Moloch* and *Phrynosoma* (Pianka and Pianka, 1970; Pianka and Parker, 1975), termite specialists such as *Typhlosaurus* and *Rhynchoedura* (Huey and Pianka, 1974; Huey, Pianka, Egan, and

Coons, 1974; Pianka and Pianka, 1976), various herbivorous species including *Dipsosaurus*, *Sauromalus*, and *Uromastyx*, and secondary carnivores like *Crotaphytus*, *Heloderma*, *Lialis*, and some *Varanus*, all of which prey primarily

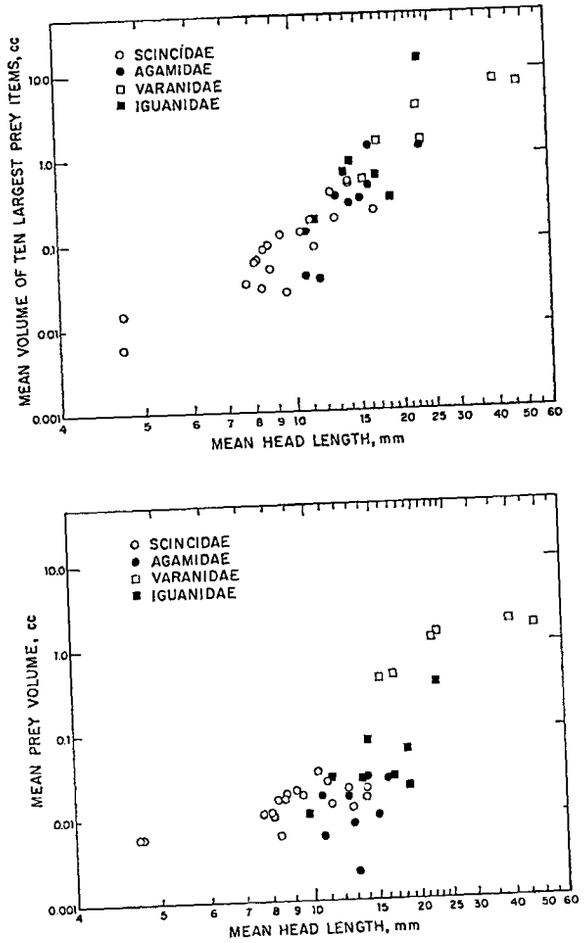

FIG. 13. Log-log plots of mean prey volume and the mean volume of the ten largest prey items against mean head length for 40 species of lizards in four families, coded by symbols as indicated in graphs.

upon eggs and/or young of vertebrates and adults of smaller species. Such foods are often either concentrated in space or temporarily abundant, conferring an advantage on food specialization (MacArthur and Pianka, 1966; Pianka, 1974a).

Though most lizards are fairly opportunistic feeders, differences in foraging techniques (below), microhabitat usage, and time of activity may usually result in exposure to different spectra of prey. I recognize two extreme types of foragers (Pianka, 1966a; Schoener, 1971). In the *widely foraging* "strategy," an animal actively searches out its prey, whereas in the *sit and wait* "strategy" the consumer simply waits more or less passively until a mobile prey item gets within range and then ambushes the prey. This dichotomy is clearly somewhat artificial in that these two tactics actually represent pure forms of a variety of possible foraging strategies. However, because actual foraging techniques used by lizards (and snakes) are often strongly polarized, the dichotomy has considerable utility. For example, many lacertids and varanids, and most skinks and teiids, are extremely active and forage widely, typically being almost continually on the move. In contrast, agamids, geckos, and iguanids are generally relatively sedentary lizards, foraging primarily by sitting and waiting. Among snakes, racers and cobras are very active, widely foraging, predators, whereas most vipers and boids typically forage by sitting and waiting and ambushing their prey. Such differences in mode of foraging doubtlessly influence the exact prey types encountered and hence the composition of an animal's diet. The effectiveness of the sit and wait tactic depends upon either a high prey density or mobility, and/or a low energy demand by the predator. The success of the widely foraging tactic also requires prey that are sufficiently dense to satisfy the predator's energy requirements, but in addition the prey's distribution in space and the predator's searching abilities also assume substantial importance. Among lizards, sit and wait foragers typically tend to capture relatively active prey (as might be expected), whereas widely foraging predators often consume somewhat more sedentary prey types, such as termites, which are relatively concentrated in space. Moreover, diets of sit-and-wait foragers tend to be somewhat broader than those of sympatric widely-foraging species.

