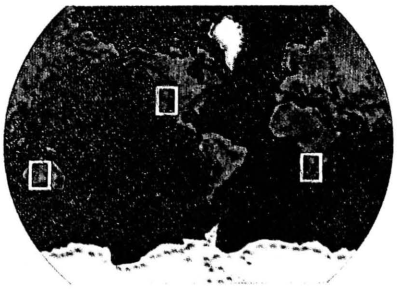
Eric R. Pianka

Some Intercontinental Comparisons of Desert Lizards



Independently evolved lizard assemblages from three continents are described and compared, with particular reference to species richness and patterns of resource utilization. Both differences and similarities are examined. Lizard diversity is relatively low on flatland study sites in the Mojave and Sonoran Deserts of western North America (six to 11 species), intermediate in the Kalahari Desert (really a semidesert) of southern Africa (11 to 17 species), but quite high in the Great Victoria Desert of western Australia (from 15 to 42 species). Detailed ecological work enables quantification of patterns of utilization of microhabitat and prey resource states. Overall diversity of resources used by entire saurofaunas varies by continent, although not necessarily in direct concordance with lizard diversity. Certain species are specialists and others generalists, but average niche breadth is similar on all three continents, both for diet and microhabitat. Crude counterparts that occupy similar niches in different lizard faunas, or "ecological equivalents," can be identified.

Basically similar ecological systems have arisen more or less independently in similar climates at widely divergent localities around the planet. One of the more striking examples is so-called chaparral, a drought-resistant, evergreen, tough-leaved type of vegetation, found in five geographically disparate regions that share a unique winter-wet, summer-dry climate: around the Mediterranean Sea, along the southernmost edge of Africa, in southwestern Australia, in central Chile, and also in parts of southwestern California. Chaparral plants are broadly similar in growth form, but different species have apparently arisen independently in each of the regions (DiCastri & Mooney 1973). Such convergent evolutionary responses to similar physical environments has led to the recognition of biomes (Allee et al. 1949).

Ecologically comparable species that occupy similar niches in different regions are known as ecological equivalents (Grinnell 1924, Hesse et al. 1937). Among desert lizards, one of the prime examples involves adaptations to loose sand (Mosauer 1932). Under such circumstances toe lamellae have been enlarged to form fringed toes (Figure 1, *right*) so they can "swim" in the sand, and snouts have become flattened to shovel-shaped noses. Fringed toes have evolved independently in five different lizard families (probably several times in each): agamids, iguanids, lacertids, skinks, and geckos. Examples of three such sand-swimming lizards are: an American desert fringe-toed iguanid *Uma scoparia* (Figure 1), a Sahara Desert skink *Scincus scincus,* known as a sandfish (Fig-

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further when species richness is considered (Pianka in press). In the North American warm deserts, flatland study areas support from six to 11 species of lizards, depending on the complexity of the vegetation (Pianka 1967, in press). In the Kalahari, between 11 and 17 species of desert lizards coexist on various study sites (Pianka 1971b). In the Great Victoria Desert of western Australia, lizard species richness on various study areas reaches its apogee, varying from 15 species to a phenomenal 42 species (Pianka 1969, in press). Reasons for these differences in diversity are complex and are considered below.

Table 1. **Numbers of Species of Lizards in Different Families Found in Sympatry on Desert Study Sites**

	North America		Kalahari		Australia	
Lizard Family	**Spp./ Site**	**Family Total**	**Spp./ Site**	**Family Total**	**Spp./ Site**	**Family Total**
Agamidae	—	—	1	1	2–8	11
Chameleontidae	—	—	1	1	—	—
Gekkonidae	1	1	4–7	7	5–9	13
Helodermatidae	1	1	—	—	—	—
Iguanidae	3–8	9	—	—	—	—
Lacertidae	—	—	3–5	7	—	—
Pygopodidae	—	—	—	—	1–2	3
Scincidae	—	—	3–5	6	6–18	28
Teiidae	1	1	—	—	—	—
Varanidae	—	—	—	—	1–5	5
Xantusidae	1	1	—	—	—	—
Total*	4–11	13	12–18	22	18–42	61

**Based on actual study site data (not given).*

Methods

To gather data on the ecological relationships of these lizard faunas required walking thousands of kilometers through 30-odd study sites observing lizards. Study areas vary in size from half a square kilometer to several square kilometers. Study sites are spaced over hundreds of kilometers (maps can be found in Pianka in press). Average distances to the nearest other study area for North America, the Kalahari, and Australia, in that order, are 190, 61, and 87 km, respectively (standard deviations, 63, 31, and 120). Five full years were spent in the field between 1962 and 1979 and nearly 12 person-years collecting data on lizards (sites were visited repeatedly over essentially the entire seasonal period of lizard activity). Snakes, birds, and mammals observed were recorded, and, in some cases, collected. Microhabitat and time of activity were recorded for most lizards encountered active aboveground. Body temperatures and air temperatures were measured for most active lizards. Whenever possible, lizards were collected so that their stomach contents and reproductive condition could be assessed later in the laboratory. Resulting collections of some 4000 North American, more than 5000 Kalahari, and nearly 6000 Australian specimens, representing some 90 species, are permanently lodged in the Los Angeles County Museum of Natural History, the Museum of Vertebrate Zoology of the University of California at Berkeley, and the Western Australian Museum in Perth.

In all three desert–lizard systems, the same 15 basic microhabitats were recognized: subterranean (for unknown reasons, no subterranean lizards live in the North American deserts), open sun, open shade, grass sun, grass shade, bush sun, bush shade, tree sun (on ground beneath), ure 2), and a Namib Desert lacertid *Aporosaura anchietae* (Figure 3).

Appropriately selected "natural experiments" may actually allow a limited measure of control over prehistoric phenomena such as the Pleistocene glaciations. Differences between independently evolved faunas occurring in areas with comparable present-day climates and vegetation structures presumably reflect such prehistoric factors (Orians & Solbrig 1977). Natural variation is also frequently very useful because experimental manipulation of ecological systems is often extremely difficult and therefore impractical. For example, a fruitful natural experiment on competition may exist when a species occurs both with and without a potential competitor in similar habitats in different parts of its geographic range. Such situations have been considered analogous to removal–addition experiments, and, if chosen and studied with enough care, niche shifts can sometimes be related to the underlying effects of interspecific competition. Comparing ecological systems known to be independent but basically comparable has sometimes helped ecologists to assess the predictability of evolutionary pathways. Just how deterministic is the outcome of the evolutionary response of a particular body plan in a given environmental regime?

