

Long-Term Changes in Lizard Assemblages in the Great Victoria Desert

Dynamic Habitat Mosaics in Response to Wildfires

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I. BACKGROUND

The Australian deserts house the most diverse lizard assemblages on planet Earth. Nowhere else can so many kinds of lizards be found together—at least 47 species (now 53 species; see Appendix) coexist at a sandridge site in the Great Victoria Desert. These include agamids such as the ant-eating “thorny devil,” *Moloch horridus*; 6 species of predatory monitor lizards such as the gigantic perentie, *Varanus giganteus*; a dozen species of exquisitely beautiful nocturnal geckos; more than a dozen wary and secretive skinks; and many other species including several snake-like, flap-footed, legless pygopodid lizards.

At least a dozen factors contribute to the very high lizard diversity in the

Australian deserts (Pianka, 1989). One of the most important is frequent natural wildfires, which generate a patchwork of habitats in different states of recovery, each of which favors a different subset of lizard species (Pianka, 1992). Inland Australia is one of the last remaining areas where natural wildfires remain a regular and dominant feature of an extensive semi-pristine natural landscape largely undisturbed by humans. In this region, an important fire succession cycle generates spatial and temporal heterogeneity in microhabitats and habitats. Habitat-specialized species can go locally extinct within a given habitat patch (fire scar) but persist in the overall system by periodic reinvasions from adjacent or nearby patches of suitable habitat of different age. Such spatial-temporal regional processes facilitate local diversity. This system is currently being studied at the local level in the field in Western Australia and at the regional level at the University of Texas at Austin using aerial photography and Landsat multispectral satellite (MSS) imagery. Satellite imagery offers a powerful way, heretofore underutilized by biologists, to acquire regional-level data on the frequency and phenomenology of wild fires and thus on the system-wide spatial-temporal dynamics of disturbance.

Compared to Australia, North American deserts are impoverished, with a mere dozen species of lizards (Pianka, 1986). On 12 North American study sites, lizard species diversity¹ ranges from 1.4 to 4.9 with an average of 3.0. In the Kalahari semi-desert of southern Africa, only 20 species occur (at 10 Kalahari sites, lizard diversity varies from 2.5 to 8.7; mean = 6.3). Ten study sites in Australia's Great Victoria Desert support from 15 to 47 species of lizards (now 53 species; see Appendix)—species diversity there ranges from 6.2 to 14.4 (mean = 8.6). Many species of Australian lizards are quite uncommon. There are two components to species diversity: (1) number of species, or species richness, and (2) equitability of relative abundances, which can be measured by the ratio of observed diversity divided by maximum possible diversity (i.e., species richness). Averages of such ratios for all study sites in North America, the Kalahari, and Australia, are, respectively, 0.44 (SD = 0.19), 0.42 (SD = 0.10), and 0.31 (SD = 0.11). Equitability is lower in Australia than in either of the other continental desert-lizard systems, an indication that there are more rare species in Australia than in North America or in the Kalahari.

Why are the Australian deserts so rich in lizard species? Explaining this high diversity, and understanding what goes on between and among component species, is exceedingly difficult. How do so many species of lizards avoid competition and manage to coexist in the Australian desert? How do they partition resources such as food and microhabitats? What historical and ecological fac-

¹All diversity and niche breadth measurements reported here were calculated from relative abundances or resource utilization spectra using the reciprocal of the diversity index of Simpson (1949).

tors have led to the evolution and maintenance of such high biodiversity? Ecologists still know surprisingly little about exactly how diverse natural ecological systems function—such ecological understanding is much needed and will obviously be crucial to our own survival as well as that of other species of plants and animals. In fact, the Australian deserts may well offer the last opportunity to study the regional effects of disturbance on local diversity.

