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Author(s): Eric R. Pianka
Source: *Ecology*, Vol. 52, No. 6 (Nov., 1971), pp. 1024-1029
Published by: Wiley
Stable URL: http://www.jstor.org/stable/1933808
Accessed: 14-12-2016 14:31 UTC

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# LIZARD SPECIES DENSITY IN THE KALAHARI DESERT[1]

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*Abstract.* From 12 to 18 species of desert lizards occur in ecologic sympatry on 10 study areas in the Kalahari desert of southern Africa. The number of species of diurnal lizards is similar to the number in the North American deserts, while the nocturnal component of the saurofauna is more comparable to that occurring in the Australian deserts. The between-habitat component of species density is similar in the American and the Kalahari deserts, but is markedly greater in the Australian desert. A variety of climatic and vegetational statistics are examined for the 10 areas, and correlations with lizard species density are discussed.

In previous work on North American and Australian deserts (Pianka 1966*b*, 1967, 1969*a*, 1969*b*), I demonstrated that the number of species of lizards coexisting within habitats is a complex function of climate, history, and habitat complexity (spatial heterogenity). Here I present and discuss data on a third desert-lizard system, one that is independently derived and evolved but otherwise ecologically similar: the lizards of the Kalahari desert in southern Africa.

## STUDY AREAS AND METHODS

Ten study areas were selected, varying in physiography, topography, climate, and vegetative structure. Areas were deliberately chosen along a rainfall gradient in order to test the effect of productivity on the number of species of lizards [for discussions of the relationship between precipitation and production in desert regions see Pianka (1967, 1970)]. The easternmost four areas (arbitrarily designated G, D, R, and T) have an average annual rainfall of over 200 mm, whereas the six more westerly areas have a long-term mean annual precipitation of less than 200 mm. These latter six study sites (L, K, M, B, A, and X) all lie within the "dune area" of the southern Kalahari as delineated by Leistner (1967). Locations of nine of the ten study areas are given by Pianka and Huey (1971); area M is at latitude 26°22′ S and longitude 19°49′ E.

The dune area of the southern Kalahari, also called the "sandveld" or the "duneveld," supports a vegetation composed largely of various perennial grasses such as *Stipagrostis amabilis* (dune crests), *S. ciliata, S. obtusa, S. uniplumis, Asthenatherum glaucum,* and *Eragrostis lehmanniana.* Common woody shrubs in interdune areas ("streets") are *Rhigozum trichotomum* and *Grewia flava,* both of which are reminiscent of the North American creosote bush *Larrea divaricata.* Various species of small acacias, such as *Acacia mellifera* and *A. hematoxylon,* are widespread. Small trees, especially *Acacia giraffae* and *Boscia albitrunca,* are scattered throughout the region, being common enough in some areas to suggest a savannalike vegetation. Detailed descriptions

of the vegetation, with photographs, may be found in Leistner (1967).

Areas A, X, L, and K are crossed by long, stabilized sandridges, characteristic of the easternmost portion of the southern Kalahari. Rolling, irregular dunes, rather than longitudinal sandridges, cover area M. On area B, sandridges are quite far apart, resulting in extensive interdunal flats, sometimes up to 2–4 km wide. Lizards were collected both on dunes and in interdunal flats. (The resulting collection has been deposited in the Los Angeles County Museum of Natural History.) Area G is a flatland shrub desert, with a vegetation consisting primarily of small chenopodeaceous perennials. Area D, on generally flat terrain, supports a mixture of small to large shrubs, including *Acacia mellifera, Rhigozum trichotomum,* and *Grewia flava;* area R is a nearly "pure" *Rhigozum* site. Area T is a mixed, open, forest-savanna area with a substantial number of trees; for convenience this study area is treated as two distinct areas, the savanna ($T_s$) and the forest ($T_f$). Area $T_s$ is a gently rolling sandplain dominated by perennial grasses withan occasional *Grewia* or *Acacia* bush and a few scattered trees. Area $T_f$, on the other hand, has very few grasses and small shrubs but many trees and large bushes, including *Boscia albitrunca, Acacia giraffae*(?), and *Acacia mellifera.* Lizards were censused on most areas from December 1969 through October 1970.