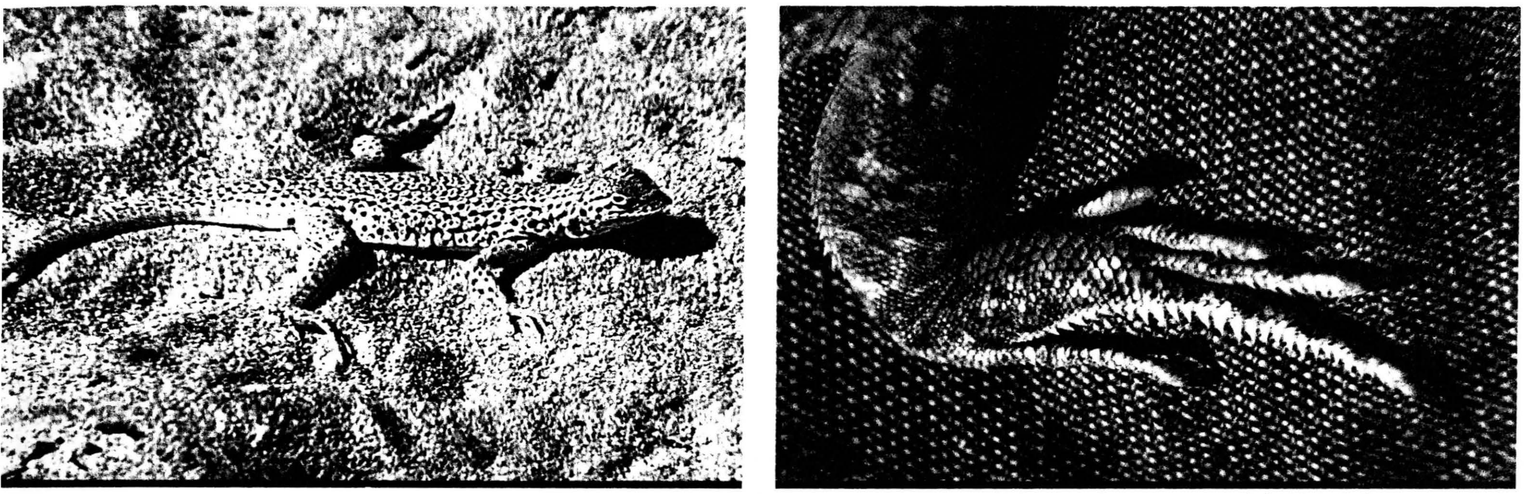
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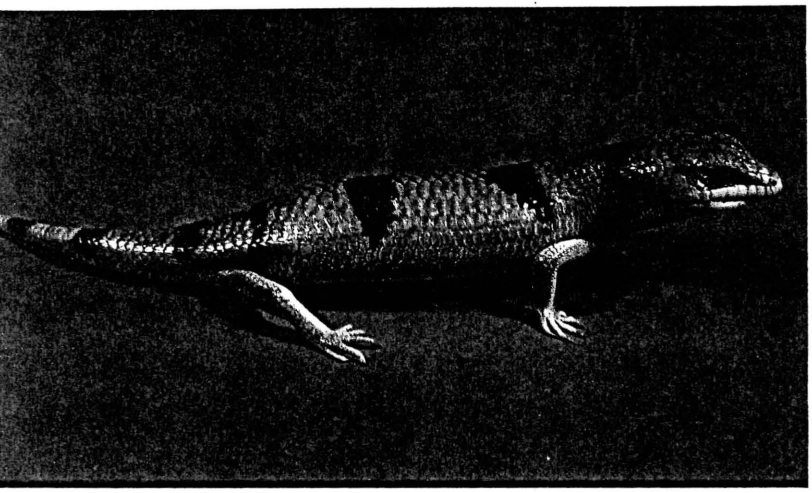
Figure 1. Left: Uma scoparia, *a sand-adapted iguanid lizard from sand dune desert regions of western North America. These lizards have evolved both shovel noses and fringed toes* (right).

Over the past two decades, the author has examined various aspects of the ecology of lizards in warm deserts of three continents: western North America (the Mojave and Sonoran Deserts), southern Africa (the Kalahari Desert), and western Australia (the Great Victoria Desert). Lizards have evolved independently from partially different stocks in each of these three continental desert–lizard systems, and it proves instructive to examine the extent of ecological similarity as well as the degree of lack of convergence.

Taxonomic Richness

At the highest taxonomic level, the three systems are similar in diversity, with five families of lizards represented in each; however, the identities of these five families vary among continents (Table 1) — only Gekkonidae occurs in all three. Of the 15 recognized families of extant lizards, 11 are represented in these three different continental desert–lizard systems. At the generic level, North America and the Kalahari are similar with 12 and 13 genera, respectively, whereas Australia shows double the diversity (24 genera). Intercontinental differences are magnified still tree shade (on ground beneath), other sun, other shade, low sun (≤ 30 cm aboveground), low shade, high sun, and high shade (> 30 cm aboveground). For some purposes, finer microhabitat resource states were used. Lizards at an interface between two or more microhabitats were usually assigned fractional representation in each. Only undisturbed lizards were used in analyses of microhabitat utilization.

In analysis of stomach contents, the same 20 very crude prey categories were distinguished on all continents. Both volume and number of prey items were estimated for each of these categories (the resulting data consist of nearly half a million individual food items).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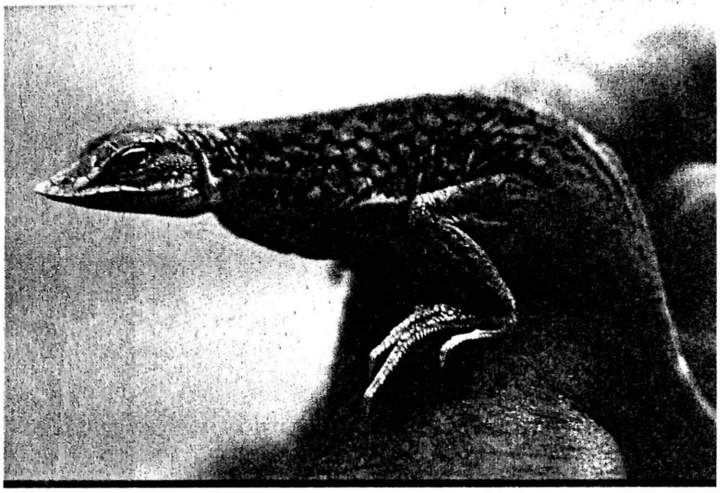
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Figure **2.** Scincus scincus, *a Sahara Desert skink known locally as the sandfish.* **3.** Aporosaura anchietae, *a sand-swimming lacertid lizard from the Namib Desert of southwest Africa.*

Niche breadth was estimated for both diet and microhabitat for all species using proportional utilizations by volume in a simple index of diversity (Simpson 1949). Resource diversity, based on the overall utilization by an entire saurofauna, was estimated similarly.

