50 Diversity and adaptive radiations of Australian desert lizards

Eric R. Pianka

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1. Introduction

At least 39 and probably 40 species of lizards coexist in sympatry on about a square kilometer of sandridge habitat at one site in the Great Victoria Desert in Western Australia (Pianka, 1969a). Several other sandplain sites support about 30 different species of lizards, while two sites with simpler vegetation (a pure spinifex flat and a shrubby dry lakebed) contain about 15 to 20 species. Physiognomically and climatologically nearly identical sand-ridge areas in the Kalahari desert of southern Africa support only 14 to 18 species of lizards; two Kalahari shrubby flats have 11 and 13 species (Pianka, 1971). Study plots in the flatland deserts of western North America are still more impoverished, with a maximum of 10–11 species of lizards and a minimum of 4 to 6 species depending upon vegetative structure and geography (Pianka, 1966b, 1967, 1973, 1974, 1975). Table 1 summarizes the number of species in different lizard families that coexist on these study sites. Higher taxonomic levels contribute little or nothing to differences in diversity as indicated by the fact that exactly five lizard families are represented in each continental desert-lizard system. At the generic level, Australian deserts are somewhat richer (about 23 genera) than either the Kalahari (13 genera) or North American deserts (12 genera). A relatively recent burst of speciation is thus suggested in the Australian desert saurofauna.

Quite clearly, then, the Australian deserts support an extraordinarily rich lizard fauna, very probably the richest in the entire world. What sorts of biogeographic and ecological conditions have allowed such phenomenal diversification of Australian desert lizards?

Within the vast and heterogeneous area climatologically defined as desert, various natural subregions have been recognized (Fig. 1). Boundaries of the three great sandridge deserts, the Great Sandy, Simpson and Great Victoria deserts, are generally fairly sharp, especially where these sandy subregions contact the stony desert areas such as the Gibson desert, Sturt's Stony desert, the Pilbara region and the Stony Salt Lake country of northern South Australia. Boundaries of the three major sandridge deserts are somewhat less well defined where these deserts grade into the extensive areas of sandplain that occur with some scattered sandridges in the Central Ranges and the Tanami desert of the Northern Territory. Some sandplain also occurs in the Port Hedland and Exmouth Gulf areas. In the sandy desert regions, vegetation is dominated by spinifex or porcupine grass (*Triodia*) and *Eucalyptus* trees, whereas the vegetation of stony regions is usually composed primarily of chenopodeaceous shrubs and *Acacia* trees, particularly mulga and myall. A belt of such shrubby habitat runs east–west for over 3000 km along the southern edge of the desert region (Fig. 2). Another, more northern, band of shrub-*Acacia* habitat ('mulga') in the

Table 1. Numbers of species of lizards in different familes found in sympatry on desert study areas on three continents (total number of different species in each family is listed in parentheses).

Lizard family	North America	Kalahari	Australia
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)		
TOTALS	4–11(13)	12–18 (22)	18–40 (60)

southern part of the Gibson desert and the Lake Carnegie region (the Giles Corridor) connects shrubby habitats of northern South Australia and the south-central Northern Territory with those in central Western Australia (Fig. 2). Geographic distributions of about 150 of the 350-odd described species of Australian lizards (Cogger, 1975) penetrate the boundary of the desert region as depicted in Fig. 1 and 2. Many desert lizards show various
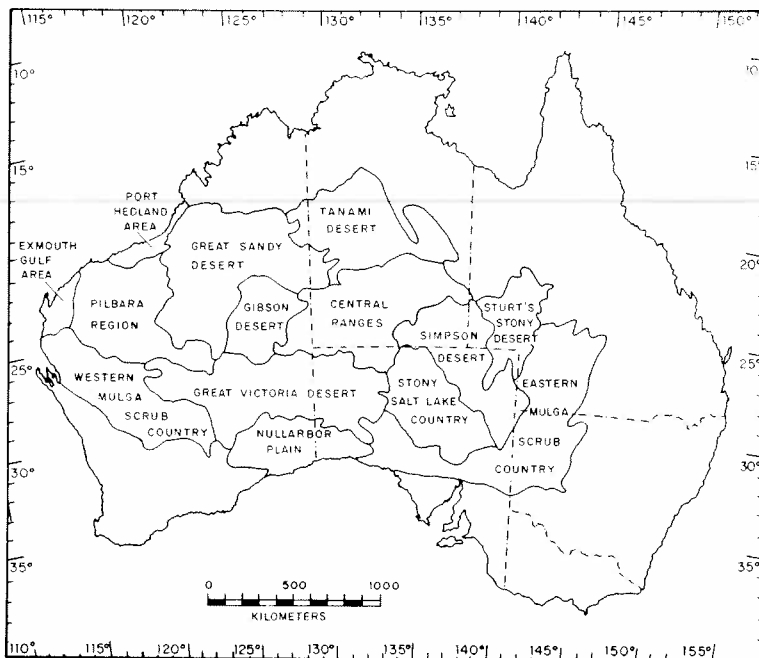