E. Niche Breadth

Actual diversities of use of the temporal, spatial, and trophic dimensions of the niche (niche breadths) vary considerably both among lizard species within saurofaunas and between continental desert-lizard systems (Pianka, 1973, 1975). Correlation coefficients among niche breadths along various dimensions are generally not statistically significant, except for a weak positive (but significant) correlation between the diversity of microhabitats used by various species and their diversity of time of activity ($r = 0{\cdot}389$, $P < 0{\cdot}001$). Table IV summarizes the average diversity of use of foods, microhabitats, and times of activity by all the species within each of the

three continental systems. Diversity of use of the trophic dimension is low in the Kalahari, whereas use of the spatial (microhabitat) niche dimension is relatively restricted in North America. Average use of the three dimensions is less variable in Australia, where an average lizard species exploits all three niche dimensions rather more equally. Confidence limits on means within continental desert-lizard systems, however, overlap broadly (Table IV),

Table IV

Means and 95% confidence limits (in parentheses) on niche breadths and niche shapes in the three desert-lizard systems

Niche dimension	North America	Kalahari	Australia
Trophic	0·232 (0·168–0·296)	0·198 (0·196–0·312)	0·214 (0·202–0·278)
Spatial	0·146 (0·108–0·184)	0·228 (0·186–0·270)	0·201 (0·177–0·225)
Temporal	0·241 (0·167–0·295)	0·254 (0·148–0·248)	0·240 (0·180–0·248)
Overall summation	0·206 (0·178–0·234)	0·237 (0·205–0·269)	0·218 (0·196–0·240)
Overall multiplicative	0·077 (0·045–0·109)	0·138 (0·078–0·198)	0·112 (0·078–0·146)
Shape	2·57 (2·410–2·730)	2·72 (2·610–2·830)	2·59 (2·510–2·670)

and no statistically significant variation in niche breadth is evident among continents. Niche breadth does vary inversely with lizard species density within continents, but the correlations are not statistically significant. When all 28 areas are considered one reaches the surprising conclusion that niche breadths do *not* decrease with increased diversity, provided niche dimensionality remains constant. Indeed, if anything, niches tend to be slightly broader in more diverse saurofaunas (Pianka, 1973, 1975). Hence diversity in these lizard communities is not enhanced by reduced niche breadths in the more diverse communities.

F. Niche Overlap Patterns

Elsewhere (Pianka, 1973, 1974b, 1975), I have examined patterns of niche overlap among desert lizards in some detail. These analyses demonstrate that overlap generally *decreases* with increasing lizard species diversity (Fig. 14). Possibly species densities or diversities of competitors are themselves determinants of tolerable niche overlap. A greater number of competing species, or stronger "diffuse competition" (MacArthur, 1972), demands greater average niche separation among coexisting species. High overlap

with fewer competitors might actually be roughly similar to lower overlap with more competitors. The actual intensity of interspecific competition per species, or the total of the interspecific inhibitory effects, could thus be similar in communities of widely divergent species densities. Such adjustments of overlap with species density might result in a relatively constant level of interspecific competitive inhibition among a community's component species. If so, it may not be overlap between average interspecific pairs that