## METHODS

Methods follow closely those used in earlier studies (Pianka 1965, 1966*b*, 1967, 1969*a*, 1969*b*, 1970), and are only outlined briefly here. At least 32 large quadrats (58 to 232 m²) were staked out on each study area, and all perennial plants within these quadrats were measured and counted. Linear measurements of the approximate height and width of shrubs and trees were made (to the nearest decimeter) and used to estimate plant volumes, using formulae for the volumes of oblate and prolate spheroids ($V = 4/3\pi a^2 b$, and $V = 4/3\pi a b^2$, where *a* and *b* are the major and minor semi-axes, respectively) depending upon the general shape of each shrub and

TABLE 1. Lizard censuses from 10 Kalahari Desert study areas varying in climate, vegetation, and topography. $T_s$ and $T_f$ are subareas of area T

| Lizard species | | L | K | M | B | A | X | G | D | R | $T_s$ | $T_f$ | T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chondrodactylus angulifer | NT | x | x | x | x | x | x | x | x | x | x | x | x |
| Ptenopus garrulus | NT | x | x | x | x | x | x | x | x | x | x | x | x |
| Colopus wahlbergi | NT | x | x | x | x | x | x | x | x | e | x | x | x |
| Pachydactylus rugosus | NA | x | x | x | x | x | x | | x | | | | |
| Pachydactylus capensis | NS | x | e | x | x | x | x | x | x | x | x | x | x |
| Pachydactylus bibroni | NA | x | x | | x | | x | | | | | x | x |
| Pachydactylus punctatus[a] | NT | | | | | x | | | | | | | |
| Lygodactylus capensis | DA | | | | x | | | | | | | | |
| Agama hispida | DS | x | x | x | x | x | x | x | x | x | x | x | x |
| Typhlosaurus lineatus | F | x | x | x | x | x | x | | x | x | x | x | x |
| Typhlosaurus gariepensis | F | x | x | x | x | x | x | | | | | | |
| Mabuya striata sparsa | DA | x | x | x | x | x | x | x | | x | | | |
| Mabuya punctatissimus | DA | | x | | | | | | x | | x | x | x |
| Mabuya occidentalis | DT | x | x | | x | x | x | x | x | x | x | x | x |
| Mabuya longiloba | DT | | | x | x | x | x | x | x | | x | | x |
| Eremias lineo-ocellata | DT | x | x | x | x | x | x | x | x | x | x | x | x |
| Eremias namaquensis | DT | x | x | | x | | x | x | | x | | x | x |
| Eremias lugubris | DT | x | x | x | e | x | x | x | x | x | x | x | x |
| Nucras tessellata | DT | x | | | x | x | | | | | | | |
| Nucras intertexta | DT | | | | | | | | | | x | | x |
| Meroles suborbitalis | DT | x | x | x | x | x | x | x | x | x | | | |
| Ichnotropis squamulosa | DT | | | | | | | | x | | x | | x |
| Chamaeleo dilepis | DA | | | | | | | | e | | x | e | x |
| Totals (x only) | | 16 | 15 | 14 | 17 | 15 | 16 | 13 | 13 | 11 | 14 | 12 | 16 |
| Totals (x + e) | | 16 | 16 | 14 | 18 | 15 | 16 | 13 | 14 | 12 | 14 | 13 | 16 |

NOTE:
x = collected
e = highly expected
NT = nocturnal terrestrial
NA = nocturnal arboreal
NS = nocturnal semiarboreal
DA = diurnal arboreal
DS = diurnal semiarboreal
DT = diurnal terrestrial
F = fossorial
[a] Pachydactylus punctatus is omitted from the totals (see text).

tree. The area covered by a plant was estimated from its average width (diameter) and the formula for the area of a circle ($A = .7854d^2$, where $d$ is the diameter). No allowances were made for differences between plants in foliage density. These values were then used to compute various vegetational statistics for the number of plants per quadrat, percentage coverage, and the volume of plants per quadrat. Shannon's (1949) information theory function, $H = -\Sigma p_i \log_e p_i$, was employed to calculate *plant species* diversities, using as $p_i$'s the proportion of the total number, the total coverage, and the total volume of perennials belonging to the $i$th plant species. The same formula was employed to calculate (i) *plant height diversities*, using the proportion of plants over 2 dm belonging to three height categories (3–6 dm, 7–14 dm, and over 15 dm) as $p_i$'s [frequency distributions of plant heights are given by Pianka and Huey (1971)], and (ii) *plant volume diversities* irrespective of species, using the proportion of plants in the $i$th volume category as $p_i$'s in Shannon's equation. Two different plant volume diversities were calculated; one, designated $H_3$, was based on the three volume categories of Pianka

(1967), the other, designated $H_{19}$, uses 19 volume categories.