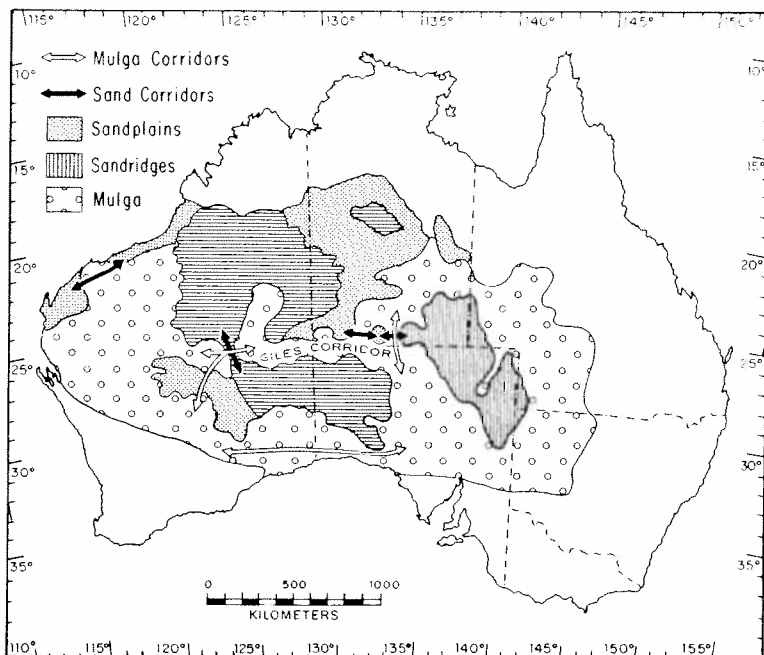Fig. 1. Subregions of the Australian desert. Compare with Fig. 2.

Fig. 2. Approximate distributions of the three major habitats to which lizards have become specialized – sandplains, sandridges, and shrub-*Acacia* or 'mulga' habitats. Several of the more important corridors between various subregions are also noted.

degrees of habitat specificity (Pianka, 1969a, 1972), with some species being restricted to sandridge habitats, others to sandplain-*Triodia* areas, and still others to shrub-*Acacia* (or mulga) habitats. Distributions of these major habitat types (Fig. 2) provide a convenient and potent background in which to interpret geographic patterns of diversity and mechanisms of lizard speciation (see section on Speciation below).

2. Structural types

As might be expected, Australian desert lizards have evolved essentially the entire range of lizard body plans (Fig. 3). Pygopodid lizards are almost entirely legless, basically snakelike creatures. Fossorial species, particularly those in the genus *Lerista*, are typically tiny with very reduced legs. Except for changes in size and slight modifications of bodily proportions, *Varanus* morphological evolution has been relatively conservative; most species have long noses, necks and bodies (the miniature and compact *V. brevicauda* is perhaps an exception). The unique spinily-armored ant specialist *Moloch horridus* is well known. A variety of saxicolous and arboreal body plans range from long-tailed slender species (*Lophognathus* and *Diporiphora*) to stout spiny-tailed forms (*Egernia depressa*) to somewhat more typical lizards (*Cryptoblepharus boutoni, Amphibolurus minor, Varanus gilleni* and *V. tristis*). Gekkonid toe pads represent still another avenue to an above ground existence (some climbing geckos, such as *Diplodactylus elderi* also have
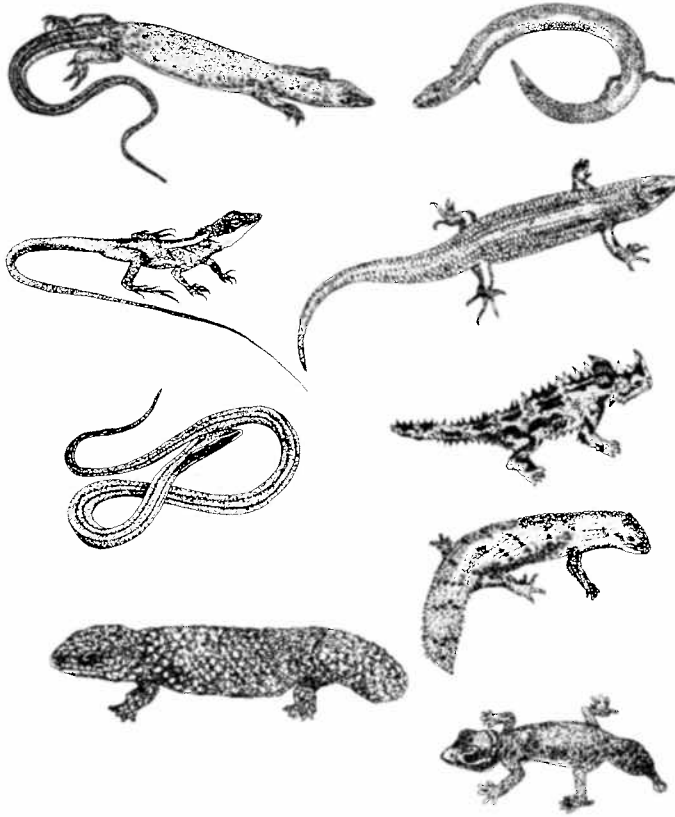
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Fig. 3. Some examples of the great diversity of lizard body plans in Australian deserts. Clockwise from top right: a *Lerista* skink, a 'typical' skink such as a *Ctenotus*, the agamid *Moloch horridus*, *Egernia depressa*, *Nephrurus levis*, *Tiliqua rugosa*, the pygopodid *Lialis burtoni*, *Lophognathus longirostris*, and *Varanus eremius*. (top left).