In the Great Victoria Desert (Fig. 1), the rusty-red sands are rich in iron and laced with long, undulating, stable sandridges parallel to prevailing winds. Evergreen marble gum trees (*Eucalyptus gongylocarpa*) with smooth white bark adorn this landscape. Various species of *Acacia* and *Eremophila* shrubs, plus shrub-like large mallee, as well as an occasional mulga tree, are also scattered

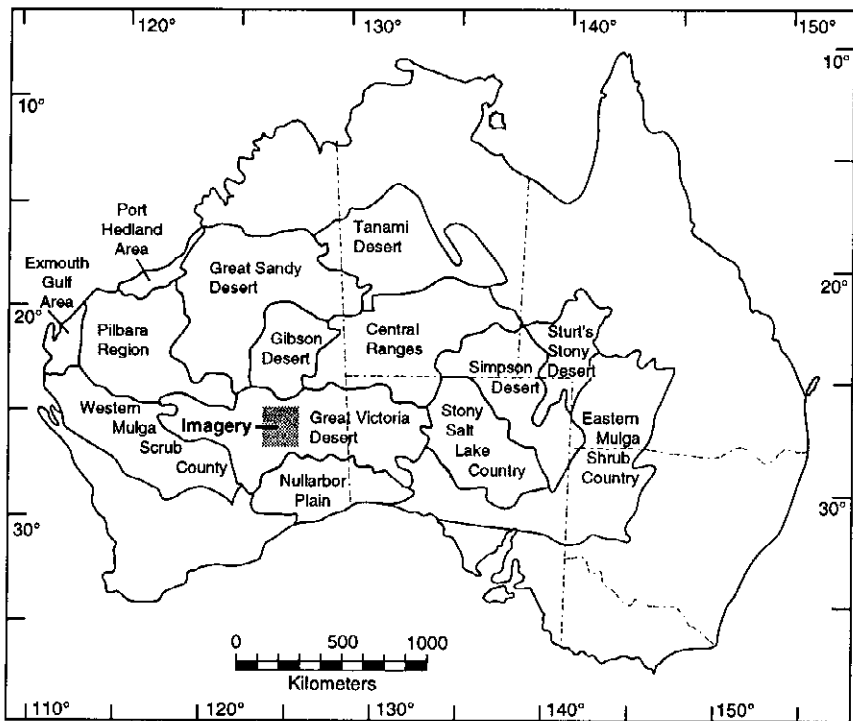


FIGURE 1. Map showing locations of various arid zone regions within Australia. The Great Victoria Desert stretches from western South Australia over 1000 kilometers into south-central Western Australia. Other areas referred to in the text include the Central Ranges and Tanami Desert in the Northern Territory and the Simpson Desert (southeastern Northern Territory, northwestern South Australia, and southwestern Queensland). Approximate position of imagery is shown. See color plate (Fig. 2) facing page 196.

about. The dominant ground cover is porcupine grass or spinifex (*Triodia basedowi*), a fire-prone perennial grass that grows in hummocks or tussocks. Rain is infrequent and clear, blue skies prevail most of the time.

II. FIRE ECOLOGY IN SPINIFEX GRASSLANDS

Spinifex tussocks are almost perfectly designed for combustion, consisting of hemispherical clumps of numerous blades of dry grass filled with flammable resins that are rolled into hollow match-stick sized cylinders, loosely interpenetrating one another and laced with ample air spaces among blades. Spinifex is nearly optimal tinder (Burrows *et al.*, 1991) and has been called an "ideal pyrophyte" (Pyne, 1991). Following a fire caused by lightning, sands are frequently wetted by thundershowers, facilitating rapid regeneration of spinifex, both from live roots as well as from seedling establishment (Burbidge, 1943). Newly-burned areas are usually quite open with extensive bare ground and tiny, well-spaced, clumps of *Triodia*. Unburned patches, in contrast, are composed of large ancient tussocks, frequently quite close together with little open space between them. As time progresses, *Triodia* clumps grow, simultaneously increasing the amount of combustible material and reducing gaps between tussocks. Both increase the probability that a new fire will spread. Marble gum trees are fire-resistant and usually survive a hot but brief ground fire carried by the exceedingly combustible spinifex grasses. The above-ground parts of mallees, however, burn but the root bole survives and sends up new growth after a fire.