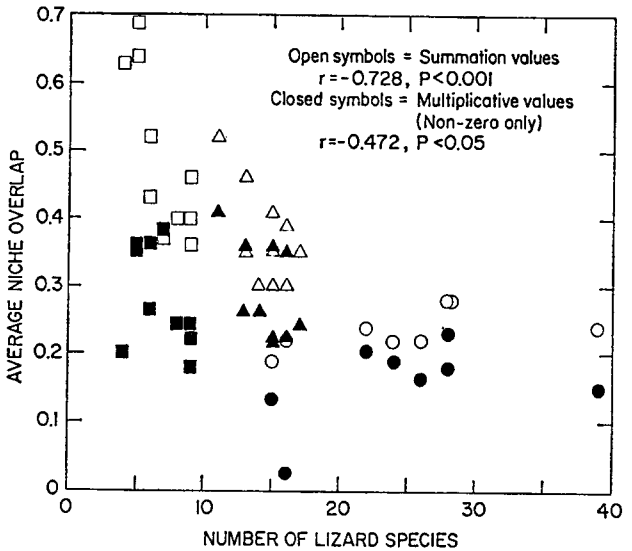

FIG. 14. Average niche overlap plotted against the number of lizard species occurring together on 28 desert study sites on three continents (continental desert-lizard systems are coded by shape as in Figs. 3, 4, 10, and 12). Two measures of overlap are plotted, and both decrease significantly with increasing lizard species density. Other measures of maximal tolerable niche overlap are similarly inversely correlated with lizard species densities (Pianka, 1974b, 1975).

remains constant, but rather the total degree of competitive inhibition tolerated by the individuals that comprise an average species.

Niche overlap therefore does not act to enhance diversity, but rather contributes negatively to it, since overall overlap decreases, rather than increases, with diversity. Indeed, I have argued that the product of the number of neighbors in niche space times the average overlap could actually approximate a constant (Pianka, 1975), so that the term $(1 + C\bar{\alpha})$ in MacArthur's diversity equation may change little with diversity. Above I showed that mean niche breadth does not vary consistently with lizard diversity, so that only one of the four components of the diversity equation is

implicated as a major determinant of the number of species coexisting in these lizard communities; this is the size of the lizard niche space as measured by the diversity of resources actually utilized by lizards, or D_R. Thus the diversity equation might be greatly simplified for desert lizard communities, with species diversity being simply proportional to the diversity of resources utilized by lizards.

IV. Interactions with Other Taxa

A. General

Reptiles interact with other taxa both directly and indirectly and in several important ways. In some cases, such as the snake species density study alluded to above (Arnold, 1972), a direct dependence upon another taxon or taxa is evident. In other situations, reptiles appear to usurp the ecological roles of other taxa so that a complementary relationship (replacement) is indicated. Some examples of both are given below.

B. Dependence Upon Other Taxa

Southern Africa is well known for its diverse termite fauna; in this desert-lizard system, termites comprise over 40% by volume of all the food eaten by all lizards (Pianka, 1973). Moreover, two species of termite-specialized fossorial skinks (*Typhlosaurus*), the diets of which consist of 95% termites by volume, exist in the Kalahari desert, frequently in sympatry (Huey *et al.*, 1974). Clearly, the abundance and diversity of termites probably allowed the evolution of such termite-specialized species (Huey and Pianka, 1974).

In the North American desert-lizard system, lizard species density is significantly correlated with the diversity of foods eaten by all lizards (Pianka, 1975). Lizard diversity in this system could thus be partially dependent on prey diversity, much as is the case in certain snake assemblages (Arnold, 1972). The prevalence of arboreal nocturnal lizards in the Kalahari and Australia, but absence of this lizard guild in the North American deserts is puzzling (Pianka, 1973, 1975), and might be attributable to a reduced availability of nocturnal insects on the branches and trunks of trees and shrubs in the latter system. The presence of the herbivorous genus *Dipsosaurus* in the North American desert system can be similarly attributed to the presence of its major food plant, creosotebush (*Larrea divaricata*) which blooms profusely during certain times of year (Pianka, 1965, 1967).