prehensile tails). Peculiar species such as the shingle-back or bobtailed skink (*Tiliqua rugosa*), the earless agamid genus *Tympanocryptis*, and the knob-tailed geckos (*Nephrurus*) also merit comment. Considerable morphological diversification has, of course, also taken place even among the more standard lizard-like genera, such as *Amphibolurus* and *Ctenotus*. In the latter genus and in desert geckos, relative hindleg length is correlated with the percentage of animals first encountered in the open (Fig. 4). Presumably longer legs increase running speed and facilitate the use of space farther from cover; moreover, long-legged species such as *Amphibolurus isolepis* move clumsily through dense vegetation suggesting that there is actually a premium on shorter legs in species that exploit such closed-in microhabitats. An analogous anatomical correlate of feeding ecology also exists, with lizard species that have longer heads taking larger prey items than smaller-headed species (Fig. 5).
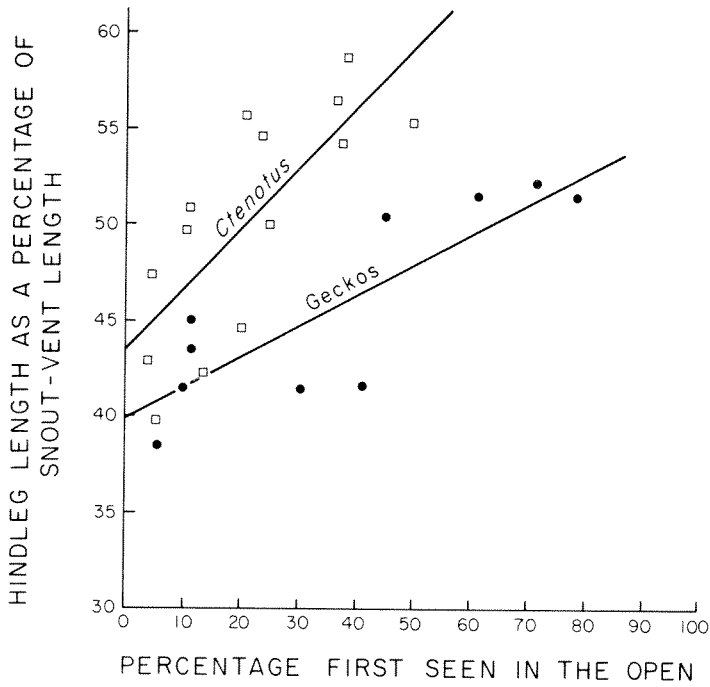
Fig. 4. Hindleg length expressed as a percentage of snout-vent length plotted against the percentage of lizards first sighted in the open spaces between plants among 14 species of *Ctenotus* skinks and 10 species of geckos.

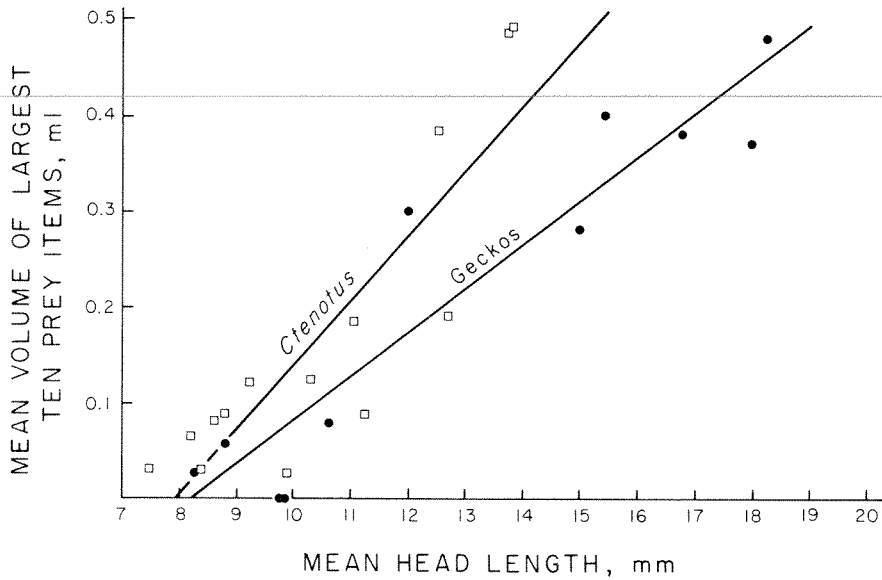

Fig. 5. Prey size is correlated with head length in most lizards.