A major virtue of these data is that identical methods and the same resource categories were used by a single investigator in each of three continental desert–lizard systems, enabling meaningful intercontinental comparisons. This unique body of data thus allows fairly detailed analyses of patterns of resource utilization and community structure in these independent saurofaunas. Moreover, both dietary and microhabitat niche breadths and overlaps can be estimated as well as species diversities and the spectra of resources actually exploited by entire lizard faunas varying widely in number of species. Still another dimension that can be profitably exploited is area-to-area variation in species utilization patterns (Pianka in press).

Results

Considerable fidelity in microhabitat utilization is evident. Many species separate out using just the above 15 very crude microhabitat categories. For example, some species frequent open spaces between plants to the virtual exclusion of other microhabitats, whereas other species stay much closer to cover.

Desert lizards vary widely in their modes of thermoregulation (Pianka in press). Some species, particularly nocturnal ones such as most geckos, exhibit relatively passive "thermoconformity," with their body temperatures mirroring ambient thermal conditions. Other species, particularly active diurnal heliotherms, show considerable precision in controlling their body temperatures by behavioral means. Linear regressions of body temperature among individual lizards on ambient air temperature in such species are often fairly flat with slopes not appreciably different from zero (Huey & Slatkin 1976, Pianka in press). In contrast, regressions of body temperatures against air temperatures for thermoconformers are steep, with slopes that do not differ significantly from one (Pianka in press). Other species display intermediate slopes and thermoregulatory tactics. Various species can be placed on a unidimensional, linear, thermoregulation continuum (Figure 4). The remarkably good fit to a transcendent straight line does not seem to be a statistical artifact, but rather a reflection of an innate physiological design constraint on the vertebrate body plan. Positions of different species along this spectrum reflect a great deal about their complex activities in both space and time, and are correlated with patterns of microhabitat utilization.

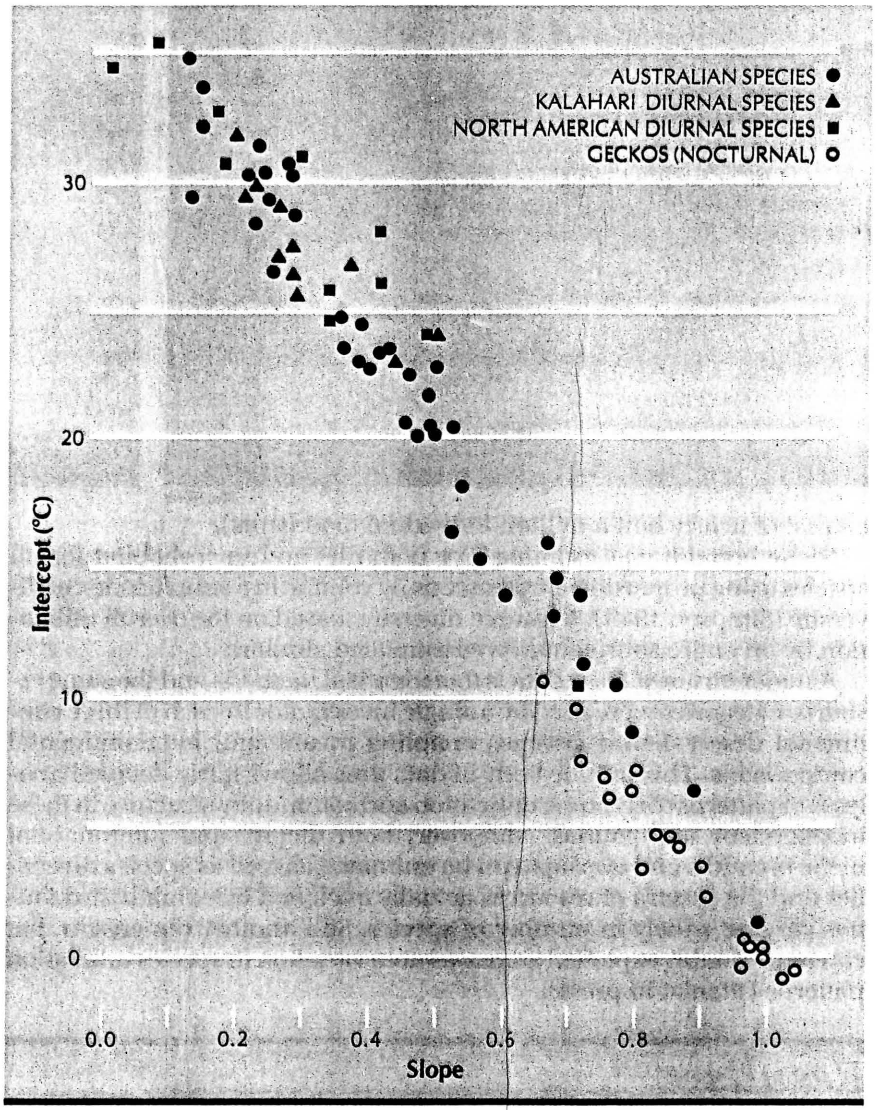


Figure 4. Each datum point represents the least-squares linear regression of body temperature against air temperature for a given species of desert lizard (data given in Pianka in press). Sample sizes are usually substantial (mean N = 145; data on a total of 11 924 individual lizards were used to make this plot). The ordinate represents the spectrum of thermoregulatory tactics ranging from active thermoregulators (slope of zero) to entirely passive thermoconformity (slope of one). The intriguing "intercept" of the intercepts (38.8°C) approximates the point of intersection of all 82 regression lines and presumably represents an innate design constraint imposed by lizard physiology and metabolism. Even so, this statistic varies among taxa, ranging from only 29.4°C in 19 species of nocturnal geckos to 39.1°C in 13 species of diurnal agamids. (In other diurnal groups, such as skinks and iguanids, it is about 36.5 to 37°C.)

Considerable consistency in diet is also evident among species. For example, some species eat virtually nothing but termites, whereas others never touch them. Moreover, diets of many species change little in space or time (Pianka in press). Indeed, using just the 20 very crude prey categories (Figure 5) allows reasonably clean separation of many pairs of lizard species on the basis of foods eaten (Pianka in press). When prey items are analyzed by either number or size, separation of pairs of lizards is substantially less than when the proportional representation of each food category by volume is used. For some purposes, much finer prey categories could be used. Termites were identified to species and caste for Kalahari lizards. Similarly, prey were identified to the finest possible categories for a subset of the Australian data (for example, ants and termites were placed into various size and color categories by family to generate some 97 ant and 58 termite resource states). (These very detailed data are however only of limited utility for comparative purposes.)