C. Reciprocal Relations

One reason that the Australian deserts support such high lizard species diversities is that competition with, and perhaps predation pressures from,

snakes, birds, and mammals are probably reduced on that continent. Australian desert lizards have clearly usurped some of the ecological roles occupied by other animal taxa in the Kalahari and North American deserts (Pianka, 1969a, 1973, 1975). Pygopodid and varanid lizards in Australia are rough ecological equivalents of certain snakes and of mammalian carnivores in the other two desert systems. Moreover, the mammalian fauna of the Australian desert is conspicuously impoverished, and the snake fauna less so. Such usurpation of the niches of other taxa clearly has expanded the diversity of resources and of the overall niche space exploited by desert lizards in Australia. These mammal-like and snake-like lizards, however, contribute relatively little to the increased lizard species density in Australia, ranging from about one to four species on various study areas (Pianka, 1969a, 1975). Thus Australia also supports many more "lizard-like" lizard species than the other two continents.

More elusive interactions between taxa also occur. For example, on my North American study areas, lizard biomass varies inversely with the biomass of small mammals (largely seed-eating species such as *Dipodomys*, *Perognathus*, and *Peromyscus*). Presumably a quantum amount of primary productivity can be channelled either into leaves or seeds: if it is diverted to vegetative tissue, the plants support herbivorous insects which in turn feed lizards (hence increased lizard biomass), but if products of photosynthesis are channelled into seeds, the biomass of granivorous mammals is increased.

Perhaps equally cryptic, but nevertheless important, competitive interactions doubtlessly occur between lizards and birds (Pianka and Huey, 1971; Lein, 1972). As total community diversity increases, lizard species density increases faster than bird species density in Australia, whereas the reverse is true in the Kalahari and North American deserts (Pianka, 1971, 1973, 1975). Reasons for these differences are elusive but they suggest that lizards have somehow obtained the "upper hand" in competition for the insect resources of Australian deserts, whereas birds have managed to prevail in the other two continental systems. Interestingly, there are proportionately more species of ground-dwelling insectivorous birds in the Kalahari than there are in Australia, which suggests that competition between lizards and birds could be keener in southern Africa (Pianka, 1971; Pianka and Huey, 1971). Poikilothermic lizards may be able to capitalize on scant and variable amounts of primary production better than birds and this could well contribute to their relative success over homoiothermic birds in deserts (Pianka, 1967, 1975). Variability in annual rainfall, and presumably in primary production and therefore availability of insects, is greater in the Australian deserts than in either the Kalahari or North America, which supports this hypothesis.

Other differences between the lizard faunas of the three continental

desert-lizard systems could also stem from reciprocal interactions with other taxa. The higher incidence of arboreal and nocturnal lizard species in the two southern hemisphere deserts, as compared with North America, could well be related to fundamental differences in the niches occupied by other members of these communities, such as arthropods, snakes, birds, and mammals. Thus the high diversity of nocturnal lizards in the Kalahari and Australia, but reduced diversity of nocturnal species and total absence of arboreal ones in North America could indicate that the ecological roles of nocturnal lizards are filled in North America by other taxa, perhaps by solpugids and/or spiders. Differences in the numbers and/or species densities of insectivorous and carnivorous nocturnal snakes, birds, and mammals might well also play a role (Pianka, 1975).

Kiester (1971) reported a longitudinal complementarity between mammalian species density and reptilian species density in the continental United States, and discussed similar mechanisms for such an inverse relationship.

D. An Analysis and Some Comparisons with Birds and Mammals

The sorts of complementary interactions among taxa described above prompted me to examine species densities of North American reptiles, birds and mammals. I thank A. Ross Kiester and Robert E. Cook for generously providing me with copies of their reptile and birds species density maps, respectively. [Kiester also gave me Simpson's (1964) mammalian species densities.]