3. Contemporary desert radiations

Some genera that have undergone adaptive radiations are listed in Table 2 along with the total number of species and the number that have penetrated the desert region. Using the range maps of Cogger (1975), I constructed approximate maps of the numbers of species in various genera occurring over different parts of the Australian continent. A major adaptive radiation into the desert has clearly occurred in the scincid genus *Ctenotus* (Fig. 6). Somewhat less extensive desert radiations have taken place in the gekkonid genus *Diplodactylus* (Fig. 7) and the scincid genus *Lerista* (Fig. 8). Although perhaps a polyphyletic genus, *Amphibolurus* has also radiated into many desert niches (Fig. 9). Varanid species densities are fairly high in the desert region, too (Fig. 10). Interesting, if somewhat more minor, adaptive radiations have also taken place in the scincid genus *Egernia* (22 species of which 8 occur in the desert region), the pygopodid genus *Delma* (6 of the 13 species are desert dwellers in at least part of their range), and the gekkonid genus Nephrurus (all 6 species enter the desert region). Most of these radiations have been facilitated by habitat specificity (see 'Speciation' below), and many of these genera have species that are restricted either to sandridge, shrub-*Acacia*, or sandplain-*Triodia*, habitats. For example, among *Nephrurus*, *N. laevissimus* is a sandridge species, *N. levis* is found on sandplains, and *N. vertebralis* occurs in shrub-*Acacia* habitats (Pianka, 1969a, 1972). Table 2 in Pianka (1972) lists many other examples. Pairs of closely related and ecologically similar species, especially in the scincid genus *Ctenotus*, also frequently occur in sympatry in the same habitat (see Table 3 of Pianka, 1972).

Table 2 Number of species in some lizard genera that have undergone adaptive radiations. The number and percentage that penetrate the desert region are also given (based on Cogger, 1975).

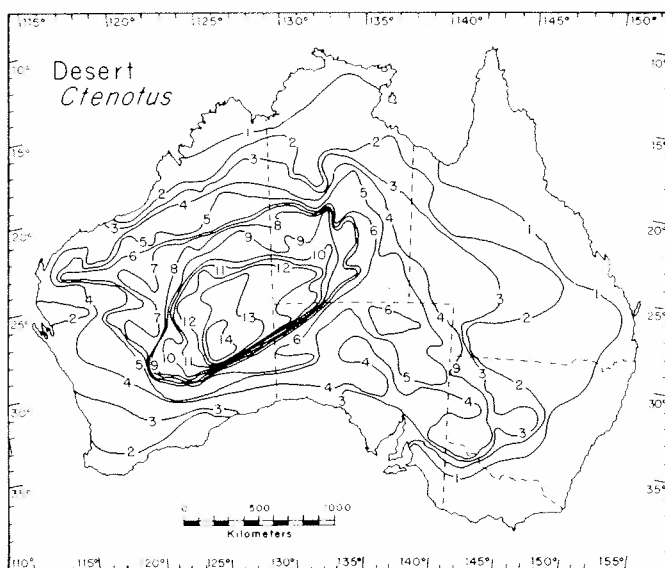| Family and genus	Total Number of species	Number of species penetrating desert	Percentage Eremaean
Agamidae			
*Amphibolurus**	26	19	73
Diporiphora	10	3	30
Tympanocryptis	6	5	83
Gekkonidae			
Diplodactylus	22	16	73
Nephrurus	6	6	100
Pygopodidae			
Delma	13	6	46
Scincidae			
Ctenotus	42	23	55
Egernia	22	8	36
Lerista	30	14	47
Varanidae			
Varanus	21	8	38

* Perhaps polyphyletic.

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Fig. 6. Species density of desert *Ctenotus* (23 species total).

4. Adaptations

Lizards are somewhat 'preadapted' to exploit desert environments. Ectothermy facilitates metabolic inactivity on both a daily and seasonal basis (via brummation and aestivation) and hence allows lizards to capitalize on scant and unpredictable food supplies. This may well contribute to their
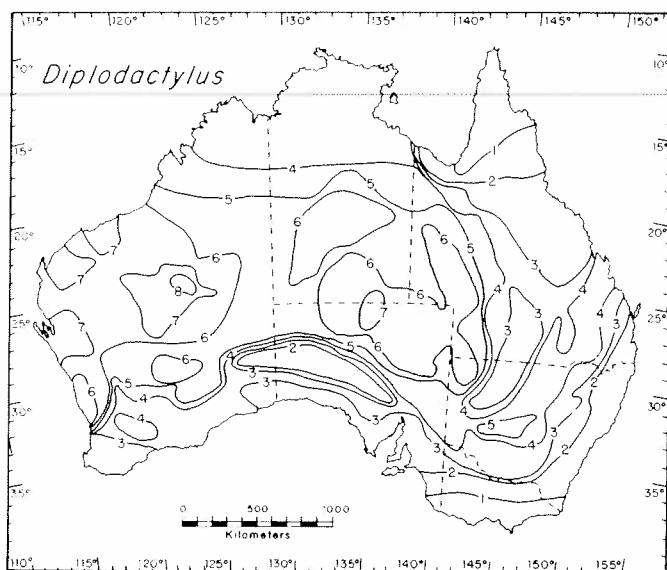