Standard symbols are used for the mean ($\overline{X}$), standard deviation (SD), sample size ($N$), and correlation coefficient ($r$) in text and tables.

## RESULTS AND DISCUSSION

Lizard censuses on 10 study areas presented in Table 1 demonstrate that local species densities in the Kalahari (12 to $18^2$ species) are intermediate between those in the western part of the North American desert system [4 to 10 species (Pianka 1967)] and the western Australian deserts [18 to 40 species (Pianka 1969a)]. The range from area to area in the number of species living together (relative to the number of species on the area with the fewest species) is smaller in the Kalahari than in either the North American or the Australian deserts. There appears to be a distinct upper limit of about 16 species of lizards on most of the Kalahari study areas (Table 1), with the exception of area B which supports 18 species.

[2] *Pachydactylus punctatus*, which does not occur in the Kalahari desert proper, is extralimital on area B and is therefore omitted from consideration here.

In Table 2, species counts are classified into several components, namely the numbers of species which are (i) diurnal and terrestrial, (ii) diurnal and arboreal, (iii) nocturnal and terrestrial, (iv) nocturnal and arboreal, and (v) fossorial (burrowing) species. Examination of this table reveals that, while the numbers of diurnal lizard species in the Kalahari are similar to those in North America, the numbers of nocturnal species are intermediate between those in the North American and Australian deserts. Although the range in numbers of fossorial species is the same in both the Kalahari and the Australian deserts (1-2), the mean number of fossorial species per study area is slightly higher in the Kalahari, due to extensive sympatry of two species of *Typhlosaurus* (Huey, Pianka, Egan, and Coons, manuscript). The major source of difference between the Kalahari and Australia is in the numbers of *terrestrial* species (both diurnal and nocturnal), although there are slight differences in the numbers of arboreal species as well. A large part of the two- to threefold variation in lizard species densities between the three continents is a result of the success of nocturnal geckos (and nocturnal skinks in Australia) in the deserts of the southern hemisphere (Table 2), which fact in turn is perhaps best interpreted as historical accident. [It is generally accepted (Darlington 1957, 1965) that the climatic effects of the Pleistocene glaciations were more pronounced in the northern hemisphere.] Present-day climates in portions of the three desert systems are relatively similar, making it unlikely that climatic differences are a cause of existing present-day differences in the number of nocturnal species.

Two extremes in the mode of foraging of carnivorous animals are (i) the "sit-and-wait strategy," in which a predator waits passively until a moving prey item offers itself and then "ambushes" the prey, and (ii) the "widely foraging strategy," in which the predator actively searches out its prey (Pianka 1966b, Schoener 1969). Ordinarily, the success of the first method requires one or more of the following conditions: a fairly high prey density, high prey mobility, low predator energy demand. The success of the second method is also a function of the density and mobility of prey and of the predator's energy requirements, but here the distribution of prey in space and the searching abilities of the predator take on paramount importance. Obviously, the dichotomy of "sit-and-wait" versus "widely foraging" is somewhat artificial in that these two "strategies" are actually endpoints of a continuum of foraging strategies. However, because the actual foraging techniques used by lizards are often rather strongly polarized (Pianka 1966b, 1969b), the dichotomy has substantial practical value and it is employed here in that spirit.

TABLE 2. In the top part of the table, lizard species density is broken down into various components for each continental desert system.[a] At the bottom, the number of study areas with different lizard faunas and the coefficients of community similarity are listed. Both ranges and means are given, the latter in parentheses

|  | NORTH AMERICA | KALAHARI[a] | AUSTRALIA[a] |
|---|---|---|---|
| Diurnal terrestrial | 4-7 (5.4) | 4.5-7.5 (6.3) | 9-21.5 (14.4) |
| Diurnal arboreal | 0-3 (0.9) | 1.5-2.5 (1.9) | 0-5.5 (2.6) |
| Nocturnal terrestrial | 0-2 (1.1) | 3.5 (3.5) | 6-9 (7.6) |
| Nocturnal arboreal | 0 (0.0) | 0.5-2.5 (1.6) | 1-4 (2.6) |
| Fossorial | 0 (0.0) | 1-2 (1.4) | 1-2 (1.1) |
| Number of areas | 9 | 10 | 8 |
| Coefficients of community similarity | .40-.90 (.66) | .43-.88 (.67) | .26-.69 (.49) |

[a]Half lizards are split between terrestrial and arboreal categories.