Using the continental United States portions of these three data matrices of species densities, based on Simpson's grid size of 150 miles on a side, and climatic data from Visher (1954), I performed a correlation analysis on the following six variables:

1. Reptilian species density
2. Avian species density
3. Mammalian species density
4. Average annual sunfall
5. Average annual precipitation
6. Average annual actual evapotranspiration

All but three of the fifteen possible correlation coefficients among these six variables are statistically significant (Table V). The number of reptilian species is most strongly correlated with average annual sunfall (Fig. 15); notably, reptile species density is inversely correlated with the number of bird species (Fig. 16). This correlation is improved when the effects of sun-

TABLE V

Correlation coefficients among the six variables (above diagonal). Partial correlation coefficients holding sunfall constant are shown below the diagonal. All values are significant at the $P < 0{\cdot}001$ *level except the three marked with asterisks*

	Mammal species density	Bird species density	Reptile species density	Sunfall	Long-term mean annual precipitation	Average annual actual evapotranspiration
Mammal species density	—	0·65	0·11*	0·67	−0·59	−0·47
Bird species density	0·77	—	−0·40	0·13*	−0·64	−0·58
Reptile species density	−0·59	−0·65	—	0·66	0·33	0·45
Sunfall	—	—	—	—	−0·31	−0·14*
Long-term mean annual precipitation	−0·53	−0·64	0·76	—	—	0·88
Average annual evapotranspiration	−0·52	−0·57	0·73	—	0·89	—

fall are held constant by partial correlation (Table V). Reptilian species density is not significantly correlated with mammalian species density. Further, both avian and mammalian species densities are *inversely* correlated with both the long-term mean annual precipitation and the average annual actual evapotranspiration (proportional to productivity—see Rosenzweig, 1968), whereas reptilian species density is *postively* correlated with both long-term mean precipitation and actual evapotranspiration. These

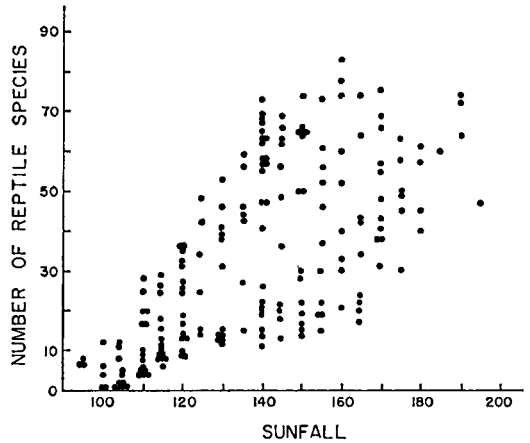

FIG. 15. Number of reptile species plotted against sunfall (in kilocalories per m^2 per year) in 193 quadrates in the continental United States.

correlations suggest that different physical factors operate to regulate diversity of the different taxa; moreover, the inverse correlation between reptilian density and number of bird species lends credence to the above-mentioned hypothesis that ectothermic reptiles might enjoy a degree of competitive superiority over endothermic birds in arid environments.

V. Conclusion

Clearly a great deal more remains to be learned about reptilian species diversity. Even so, studies on this taxon have already contributed substantially both to documenting patterns of diversity and to our understanding of them. Thus, latitudinal gradients in reptilian species densities have been demonstrated (Figs. 5, 6 and 7) and studied (Pianka, 1967). Reptiles have been used in the study of species density-area relationships as well (Figs. 8 and 9) and in examining the taxonomic composition of communities (Lloyd *et al.*, 1968; Heyer and Berven, 1973; Pianka, 1973). Correlations between reptilian species diversity and the diversity of resources they

actually utilize are known (Figs. 10 and 12). The group of reptiles that has been most thoroughly studied from the point of view of determinants of diversity are desert lizards (Pianka, 1967, 1969a, 1971, 1973, 1974b, 1975). Species densities and diversities of these lizards are directly proportional to