Fig. 7. Species density of *Diplodactylus* geckos (22 species total).
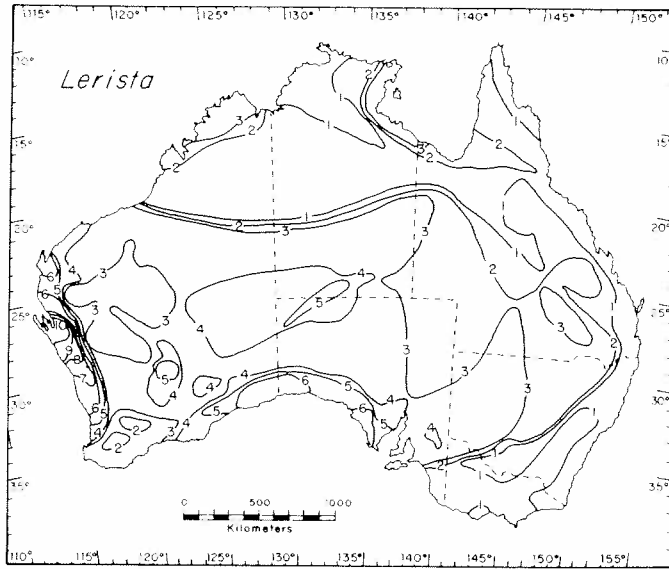
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Fig. 8. Species density of *Lerista* skinks (30 species total).

relative success over endothermic birds and mammals in arid regions (Pianka, 1967, 1978), which typically support the richest saurofaunas. By becoming inactive during harsh periods, lizards can effectively reduce temporal heterogeneity; in contrast, diurnal birds and mammals must wait out the hot mid day period at a considerably higher metabolic cost. An effective way to escape the desert heat, of course, is nocturnality; most species of pygopodids, all geckos, many skinks, as well as some bird and most mammal
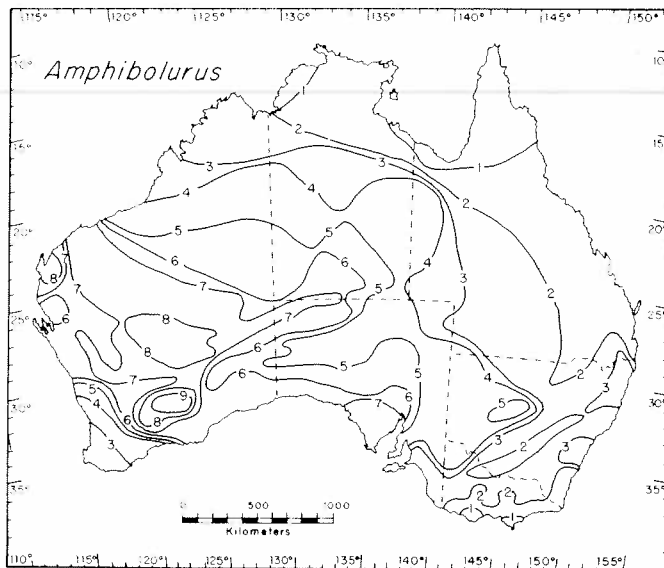

Fig. 9. Species density of the agamid genus *Amphibolurus* (26 species total).
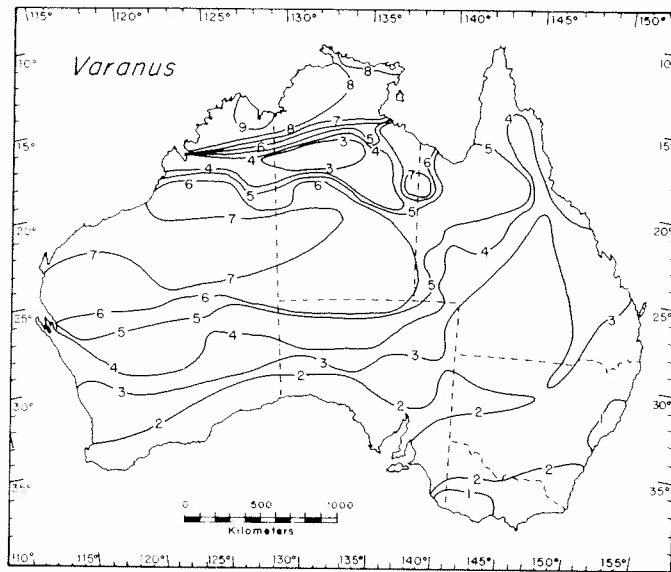
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Fig. 10. Species density of *Varanus* (21 species total).