Deserts in other regions, such as the Sonoran desert of North America, do not usually accumulate enough combustible material to carry fires. Fires do, however, occur regularly in the Kalahari semidesert of southern Africa, an open savanna woodland. Fires are a predictable event in arid Australia, particularly in spinifex grasslands (Catling and Newsome, 1981; Gill, 1975; Gill *et al.*, 1981; Pyne, 1991; Winkworth, 1967). Bush fires are usually started by lightning, raging completely out of control for weeks on end across many square kilometers of desert. Thunderstorms and lightning are regular during summer. Lightning-induced fires are most frequent during the months of November and December (Ralph, 1984). Over the 35-year-period from 1950 through 1984, approximately 60% of natural wild fires in the Northern Territory were estimated to have been caused by lightning (Griffin *et al.*, 1983, 1988). During that same period, there was a movement of aborigines out of the bush, reducing the numbers of fires started by humans. Aborigines have increasingly been moving back to reside on tribal lands, except that nowadays aborigines seldom walk, preferring to ride in vehicles. They still set fires but seldom very far away from roads. Most early explorers and historians of Australia commented on the extent

to which the aborigines exploited fire. Spinifex grasses give off dark smoke that can be seen from afar. Australian aborigines used fire to send long-distance smoke signals, to manage habitats and keep terrain open, as well as to facilitate capture of various animals for food. Some think that the extensive grasslands in Australia were formed and maintained by regular aboriginal burning over many thousands of years and that aborigines acted to select members of plant communities for resistance to fire or for an ability to come back quickly following a fire.

Some Australian land management authorities are attempting to mimic aboriginal burning patterns to create a spatial mosaic of fire-disturbed habitat patches of differing ages and sizes. By acting as fire breaks, small burns prevent extensive burns from taking place which homogenize the landscape (Minnich, 1983, 1989).

All spinifex communities are in a state of cyclic development from fire to fire (Winkworth, 1967). In the Northern Territory, only about 20% of some 150,000 km² of spinifex habitat is in a "mature" climax state, with the other 80% either in regenerative stages following fires or in a degenerative state owing to drought. A single fire in this region covered about 10,000 km² (Winkworth, 1967). An even larger fire in 1982–1983 burned 30,000 km², an area more than twice the size of the state of Massachusetts. Over the 35-year-period from 1950 through 1984, an average of 143 fires per year occurred in this region, most set by lightning (Griffin *et al.*, 1983; Ralph, 1984). Such an exceedingly high level of disturbance requires a rapid rate of recovery. In the Northern Territory, fire-return intervals are short. Some areas will carry another burn within 4–5 years (Perry and Lazarides, 1962). Burned plots converge on their original state quickly; in 7 years, dry weight production of spinifex totalled 823 kilograms per hectare, approximately one quarter of the standing crop of "mature" stands at a nearby site (Winkworth, 1967). Fire-return intervals are longer in the Great Victoria Desert due to lower precipitation. Time required for a burned stand to reach maturity is a function of precipitation and can require 20–25 years or longer. The probability of a burn is directly proportional to accumulated precipitation since the last fire and generally increases with the time since the last burn.

Spinifex fires in the Central Ranges and the Tanami Desert of the Northern Territory were also studied by Griffin *et al.* (1983, 1988) and Allan and Griffin (1986). Using aerial photography, every identifiable fire in the southern half of the Northern Territory between 1950 and 1984 (more than 5000 fires in some 750,000 km²) was mapped. Certain informative relationships between fire patch dynamics and rainfall were discovered. At wetter, more productive areas, fires were not only more frequent and more numerous but also patches were more variable in size and tended to be younger on average. Following periods of low rainfall, fires were less frequent and homogeneously smaller. Fuel load recovery is a function of time and total rainfall. Cumulative millimeters of precipitation is a useful temporal productivity metric against which to calibrate

fires and vulnerability to fire. Approximately 63 cm of rain are necessary for a site to accumulate sufficient fuel to burn again under extreme summer conditions (Griffin *et al.*, 1988).

III. FIRE GEOMETRY

Bush fires generate a spatial mosaic of patches of habitat at various stages of post-fire succession. The geometry of burns is rich in detail and exceedingly varied (Fig. 2). As a regular agent of disturbance, fires contribute substantially to maintaining a spatially heterogeneous patchwork of habitats, hence fostering diversity in Australian desert lizards (Pianka, 1986, 1989). Fires vary considerably in intensity and extent.