In the North American desert system, iguanid lizards forage by sitting and waiting (Pianka 1966b), whereas the teid *Cnemidophorus tigris* is widely foraging (Pianka 1970). The Kalahari and the Australian deserts support no iguanids but have been populated by agamid lizards, derived from iguanid ancestors, which forage by sitting and waiting. There are no teids in Australia or Africa; skinks and varanids are the widely foraging lizards in Australia, while skinks and some lacertids forage this way in the Kalahari. Three lacertids, *Eremias lineo-ocellata, Meroles suborbitalis,* and probably *Ichnotropis squamulosa,* usually forage by the sit-and-wait technique. The other four, *Eremias lugubris, E. namaquensis, Nucras tessellata,* and *N. intertexta,* are widely foraging; up to three of these may occur in sympatry (Table 1). Clear-cut ecological differences exist between all these lacertids, including differences in microhabitat, daily and seasonal differences in time of activity, as well as the above-mentioned differences in mode of foraging. One species, *Meroles suborbitalis,* is active all year long and mates in early winter. Snout-vent length frequency distributions of syntopic *Meroles* and *Eremias lineo-ocellata,* which have somewhat similar autecologies, are largely nonoverlapping as the young lizards grow to maturity, suggesting an avoidance of interspecific competition. Broadley (1967) demonstrated a similar temporal separation by size in two species of *Ichnotropis.* A detailed analysis of niche differences among the six species of lacertids is in preparation.

Only one of the diurnal terrestrial species in the North American desert system is widely foraging (*Cnemidophorus tigris*); in the Kalahari, from three to five of the diurnal terrestrial species forage widely, while in the Australian desert, anywhere from four to 14 such species can occur in sympatry on a given study area. The large numbers of widely foraging species of diurnal terrestrial lizards in Australia are due primarily to extensive sympatry of skinks of the

TABLE 3. Climatic statistics from weather stations near each of the study areas

| | L | K | M | B | A | X | G | D | R | T |
|---|---|---|---|---|---|---|---|---|---|---|
| **Annual precipitation (mm)** | | | | | | | | | | |
| $\bar{X}$ | 167 | 190 | 163 | 152 | 145 | 190 | 227 | 217 | 227 | 286 |
| SD | 78 | — | — | 72 | 86 | 97 | 113 | 103 | 113 | 93 |
| % dev. | 43 | — | — | 44 | 50 | 48 | 47 | 49 | 47 | 33 |
| $\bar{X}$ dev. | 71 | — | — | 67 | 73 | 90 | 107 | 106 | 107 | 95 |
| N | 29 | — | 16 | 37 | 38 | 14 | 24 | 29 | 24 | 29 |
| **Average annual temperatures (°C)** | | | | | | | | | | |
| $\bar{X}$ Jan. | 27.1° | — | — | — | — | — | 27.5° | — | 27.5° | 26.5° |
| $\bar{X}$ July | 11.7° | — | — | — | — | — | 11.8° | — | 11.8° | 11.4° |
| $\bar{X}$ daily range | 18.3° | — | — | — | — | — | 16.4° | — | 16.4° | 18.5° |

NOTE: $\bar{X}$ = mean, SD = standard deviation, % dev. = mean percentage deviation, $\bar{X}$ dev. = mean deviation, N = sample size (number of years)