species, are nocturnal and/or crepuscular in the Australian desert. Even so, some species of desert lizards including *Amphibolurus isolepis, A. scutulatus, A. inermis, Ctenotus leae* and *C. leonhardii* are active during the hottest times of day (indeed, the latter species has the highest known active body temperature of any skink!). Various other adaptations of desert lizards, including thermal relations and methods of water conservation such as excretion of solid uric acid are treated by Bradshaw & Main (1968), Cloudsley-Thompson (1971), Mitchell (1973), Heatwole (1970, 1976), Main (1976) and Bradshaw in this volume.

5. Speciation

Relatively few obvious geographic barriers, such as mountains, lakes, and/or rivers, exist in the Australian desert region (but see also Kluge, 1967). Rather, zones of unsuitable habitat evidently form the most effective impediments to lizard movements. The high degree of habitat specificity observed in Australian desert lizards, coupled with the extensive spatial patchiness in the mosaic of desert vegetation, led me to propose a simple model for lizard speciation based upon fluctuating boundaries among the three major habitat types to which lizards have evolved specificity (Pianka, 1969a, 1972). Habitat-specific lizard species, such as those restricted to shrub-*Acacia* ('mulga') habitats, are free to move along the appropriate corridors (Fig. 2). Long-term changes in climate and/or soils, such as movements of windblown sands, could easily break the shrub corridors, separating eastern from western patches of shrub-*Acacia* habitats and isolating shrub-specific lizards to diverge and speciate. Simultaneously, sand corridors are opened, allowing

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sand-specialized stocks to invade new sandy desert regions. Later in geological time, shifting sands could reverse the process, resulting in the closure of the sand corridors and forming isolates among sand species while reopening shrub corridors. Such alternating habitat junctures probably isolated eastern from western (and north from south in the center) populations of lizards restricted to shrub-*Acacia* habitats as well as northern from southern (in the west) and eastern from western population of species restricted to sandridge and/or sandplain-*Triodia* habitats (Pianka, 1969a, 1972). Geographic distributions observed in many species of desert lizards closely follow habitat boundaries (compare Figs. 6, 7, 8, 9 and 10 with Fig. 2), lending very considerable credance to the above hypothesis (see also range maps in Pianka, 1972 and Cogger, 1975). Somewhat similar mechanisms of speciation have been proposed for South American *Anolis* lizards (Williams & Vanzolini, 1966; Vanzolini & Williams, 1970) as well as for Amazonian birds (Haffer, 1969).

6. Species diversity

The efficient process of speciation described above could quite conceivably generate exceedingly high lizard diversity in a relatively short period of time. However, mechanisms leading to the origin of numerous new species need not result in their maintenance. Clearly coexistence of so many species requires appropriate ecological conditions such as spatial heterogeneity, climatic stability, high productivity, and/or a great diversity of available microhabitat and food resources (Pianka, 1966a).

Two areas can differ in the numbers of species they support in basically only three different ways (MacArthur, 1965, 1972). First, a site with a greater variety of available resources will support more species than one with fewer different resources even if the average consumer species in each community uses the same range of resources and shares these resources to a comparable extent. Secondly, two sites with exactly the same range of available resources can still differ in numbers of species provided that members of one community are more specialized in their use of resources (that is, they have narrower niche breadths). Last, areas with otherwise comparable resource bases and patterns of utilization may still differ in diversity with differences in the amount of resource sharing or niche overlap. All else remaining equal (namely niche breadths, etc.), greater overlap will allow more species to 'pack in' on a given resource base. Hence diversity should increase with the variety of available resources, with the extent of specialization in resource utilization, as well as with the amount of tolerable niche overlap. Analyses of the niche relationships of desert lizards on the three continents (Pianka, 1973, 1974, 1975) showed no intercontinental trends in average niche breadth. Although some species on each continent are food and microhabitat specialists while others are more catholic in their requirements, the diversity of foods eaten by an average species is almost as great in Australia as in North America. Microhabitat niches are actually
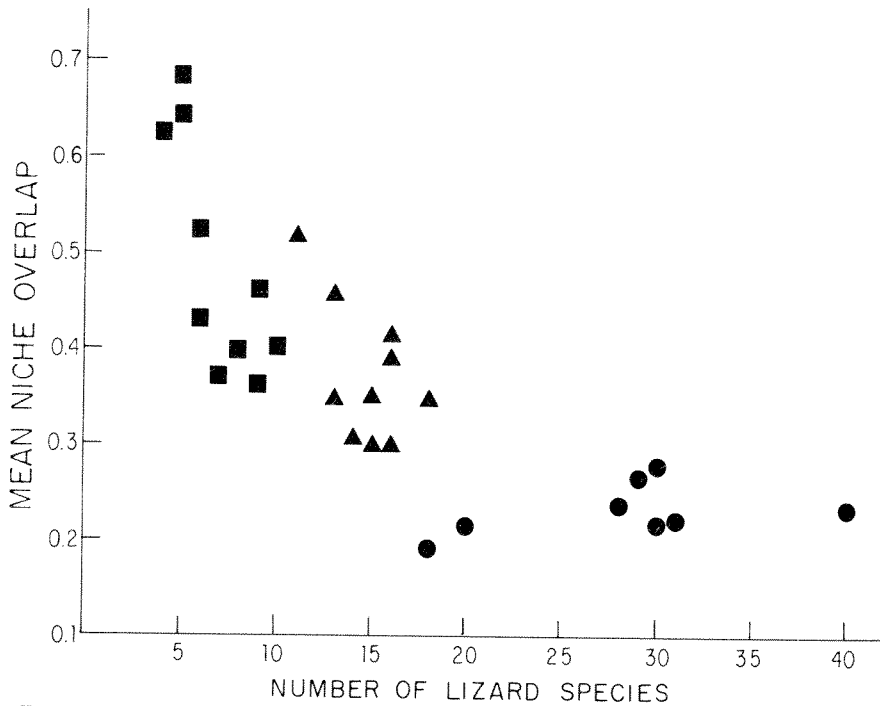
Fig. 11. Average niche overlap plotted against estimated number of lizard species (continents coded by shape—squares, North America; triangles, Kalahari; circles, Australia).