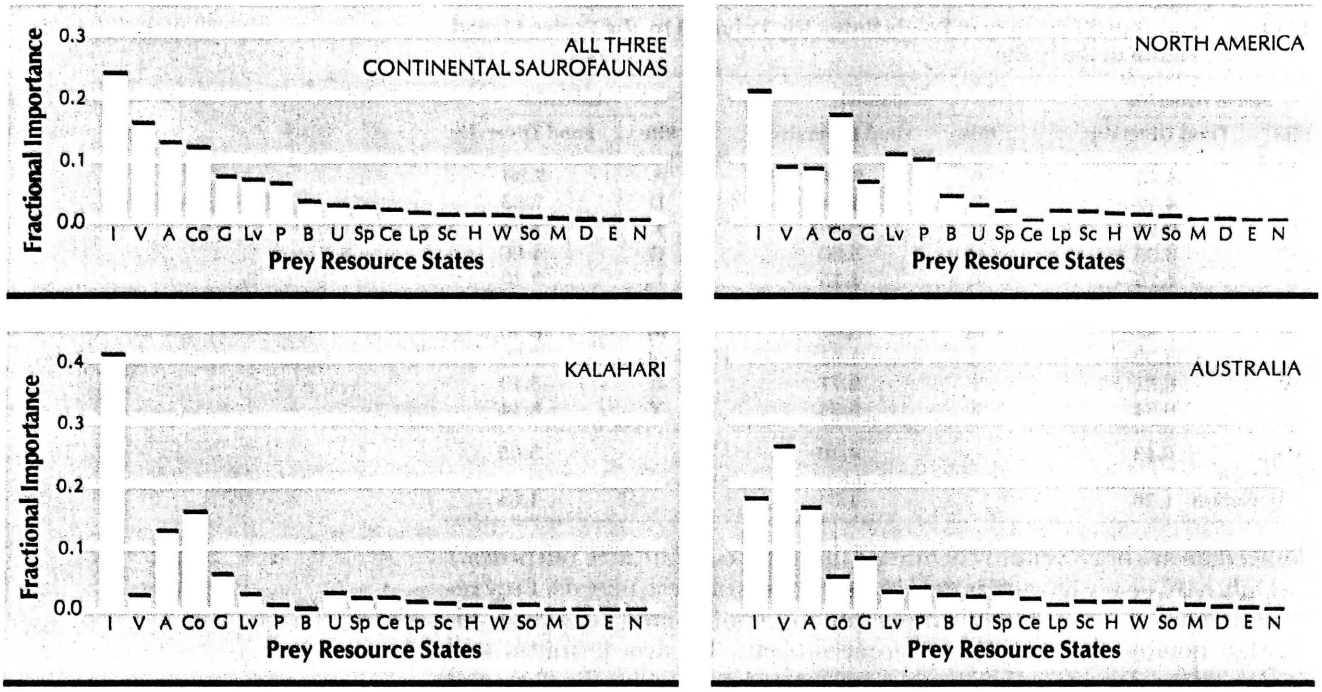
Table 2. Estimated Diversity of Foods Eaten (by Volume) by the Entire Lizard Fauna at Each Site

North America		Kalahari		Australia	
Site	Food Diversity	Site	Food Diversity	Site	Food Diversity
I	4.25	A	5.64	A	7.39
L	4.17	B	5.24	D	7.65
G	6.54	D	5.45	E	3.74
V	6.05	G	5.60	G	4.66
S	4.75	K	4.15	L_1	3.48
P	6.61	L	2.44	L_2	4.28
M	7.32	M	5.97	M	6.50
T	8.50	R	1.93	N	7.86
W	6.51	T	2.77	R	5.19
C	6.64	X	5.64	Y	6.14
Mean	6.13		4.48		5.69
Standard deviation	1.38		1.54		1.64

Only a relatively few foods dominate the diets of these lizards. Prey resource spectra are broadly similar among continents (Figure 5), although notable quantitative differences occur. Beetles, termites, and insect larvae dominate the North American diet; termites, beetles, and ants form the bulk of the diet of Kalahari lizards. In Australia the five most important food categories, in decreasing order of volumetric importance, are: vertebrates, termites, ants, grasshoppers plus crickets, and beetles. Note that the same three prey categories — termites, beetles, and ants — constitute major foods in all three continental desert–lizard systems. Termites assume a disproportionate role in the Kalahari, as do vertebrate prey in Australia (this is largely a reflection of the diets of varanid lizards). The overall diversity of foods consumed by all species of lizards is actually greatest in the least diverse North American saurofauna, lowest in the Kalahari lizards, and intermediate in Australia (Table 2). Estimates of prey diversity for different study areas correlate with various measures of the variability in average annual precipitation, and presumably primary productivity (Pianka in press).

Niche breadth, for both diet and microhabitat, does not correlate with sample size (Pianka in press), an indication that samples are adequate to characterize patterns of resource utilization among species. Frequency distributions of niche breadth for diet and microhabitat are shown in Figure 6. Intercontinental variation in niche breadth is slight and seldom statistically significant. Food-specialized species tend to exhibit narrow microhabitat niche breadth (Pianka in press).

The ecological composition of the saurofaunas of these sites is summarized in Table 3. Numbers of species with different modes of life differ among sites within continents as well as between continental systems. More than twice as many species of diurnal ground-dwelling lizards occur on a typical Australian site than on an average site in the North American and Kalahari deserts; however when expressed as a percentage of the total lizard fauna, diurnal ground-dwelling species constitute a full 74% of the North American saurofauna, compared with only 43% of the Kalahari lizard fauna and 51% of the lizard species on a typical Great Victoria Desert site. Intercontinental variation in the absolute number of species that forage by sitting and waiting for their prey (Pianka in press) is slight, but the absolute number of widely foraging species increases rather markedly from North America to the Kalahari to Australia (Table 3). When expressed as a percentage of the total saurofauna, only about 16 to 18% are diurnal sit-and-wait foragers in the southern hemisphere deserts (an average of 2.4 species in the Kalahari and 5.3 species in Australia), whereas a full 60% of the North American lizards (average, 4.4 species) fall into this category because diversity of the latter desert–lizard system is low. The percentage contribution of all diurnal species, both ground-dwelling and arboreal, to the total fauna declines as the number of lizard species increases (i.e., nocturnality increases). Arboreal, subterranean, and nocturnal species are all conspicuously more prevalent in the two southern hemisphere deserts than they are in North America; subterranean lizards and arboreal nocturnal species are entirely missing from the North American saurofaunas, yet contribute three or four species to an average site in the two southern hemisphere deserts (Table 3). Number of species of arboreal lizards and their percentage contribution to total lizard fauna both tend to increase with number of lizard species (Table 3). Arboreal lizard species are however less well represented on structurally simple sites with low lizard diversity, even within the very diverse Australian saurofaunas.