TABLE 4. Plant quadrat data, corrected to a quadrat size of 232 m²

| | L | K | M | B | A | X | G | D | R | $T_s$ | $T_f$ | T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of quadrats | 32 | 32 | 32 | 33 | 32 | 33 | 32 | 32 | 32 | 16 | 25 | 41 |
| Original quadrat size (m²) | 232 | 232 | 58 | 232 | 58 | 232 | 58 | 232 | 58 | 232 | 232 | 232 |
| Number of plant species | 14 | 15 | 9 | 13 | 13 | 10 | 8 | 17 | 7 | 9 | 16 | 17 |
| **Number per quadrat** | | | | | | | | | | | | |
| $\bar{X}$ | 279 | 64 | 220 | 195 | 228 | 210 | 388 | 88 | 532 | 599 | 25 | 249 |
| SD | 204 | 46 | 76 | 139 | 192 | 78 | 140 | 45 | 312 | 228 | 17 | 317 |
| H by species | 1.17 | 1.32 | 0.65 | 0.98 | 1.23 | 0.94 | 1.47 | 1.73 | 1.15 | 0.61 | 2.42 | 2.11 |
| **Percentage coverage** | | | | | | | | | | | | |
| $\bar{X}$ | 10.1 | 13.9 | 13.7 | 9.4 | 10.7 | 8.6 | 12.6 | 7.2 | 21.3 | 12.4 | 18.7 | 16.3 |
| SD | 5.7 | 10.1 | 7.8 | 4.6 | 6.3 | 6.4 | 3.4 | 4.2 | 11.9 | 5.9 | 8.4 | 8.0 |
| H by species | 1.91 | 1.51 | 0.97 | 1.66 | 1.42 | 1.40 | 1.32 | 1.89 | 0.90 | 1.14 | 1.66 | 1.99 |
| SD/$\bar{X}$ | .56 | .73 | .57 | .49 | .59 | .74 | .27 | .58 | .56 | .48 | .48 | .49 |
| **Plant volume per quadrat (m³)** | | | | | | | | | | | | |
| $\bar{X}$ | 10.3 | 25.2 | 12.4 | 14.1 | 11.6 | 5.0 | 5.4 | 6.6 | 16.6 | 9.1 | 82.7 | 54.0 |
| SD | 10.9 | 28.8 | 12.8 | 12.9 | 8.8 | 4.9 | 2.3 | 4.6 | 10.6 | 8.6 | 53.0 | 55.1 |
| H by species | 1.86 | 1.46 | 1.13 | 1.50 | 1.44 | 1.48 | 1.11 | 1.84 | 0.69 | 1.33 | 1.40 | 1.95 |
| SD/$\bar{X}$ | 1.06 | 1.14 | 1.03 | .91 | .76 | .98 | .43 | .70 | .64 | .95 | .64 | 1.02 |
| **Plant volumes, irrespective of species** | | | | | | | | | | | | |
| $H_3$ | 0.42 | .393 | .032 | .094 | .168 | .056 | 0.0 | .177 | .008 | .014 | .776 | .546 |
| $H_{19}$ | 0.44 | 1.74 | 0.38 | 0.75 | 1.16 | 0.25 | 0.06 | 0.64 | 0.43 | 0.14 | 1.87 | 1.35 |
| Plant height diversity | .667 | .757 | .478 | .744 | .534 | .270 | .020 | .527 | .264 | .229 | 1.02 | .581 |

NOTE: $\bar{X}$ = mean, SD = standard deviation, $H = -\Sigma\ p_i \log_e p_i$, where $p_i$ is the proportion of the $i$th species (see text).

genus *Ctenotus*, whose comparative ecology I have examined in detail (Pianka 1969b).

Table 2 also gives the range and mean values of coefficients of community similarity for each of the continental desert systems (CS = $X/N$, where $X$ is the number of species common to two "communities" under comparison and $N$ is the total number of different species occurring in both; when no species are shared CS = 0, and when two communities are identical CS = 1.0). Community similarity values are high in the North American ($\bar{X}$ = .66) and southern African ($\bar{X}$ = .67) deserts, an indication that the "between-habitat" component of diversity (MacArthur 1965) is low; moreover, the nearly identical mean values demonstrate little difference between North America and the Kalahari in the extent of "between-habitat" diversity. Lower values

of community similarity in Australia ($\bar{X}$ = .49) demonstrate that this component of diversity is considerably greater in that desert system. MacArthur (1965) has argued that there is essentially no limit on "between-habitat" diversity and that this component of diversity could well be increasing continually. It may be significant that there is a correlation between total species diversity and the between-habitat component of species density. In any case, "within-habitat" differences in diversity are ecologically more interesting (Pianka 1966a), and the present analysis was designed to probe into their causes and to attempt to explain patterns of within-habitat diversity.