broader in the Kalahari and Australia than they are in North American lizards. Average niche overlap is not greater in more diverse saurofaunas but rather varies inversely with lizard diversity (Fig. 11). Hence the higher diversity of the Australian saurofauna does not stem either from conspicuously narrower niches or from greater niche overlap on that continent. Rather, the major factor implicated in the high diversity of Australian desert lizards is the size of the niche space actually used by lizards (Pianka, 1975, 1978). The diversity of foods eaten by Australian desert lizards is no greater than those exploited by all the lizards in the Kalahari or North America, but the variety of microhabitats used and times of activity are both noticeably greater in the two deserts of the southern hemisphere (Table 3).

Several major factors that contribute to the high diversity of desert lizards in Australia are considered briefly below.

Table 3. Diversities of resources used by entire saurofaunas along three niche dimensions (means for all sites on each continent – ranges in parentheses).

Continent	Food	Microhabitat	Time of Activity
North America	0.32 (0.22–0.45)	0.19 (0.15–0.24)	0.23 (0.17–0.33)
Kalahari	0.24 (0.10–0.31)	0.46 (0.22–0.62)	0.46 (0.34–0.57)
Australia	0.31 (0.18–0.41)	0.48 (0.34–0.59)	0.48 (0.37–0.55)

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6.1. *Usurpation of ecological roles of other taxa*

Some Australian desert lizards have clearly usurped the ecological roles occupied by other taxa on other continents. Thus pygopodids and varanids replace certain snakes and mammalian carnivores such as the kit fox (Storr, 1964; Pianka, 1969a). Other exceedingly tiny Australian lizards such as *Menetia* and certain *Lerista* are essentially insect-like in their ecologies, living in litter and eating extremely small insects. However, even when these non lizard-like lizards are subtracted from the total species numbers, Australian desert saurofaunas are still much more diverse than those of the other two continents. Hence there are more species of lizard-like lizards in Australia.

Elusive, but doubtlessly important competitive interactions also occur with avifaunas. Australian desert areas support fewer species of ground-foraging insectivorous birds than do comparable sites in the Kalahari (Lein, 1972; Pianka & Huey, 1971), which may well mean that competition between lizards and birds is less intense in Australia than in southern Africa. The relationships between bird species density and lizard species density differ strikingly among the three continents (Fig. 12), implicating fundamental differences in community structure.
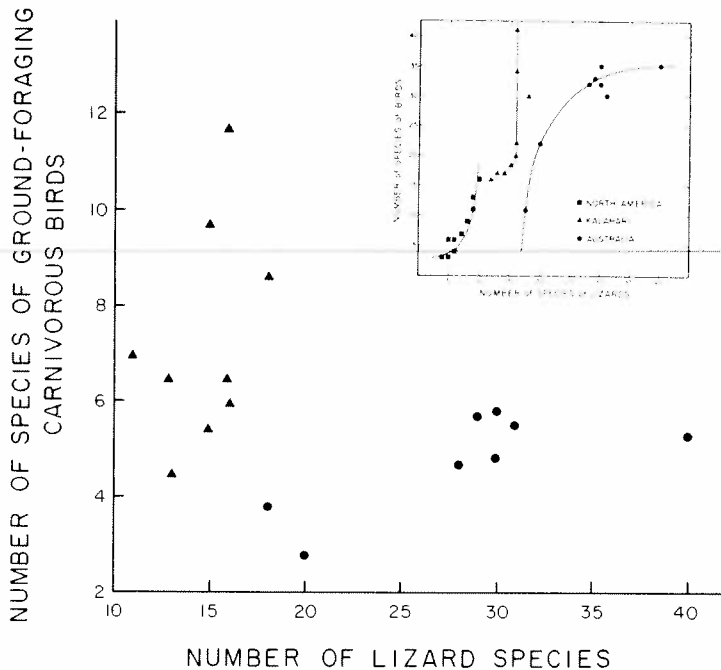

Fig. 12. Two plots of bird species numbers versus the number of lizard species. Inset shows total avifaunas whereas the larger graph plots only ground-foraging carnivorous birds.