A — ants
B — roaches (Blattaria)
Ce — centipedes
Co — beetles (Coleoptera)
D — flies (Diptera)
E — insect eggs and pupae
G — grasshoppers and crickets
H — bugs (Hemiptera and Homoptera)
I — termites (Isoptera)
Lp — butterflies and moths (Lepidoptera)
Lv — all insect larvae
M — mantids and phasmids
N — adult Neuroptera (ant lions)
P — plant material (floral, vegetative)
Sc — scorpions
So — solpugids (absent from Australia)
Sp — spiders
U — miscellaneous arthropods, including unidentified ones
V — all vertebrate material including carrion and sloughed lizard skin
W — wasps and other non-ant hymenopterans

Figure **5.** *Comparison of prey resource spectra by volume in each of the three continental desert–lizard systems and in all three systems combined. All individual lizards of all species are pooled to provide a single sample for each system; thus abundant or large species have greater weight than rare or small species.*

Discussion

The heightened relative importance of nocturnality among lizards in the Kalahari and Great Victoria Deserts could be a consequence of any or all of at least three different factors: (1) Various desert systems could differ in diversity and abundance of available resources at night, such as nocturnal insects. (2) In North America, other taxa such as spiders might fill the ecological role of arboreal nocturnal lizards. Differences in species numbers or densities of insectivorous and carnivorous snakes, birds, and mammals might also play a crucial role. (3) Effects of the Pleistocene glaciations are generally acknowledged to have been stronger in the northern hemisphere, which must certainly have influenced the evolution of nocturnal lizards. However, in at least the southernmost parts

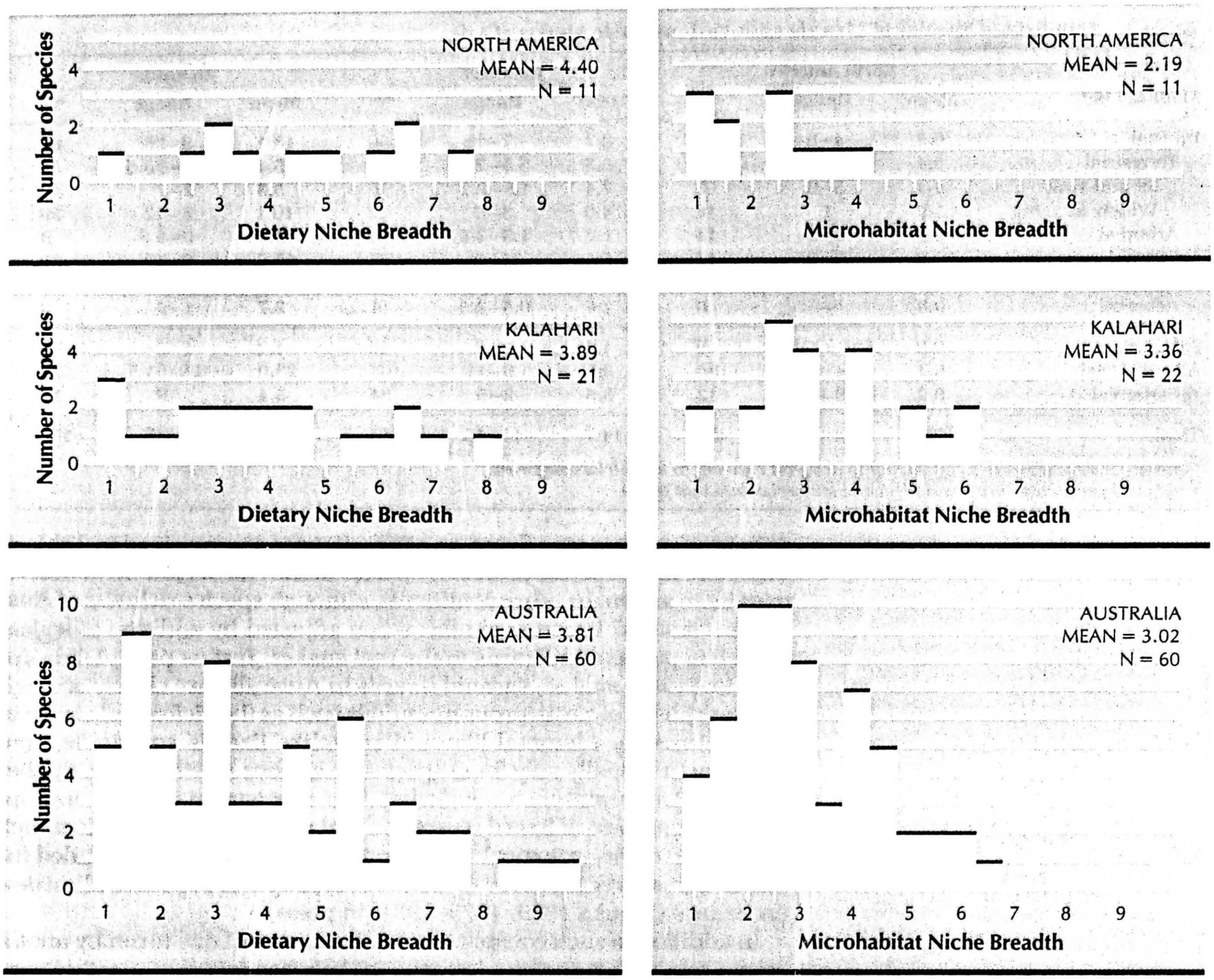


Figure 6. Observed niche breadths for food and microhabitat resources among various species in each of the three continental desert–lizard systems.

of the Sonoran Desert of North America, present-day climates are easily adequate for nocturnal lizards (Pianka in press). The eublepharine gecko *Coleonyx* thrives as a nocturnal terrestrial lizard in the Sonoran and Mojave Deserts, occurring as far north as lat 37° (some geckos reach comparable southern latitudes in Australia). As Hutchinson (1959) expressed in a slightly different context, "if one . . . species can [exist in the nocturnal terrestrial niche], . . . why can't more?" The absence of an arboreal gecko from the flatland deserts in the southern Sonoran Desert is also most puzzling, particularly since the rock-dwelling, climbing gecko *Phyllodactylus xanti* occurs nearby. A tree- or shrub-climbing gecko species might well be able to invade this desert region if given an opportunity. Without such an introduction, either accidental or deliberate, all such interpretations remain speculative.