Grassland fires burn along two "fronts" that are essentially unidimensional, each at approximately a right angle to prevailing winds burning away from one another. The "backfire" burns slowly into the wind, whereas the "headfire" burns faster, racing with the wind. Airborne flaming materials, termed "firebrands," sometimes jump over unburned areas to rekindle new fires on the downwind (leeward) side of a fire, sometimes resulting in establishment of multiple fire fronts (these can extinguish one another when one runs into another's swath).

Fires frequently reticulate, missing an occasional isolated grass tussock or even large tracts embedded within or immediately adjacent to burns (Fig. 2). Upon ignition, isolated grass tussocks generate an egg-shaped thermal field. At low wind velocities, isotherms for such fields are symmetric and close to combustibles, but as wind speed increases, thermal fields become asymmetric and extend farther out, especially downwind. If other tussocks are within such a field's threshold temperature for ignition, they too are lighted and the fire spreads. Due to the geometry of such thermal fields, fires tend to burn along broad continuous fronts at low wind velocities, whereas at higher wind velocities elongate narrow tongues of flame are produced. Fires are also more likely to reticulate at higher wind velocities due to these elongate tongues of flame.

Previously burned areas with sparser vegetation act as fire breaks. Sandridges and termitaria create smaller vegetationless areas that can also stop fires from spreading but with fundamentally different geometries and at much more local spatial scales. "Sleepers," embers created from burning hard wood of *Eucalyptus*, lay dormant in burned areas. Some of these hot coals at the edges re-ignite new secondary bush fires days or even weeks later when strong winds come up. Interesting lacinated patterns are generated that constitute qualitatively and spatially different sorts of refuges.

Major factors that determine the frequency, extent and geometry of grassfires include temperature, humidity, precipitation, combustibility, plant biomass and



0 25 50
Kilometers

FIGURE 2. Landsat false color satellite image showing the habitat mosaic. Fire scars are light beige and pale green. Dry lakebeds are blue and white (Lake Throssell and Lake Yeo). Sandridges are fine striations. Nonburnable shrub-Acacia habitats are brown and dark spots.

spatial distribution, natural firebreaks, and, of course, winds, which as explained above, are of utmost importance. With a lot of combustible material, fire fronts burn virtually everything in their paths, leaving behind almost completely burned swaths. However, when grass is green or wet and therefore less flammable and/or if tussocks are widely spaced and/or if winds are weak, fires may falter and die out. Strong winds, by supplying oxygen, "feed" fires making them burn both faster and hotter. With sufficient wind, even a relatively uncombustible area can burn. With little or no wind, however, a fire may not "take" even in a fairly combustible situation. Fires often die out at night when lower temperatures cause relative humidity to increase and winds to die down. Headfires will sometimes burn even when backfires will not. Studies of thousands of forest fires have shown that their extent is directly proportional to wind velocity (Barrows, 1951), allowing area to be used as an after-the-fact, indirect estimate of wind speed at the time of a burn. Moreover, wind direction can usually be estimated from the long axis of a fire scar.

The extent to which grassfires reticulate appears to vary between geographic regions with differences in vegetation structure. In the savanna woodland of the Kalahari semidesert in Botswana, southern Africa, for example, fires are frequent but continuous, seldom reticulating (Short *et al.*, 1976, Plate 342, p. 377). Because Australian spinifex habitats are relatively more open and because they contain various sorts of natural firebreaks, fires in those habitats reticulate more than they do in other more homogeneous areas. The unique growth form and extreme flammability of spinifex doubtlessly contributes to fire lacination in Australia as well. Intercontinental differences in winds could also be crucial in the generation of different fire geometries.