6.2. *The structure of spinifex*

Another important factor contributing to lizard diversity in Australia is the very existence of the unique hummock-grass plant life form (Beard, 1976; Pianka 1969a). As indicated in the introduction, a pure *Triodia* grass flat supports at least 16, and probably a full 20, different species of lizards, including 6–7 species of *Ctenotus* alone. Spinifex tussocks are extraordinarily well suited for lizard inhabitants, providing as they do not only protection from predators and the elements but also a rich insect food supply. Certain lizard species, including *Ctenotus piankai*, *Delma fraseri* and *Diplodactylus elderi*, appear to spend almost all their time within dense *Triodia* tussocks. Others, like *Ctenotus grandis* and *C. quattuordecimlineatus*, tend to occur around the edge of spinifex tussocks. Still other species (*Amphibolurus isolepis* and *Ctenotus calurus*, for example) frequent the more open spaces between tussocks (Pianka, 1969b, 1971d).

6.3. *Nocturnality*

Relatively large numbers of species of nocturnal lizards exist in the Australian desert (an average study site supports a full ten nocturnal species in Australia compared with only five in the Kalahari and one or two in North America). Australian nocturnal lizards include geckos, pygopodids and skinks (indeed, perhaps the only skinks known to have elliptical pupils are some of the Australian nocturnal *Egernia*).

It is instructive to compare the lizard faunas of chenopodeaceous semi-shrub sites on each of the three continents (Table 4). The vegetation on these three sites, consisting of low microphyllous chenopod shrubs, is virtually identical in structure in all three desert-lizard systems. Only 5 species are present in North America (6 species occur in the south where the terrestrial nocturnal gecko *Coleonyx* is added), whereas 13 species inhabit the Kalahari site and a full 18 species presumably occur on the Australian area (Pianka, 1969a, 1971a). Subtracting the species of lizard that are insect-like (*Mabuya variegata* and *Menetia greyi*), mammal-like (*Varanus gouldi*), subterranean (*Lerista timidus*) and nocturnal (4 species in the Kalahari, a full 8 species in Australia!), to leave only truly lizard-like lizards that are both diurnal and terrestrial* yields numbers of species that are much more comparable among continents: North America (5), Kalahari (8) and Australia (7).

6.4. *Habitat specificity*

The Kalahari desert and the Great Victoria desert in Western Australia both have summer rainfall regimes and characteristic long stabilized red sandridges. Indeed, in their physical aspects (topography and climatology), the two regions are so similar that, without recourse to their different floras and

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* *Mabuya striata* is semi-arboreal.

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Table 4. Lizard faunas on three chenopodeaceous shrubby sites with very similar vegetative structures. Very crudely approximate ecological equivalents are aligned horizontally. Nocturnal species listed in the bottom half of table.

North America	Kalahari	Australia
Cnemidophorus tigris	⎧Mabuya occidentalis ⎫ ⎨Eremias lugubris ⎬ ⎩Eremias namaquensis⎭	⎧Ctenotus schomburgkii ⎩Ctenotus leonhardii
Uta stansburiana	Eremias lineo-ocellata	Amphibolurus isolepis
Phrynosoma platyrhinos	Agama hispida (?)	Moloch horridus*
Crotaphytus wislizeni	Mabuya striata sparsa	⎧Amphibolurus inermis ⎩Amphibolurus reticulatus
Callisaurus draconoides	Meroles suborbitalis	Amphibolurus scutulatus
	Ichnotropis squamulosa	
	Mabuya variegata	Menetia greyi*
		Lerista timidus*
		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
		Sphenomorphus richardsoni

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

faunas, I would certainly be hard pressed to distinguish between the continents. Yet Australian desert lizards recognize more habitats than Kalahari lizards. For example, a full ten species are restricted to the sandridges in Australia whereas only a single Kalahari species has become so specialized. Other species are restricted to sandplain and shrubby areas in Australia. This extensive habitat specificity contributes greatly to the diversity of species on the more complex study areas in Australia with more than a single 'habitat'. The perplexing question of why haven't Kalahari lizards evolved as much habitat specificity as the Australian lizards remains unresolved. Perhaps historical factors, especially the ages of the two deserts, are involved. MacArthur (1965) may very well have been right when he argued that there is not necessarily an upper limit on the horizontal component of diversity (so-called 'between-habitat' diversity or β-diversity of Whittaker, 1965).

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