Various factors, such as degree of isolation and available biotic stock (particularly those of potential prey, predators, and competitors) have clearly shaped these lizard faunas in other ways. Certain ecological roles occupied by nonlizard taxa in North America and the Kalahari have been usurped by Australian desert lizards. Thus Australian pygopodid and varanid lizards clearly replace certain snakes and mammalian carnivores, taxa that are impoverished in Australia. Numbers of species in various vertebrate taxa found on study sites are summarized in Table 4. There are more species of snakes on sites in the North American deserts than there are on the other continents, although species richness of Australian "snakes" becomes similar when adjusted by addition of legless snakelike pygopodid lizards to the real snakes. Just as pygopodids appear to replace snakes, varanid lizards in Australia are clearly ecological equivalents of carnivorous mammals such as the kit fox and coyote in North America. Mammal-like and snakelike lizards contribute from one to eight (usually only four) species on various Australian study sites and therefore represent a relatively minor component of the overall increase in numbers of lizard species on that continent. Nevertheless such usurpation of the ecological roles of other taxa has clearly expanded the variety of resources (or overall niche space) exploited by Australian desert lizards (Pianka 1969, 1975, 1981, in press).

Table 3. Numbers of Species of Lizards with Various Basic Modes of Life

	North America			Kalahari			Australia		
Mode of Life*	**Mean**	**Range**	**%**	**Mean**	**Range**	**%**	**Mean**	**Range**	**%**
Diurnal	6.3	4–9	86	8.2	7–10	56	18.1	9–25	60
Terrestrial	5.4	4–7	74	6.3	5.5–7.5	43	15.4	9–23.5	54
Sit-and-wait	4.4	3–6	60	2.4	1.5–2.5	16	5.3	2–7	18
Widely foraging	1.0	1	14	4.0	3–6	27	10.1	4–12	36
Arboreal	0.9	0–3	12	1.9	1.5–2.5	13	2.7	0–5.5	9
Nocturnal	1.0	0–2	14	5.1	4–6	35	10.2	8–13	36
Terrestrial	1.0	0–2	14	3.5	3–5	24	7.6	6–9	27
Arboreal	0.0	—	0	1.6	0.5–2.5	11	2.7	1–4	9
Subterranean	0.0	—	0	1.4	1–2	10	1.2	1–2	4
All terrestrial	6.4	4–8	88	9.8	9–11	67	23.0	15–31.5	78
All arboreal	0.9	0–3	12	3.5	2–5	24	5.4	1–9	18
Total	7.3	4–11	100	14.7	11–18	101	29.6	18–42	100

**Semi-arboreal species are assigned half to arboreal and half to terrestrial categories.*
Totals and percentages are based on actual study site data (not given).

In addition to such conspicuous replacements of one taxon by another, more subtle competitive interactions between taxa doubtlessly occur, particularly between lizards and insectivorous birds. Fewer species of ground-dwelling insectivorous birds occur in Australia than in the Kalahari, which may reduce competition between lizards and birds in Australia. With increases in the total number of species of birds plus lizards, the number of lizard species increases faster than bird species in Australia, whereas, in North America and the Kalahari, bird species richness increases faster than lizard species richness (Pianka 1971b, 1973, in press). Reasons for these differences among continents are elusive, but one factor may be that very few birds migrate in Australia, both because of its isolation and its limited areas at high latitude. In contrast, a fair number of migrant bird species periodically exploit the North American and African deserts. Lizard faunas of the latter two desert systems could well be adversely influenced by intermittent but still regular competitive pressures from these insectivorous avian migrants.

The effect of the composition of prey taxa on the composition of saurofaunas is illustrated by the conspicuous and diverse termite fauna of southern Africa, which has apparently facilitated the evolution of termite-specialized species of skinks, lacertids, and geckos. Indeed, by volume, termites comprise a full 41% of the diet of Kalahari lizards, but, by contrast, they constitute only about 16% of the overall diet of the entire saurofauna in western North America and only about 18.5% of the diet of the lizards of western Australia (Pianka in press).

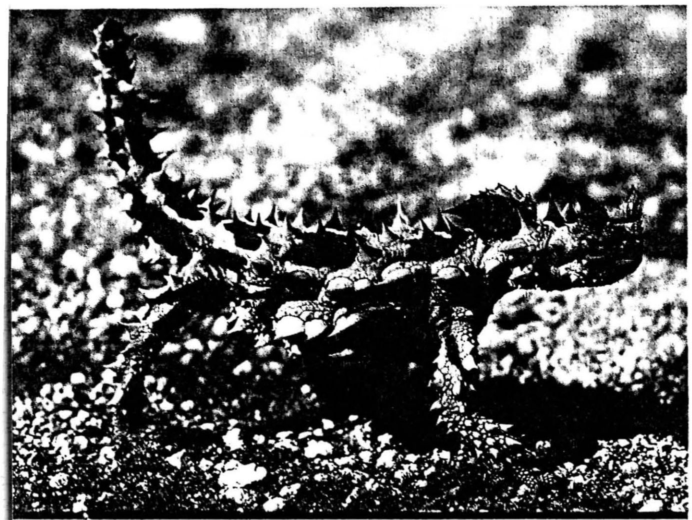

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Figure **7.** Moloch horridus, *or the "mountain devil," an ant-specialized Australian agamid.* **8.** *The desert horned lizard* Phrynosoma platyrhinos, *a North American iguanid that is a crude ecological analog of* Moloch.

Numerous more elusive interactions between taxa doubtlessly occur. For instance, one reason that the Australian deserts support such rich lizard faunas could involve reduced predation pressures from snakes, raptors, and carnivorous mammals on that isolated continent (however, many Australian lizards, both varanids and pygopodids, do prey upon other lizards). Similarly, the higher incidence of arboreal and nocturnal lizard species in the Kalahari and Australia compared with North America could well be related to fundamental differences in the niches occupied by other members of these communities, including potential competitors among arthropods, snakes, birds, and mammals.