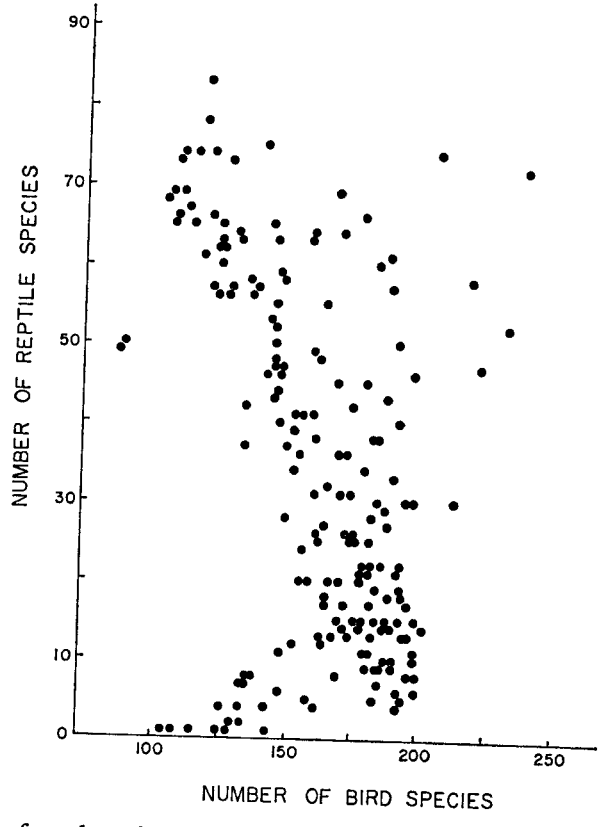

FIG. 16. Plot of number of reptile species versus number of bird species for the continental United States. The weak inverse correlation is statistically significant ($r = -0{\cdot}397$, $P < 0{\cdot}01$).

the diversity of resources exploited by them. Moreover, these studies demonstrate that both the average and the upper limit on niche overlap vary inversely with lizard species density and diversity. This result from a reptilian study may help to guide theoretical ecologists in further developing presently existing inadequate theories of niche overlap and species diversity and to make them more realistic (Pianka, 1974b).

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CHAPTER 2

Competition and the Niche

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I. Introduction

A. Historical Place of Reptiles in Competition Studies

Three approaches have historically been used to study interspecific competition. (1) Population changes in organisms forced to interact to extinction or equilibrium have been monitored under controlled laboratory conditions. (2) Species characteristics have been compared where allopatric and sympatric with similar species and used to estimate competition's role in determining ecological equilibria between species and in shaping adaptive radiation. (3) Most recently, populations have been perturbed in the field to determine competitive effects on individual and population characteristics. Reptiles played little part in the initial development of any of these approaches.

In some ways the absence of reptiles from the two experimental approaches is unsurprising. Laboratory experiments are best performed with small organisms; these often have short generation times and modest spatial requirements. Such characteristics are found in protozoa (Gause, 1934; Vandermeer, 1969; Gill, 1972) and many insects (Park, 1962; Miller, 1964; Ayala, 1971) but not in reptiles. Moving experiments into the field largely solves the space problem but not the other; short generation-time is desirable if ecologists wish to outlive their experiments. Field experiments have been performed, often with considerable success, on protozoa (Gill and Hairston, 1972), barnacles (Connell, 1961), starfish (Menge, 1972; Menge and Menge, 1974), salamanders (Jaeger, 1972), frogs (Inger and Greenberg, 1966; Wilbur, 1972) and small mammals (Sheppe, 1967; Koplin and Hoffmann, 1968; Sheppard, 1971; Grant, 1972a). While difficult to imagine for most snakes, turtles and crocodilians, such experiments may be feasible for many lizards and are now in process, but few results have yet been published.