Climatic statistics from weather stations near each of the 10 study areas are listed in Table 3. Comparison of Tables 1 and 3 indicates no tendency for

the wetter (more productive) eastern areas to support greater numbers of lizard species. In fact, although lizard species density is not significantly correlated with any climatic statistics, there is a weak *inverse* relationship ($r = -.450$, $P < .15$) with the long-term average precipitation; that is, drier and presumably less productive areas tend to support more species.

Results of the plant counts and measurements are summarized in Table 4. Only two of the measures listed are significantly correlated with the number of lizard species: mean percentage coverage ($r = -.556$, $P < .05$) and plant species diversity, by volume ($r = .623$, $P < .05$). Plant volume diversity, shown to be strongly correlated with lizard species density in North America (Pianka 1966b, 1967), was found not to be significantly correlated with lizard species density in the Kalahari.

Because these correlations are fairly weak, I ran a stepwise multiple regression (using the number of lizard species as the dependent variable) to determine the relative importance of the following four independent variables, none of which is significantly correlated with any of the others: (i) plant species diversity, weighting each species by its volumetric proportion of the total perennial volume; (ii) mean percentage coverage by perennials; (iii) plant height diversity as explained in the methods section; and (iv) long-term average annual precipitation. Two of these four variables together reduce the variance in lizard species density between study areas by nearly 61% ($r^2 = .605$): plant species diversity and the long-term mean precipitation. Given these, the other two variables, mean percentage coverage and plant height diversity, together contribute less than 1% more toward reducing the residual variation in lizard species density. Apparently, nearly all the information contained in the mean percentage coverage is also inherent in the combination of plant species diversity and long-term mean precipitation.

Unfortunately the biological significance, if indeed there is any, of these results remains obscure. One could speculate that areas with a greater diversity of perennials provide a greater variety of microhabitats and insect foods or both. Likewise, the inverse relationship with long-term precipitation and mean percentage cover could reflect the fact that many of the lizards require a certain amount of open space for basking and foraging. Alternatively, it is possible that interspecific competition with other taxa (such as birds) changes in favor of the lizard body plan with increased aridity. Elsewhere (Pianka 1967) I postulaed that lizards may capitalize on variability of primary production and that this could be an important factor contributing to their relative success over birds in desert regions.

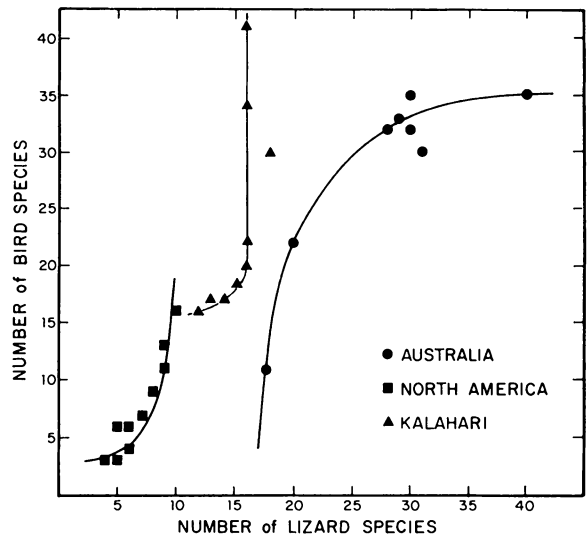Bird species densities in the Kalahari range from



FIG. 1. A plot of bird species density against lizard species density on various study areas in each of the three continental systems. Note that as overall species density increases, bird species increase faster than lizard species in North America and the Kalahari, but that lizard species increase faster than birds in Australia. The sharp upper bound on lizard species density in the Kalahari is also evident (16 species).

16 to 41 on a given study area (Pianka and Huey 1971); this represents more species than occur in the North American desert, but about the same number the occur in the Australian deserts (Pianka 1969a). Fig. 1 plots bird species density against lizard species density for study areas in each continental desert system; as overall species density increases, bird species are added faster than lizard species in North America and the Kalahari, whereas the reverse is true in Australia, where lizard species increase faster than bird species. The Kalahari supports proportionately more species of ground-foraging avian insectivores than the Australian desert (Pianka and Huey 1971); this in turn implies that competition between birds and lizards is keener in the Kalahari than in Australia. Thus this difference between the two desert systems could be one of the many causative factors impinging upon lizard species densities.

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