The physical structure of the vegetation profoundly influences the composition of lizard faunas too. In North America, sites with greater spatial heterogeneity of vegetation support more species than do sites with simpler vegetation. The mere existence of the unique hummock

Table 4. Species Densities of Various Vertebrates on Desert Study Areas

	North America		Kalahari		Australia	
Taxon	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
All lizards	7.4	4–11	14.7	11–18	29.8	18–42
Pygopodid lizards	—	—	—	—	1.7	0–3
All birds	7.8	3–16	22.8	15–40	28.3	15–35
Ground-foraging insectivorous birds	—	—	7.3	4.5–11.7	4.8	2.8–5.8
Snakes	4.5	2–9	2.2	1–6	3.6	1–3
Small mammals	5.3	4–8	—	—	1.5	1–3
Site totals*	25.0	14–40	39.7	27–63	63.2	36–80

**Totals are based on actual study site data (not given).*

grass plant life in Australia (Beard 1976) is a major factor contributing to lizard diversity on that continent (Pianka 1969, 1973, 1975, 1981, in press). A pure "spinifex" (*Triodia*) grass flat supports at least 16 species of lizards (perhaps as many as 20), including six or seven species of *Ctenotus* skinks. These grass tussocks are extraordinarily well suited for lizard inhabitants, providing not only protection from predators and the elements, but a rich insect food supply as well. Certain lizard species appear to spend almost their entire lives within dense *Triodia* clumps, while other lizards exploit the edges. Still other species forage in the open spaces between tussocks but rely on spinifex clumps for escape in emergencies. The latter species tend to have relatively longer hind legs than the former (Pianka in press) and are presumably faster runners — a trade-off exists, however, since long-legged open-dwelling species must move clumsily through dense vegetation whereas short-legged species literally swim through it with ease.

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Figure **9.** *A North American iguanid, the zebra-tailed lizard* Callisaurus draconoides. *It is a denizen of the open spaces between plants.* **10.** Ctenophorus cristatus, *a long-legged agamid of Australia.*

Lizard faunas of shrub desert sites on each of the three continents are compared in Table 5. The structure of the vegetation, consisting of low microphyllous chenopod shrubs, is virtually identical on these three sites, chosen to control vegetative structural complexity (plants of the globally distributed genus *Atriplex* occur on all three areas). On North American sites, only five species of lizards are present (a sixth species is added in the south). The Kalahari site supports 13 lizard species whereas an Australian shrubby area in a dry lake-bed presumably sustains a full 18 species (Pianka 1969, 1971b, 1981). The major differences between continents are traceable to non-lizardlike lizards and to nocturnal species. Four gecko species are nocturnal in the Kalahari while eight species of geckos and skinks are active at night on the Australian site (only one nocturnal lizard species exists on southern North American sites). Insectlike species (*Mabuya variegata* and *Menetia greyi*), a mammal-like lizard (*Varanus gouldi*), and a wormlike subterranean skink (*Lerista muelleri*) further expand the lists in the southern hemisphere. Numbers of species of truly lizardlike lizards that are both diurnal and terrestrial (or semi-arboreal) are much more comparable among the three continents: North America (five species), Kalahari (eight species), and Australia (seven species).

Effects of historical variables such as the Pleistocene glaciations could also be considerable, but are exceedingly difficult to evaluate. The North American deserts are generally acknowledged to be of relatively recent geologic origin (Axelrod 1950), although subdesert conditions must have prevailed in the general region long before the origin of true deserts. During the upper Tertiary, American deserts expanded but then became restricted to northern Mexico and the extreme southwestern United States with the onset of the Pleistocene glaciations. Presumably these deserts expanded rapidly to their present boundaries with the retreat of the glaciers about 10 000 years ago. The sands of the Kalahari are largely of eolian origin and were formed and originally distributed during the Tertiary, but later were redistributed in the Pleistocene by both wind and water. Lancaster (1979) presents evidence for a widespread humid period in the Kalahari during the late Pleistocene. Kalahari sandridges probably assumed roughly their present distribution during drier periods over the last 10 000 years; the subsequent stabilization of the

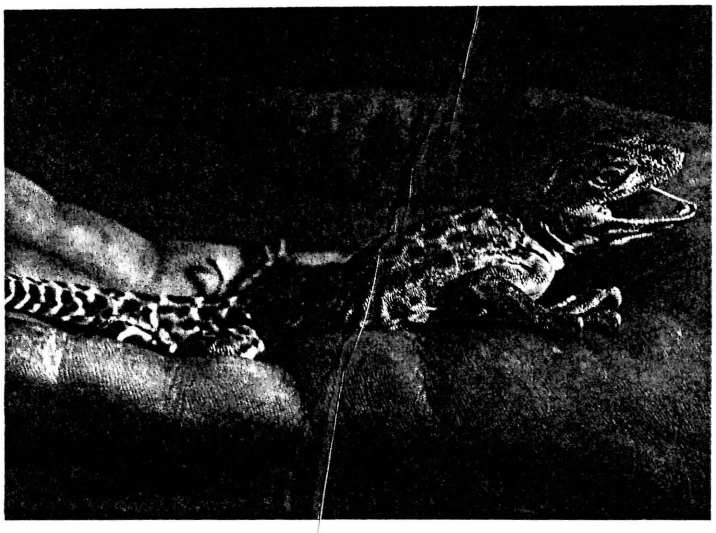

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Figure **11.** *The leopard lizard* Crotaphytus wislizeni, *a North American iguanid that specializes on other lizards in the southern parts of its geographic range.* **12.** *The convergent, Australian* Varanus eremius.

Table 5. Lizard Faunas on Chenopodeaceous Shrubby Sites

North America	Kalahari	Australia
	Mabuya occidentalis	*Ctenotus schomburgkii*
Cnemidophorus tigris	*Eremias lugubris*	*C. leonhardii*
	E. namaquensis	
Uta stansburiana	*E. lineo-ocellata*	*Ctenophorus isolepis*
Phrynosoma platyrhinos	*Agama hispida* (?)	*Moloch horridus**
Crotaphytus wislizeni	*Mabuya striata*	*Ctenophorus inermis*
		C. reticulatus
Callisaurus draconoides	*Meroles suborbitalis*	*C. scutulatus*
	Ichnotropis squamulosa	
	Mabuya variegata	*Menetia greyi**
		*Lerista muelleri**
		Varanus gouldi
Coleonyx variegata	*Colopus wahlbergi*	*Rhynchoedura ornata*
	Ptenopus garrulus	*Diplodactylus conspicillatus*
	Chondrodactylus angulifer	*Nephrurus vertebralis*
	Pachydactylus capensis	*Heteronotia binoei*
		Diplodactylus strophurus
		Gehyra variegata
		Egernia inornata
		Eremiascincus richardsoni

Atriplex *occurs on all three sites. Very crudely approximate ecological equivalents are aligned horizontally. Nocturnal species are listed in the bottom half of table.*

**Not actually collected on the area, but highly expected to occur there based on autecological considerations and occurrences on other areas.*

sandridges by vegetation suggests that a slight amelioration of the climate may have taken place in more recent times. So-called Kalahari sands are widespread in southern Africa, occurring well beyond the confines of the currently recognized Kalahari semidesert. Dry to very dry conditions have probably prevailed in most of this area since the middle to the end of the Tertiary (Lancaster 1984), although some workers have suggested otherwise. Views as to the age and history of the Australian deserts are also varied and conflicting. Crocker & Wood (1947) postulated a "Great Aridity" during the Pleistocene following the last glaciation, but others have argued for a much greater antiquity for at least portions of the continent (Bowler 1976, Bowler et al. 1976, Galloway & Kemp 1981). Australian sandridges appear to be exceedingly ancient (Bowler 1976).

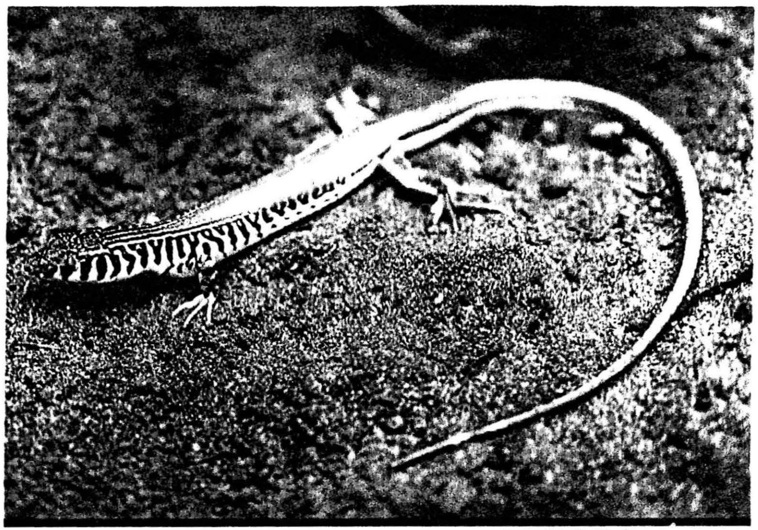

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Figure **13.** *The widely foraging Australian skink* Ctenotus. **14.** *The convergent Kalahari lacertid* Nucras.

The impact of history on these desert–lizard systems has clearly been profound, but it is overly facile, even glib, to assert that the Australian deserts are more diverse than other deserts simply by virtue of antiquity. The Namib Desert in southwestern Africa is ancient (Ward et al. 1983) and supports an extremely rich beetle fauna but yet has only a moderate diversity of lizards. Clearly, ecological factors promoting coexistence, such as resource diversity and climatic predictability, are of vital importance (Pianka 1981, in press).

Organisms that fill similar ecological niches in different, independently evolved biotas are termed ecological equivalents (Grinnell 1924). Some such convergent evolutionary responses of lizards to the desert environment, although imperfect, are evident across the three continents (Pianka 1975, in press). For example the Australian and North American deserts both support a cryptically colored and thornily armored ant-specialized species: the agamid *Moloch horridus* (Figure 7) exploits this ecological role in Australia (Pianka & Pianka 1970), while its counterpart, the iguanid *Phrynosoma platyrhinos* (Figure 8), occupies this role in North America (Pianka & Parker 1975). No Kalahari lizard has adopted such a life-style. Interestingly enough, a morphometric analysis demonstrates that *Moloch* and *Phrynosoma* are actually anatomically closer to one another than either species is to another member of its own lizard fauna (Pianka in press). Also, both North America and Australia have long-legged species that frequent the open spaces between plants: *Callisaurus draconoides* in North America (Figure 9); *Ctenophorus scutulatus, C. cristatus* (Figure 10), and *C. isolepis* in Australia; and

Crotaphytus wislizeni in North America (Figure 11) as well as the medium-sized lizard-eating lizard *Varanus eremius* in Australia (Figure 12). Active, widely foraging lizards occur in all three deserts: teiids (*Cnemidophorus*) in North America, skinks (*Ctenotus*) in Australia (Figure 13), and lacertids (*Nucras*) in the Kalahari (Figure 14). Two convergent nocturnal geckos, both often found in close association with termitaria, are shown, one on the cover of this issue (the Kalahari *Pachydactylus capensis*) and the other in Figure 15 (the Australian *Heteronotia binoei*). A few Kalahari–Australia species pairs are also crudely convergent: For example, the subterranean skinks *Typhlosaurus* and *Lerista* are roughly similar in their anatomy and ecology, as are the semiarboreal agamid lizards *Agama hispida* and *Pogona minor*.

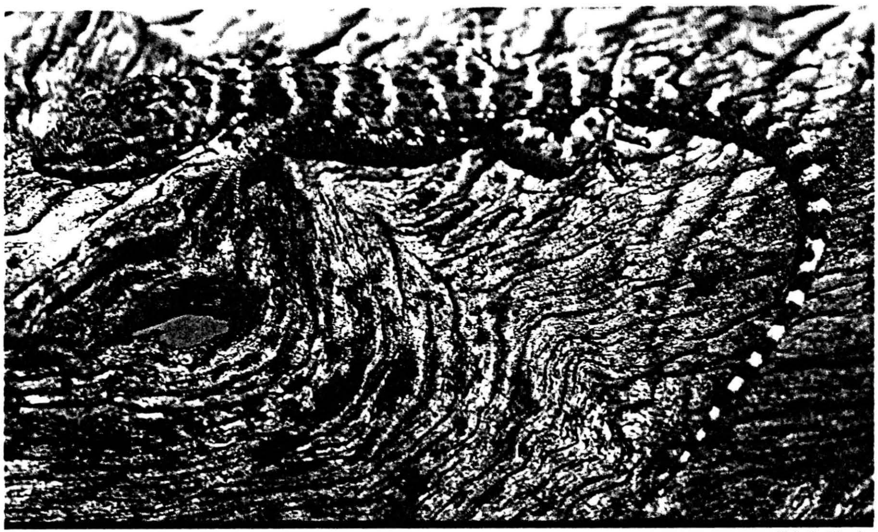

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Figure **15.** *The Australian* Heteronotia binoei, *convergent with the Kalahari* Pachydactylus capensis *pictured on the front cover. Both of these nocturnal geckos are found in close association with termitaria.*

Although pairs of approximate ecological equivalents can be identified based on similar patterns of resource utilization, relatively few convergences are apparent among all three continents. Ecologies of putatively convergent species pairs inevitably differ markedly when scrutinized (Pianka 1971a, Pianka & Pianka 1970). In fact, the differences in the ecologies of most lizard species among the three continental desert–lizard systems are much more striking than are the similarities. It is easy to make too much of convergence and one must always be wary of imposing it upon the system under consideration.

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