Throughout this process of fire succession, cover, microhabitats, and associated food resources change gradually along with reflectance properties. The prey spectrum for a recently burned area differs from those of more mature areas with relatively fewer termites but comparatively more spiders (Pianka, 1989). Presumably, by destroying litter and spinifex, fires reduce cellulose availability, hence reducing food supplies for termites. Why spiders increase in abundance is unknown. Through succession, relative abundances of various lizard species fluctuate along with such changes in available resources, with some common species becoming quite rare and vice versa. A particular habitat-specialized species can go extinct within a given area but, by surviving in an adjacent patch of appropriate habitat, still persist in the region. Such regional processes facilitate local diversity because periodic dispersal from such "source" habitats and recolonization of "sink" habitats allows such species to continue to exist as a metapopulation in the overall landscape (Pulliam, 1988; Pulliam and Danielson, 1991). An appropriate mix of subdivision or patchiness plus disturbance and dispersal can promote coexistence in competitive systems (Kareiva, 1990).

Combined effects of fires on lizards and their microhabitats are drastic yet

exceedingly heterogeneous in space (Caughley, 1985; Fyfe, 1980; Longmore and Lee, 1981; James, 1994). Certain lizard species are arboreal or associated with trees. These species are often relatively unaffected by fire. Many or even most individual lizards sometimes survive such burns, although survivorship is doubtlessly reduced for some time afterwards. Fires also attract hawks and crows which feed on fire-killed animals and take advantage of the lack of cover to catch survivors. Ectothermy may allow many lizards to become inactive and stay underground for a month or more until the vegetation and insect fauna recover.

IV. LIZARD STUDIES

Over a 16-month period from late 1966 to early 1968, I censused lizard faunas at seven study sites within the Great Victoria Desert plus one site (the A-area) slightly outside (Pianka, 1969, 1975, 1986). Study sites were chosen to represent various vegetation types and included a dry lakebed shrub-*Acacia* (mulga) site, ecotonal sites between shrubby and spinifex habitats, flat sandplain spinifex sites both with and without trees and shrubs, as well as two sandridge sites. Half a dozen undescribed species of *Ctenotus* skinks were discovered. The number of lizard species (lizard species richness) in the saurofaunas of these sites varied from 15 to 39—lizard species diversity varied between 6.3 and 11.3 (Simpson's index). Considerable habitat specificity was evident, with 8 species being restricted to shrub habitats, 10 species to sandplain spinifex habitats, and 8 species to sandridges (Pianka, 1969, 1972). Still other species are habitat generalists occurring in several habitat types.

During the past quarter of a century, my assistants and I have monitored the saurofauna at a flat sandplain study site located about 38 km east of Laverton, Western Australia (appropriately designated the L-area). The vegetation of the L-area is complex, consisting of a spinifex understory with scattered marble gums, mallee, and small *Acacia* shrubs plus an occasional mulga tree. During our first visit in 1966–1968 (hereafter referred to as 1967 for brevity), the presence of many large mature spinifex tussocks suggested it had been at least a decade since the area burned (an old reticulated fire scar is visible in a 1959 high-altitude aerial photograph). A 1969 high-altitude aerial photograph shows that a fire occurred sometime between early 1968 (when we last visited the area) and September 1969. This fire scar was lacinated, leaving behind numerous unburned refugia of varying sizes and shapes, ranging from single tussocks to areas covering many hectares. A decade later, I returned to the L-area in June 1978 and censused lizards until April 1979 (for brevity, this 1978–1979 sampling period will be referred to as 1978).

Over the decade between 1967 and 1978, lizard species richness increased

from 30 to 34, but lizard species diversity decreased from 9.9 to 6.2. Another fire burned most, but again not all, of the L-area in 1983, again leaving behind many unburned refugia of varying sizes and shapes. A third, more extensive sampling effort was undertaken during late 1989 through mid 1992 when lizard species diversity was again found to be 9.9 (the L-area is now ready to burn again). Over the past 28 years, some 37 different species of lizards have been collected at the L-area (Table I), many of which are rare. One species, a large nocturnal skink (*Egernia kintorei*), had not been seen since 1967, when it was observed just once. Another large diurnal skink, *Tiliqua occipitalis*, was not seen prior to 1990 and has been observed only twice since then. Relative abundances of many lizard species have fluctuated dramatically over this period (Table I). The abundant agamid *Ctenophorus isolepis* appears to have first increased and then decreased in abundance. Five species that have apparently increased in abundance from 1966 to 1991 are *Ctenopus calurus*, *C. quattuordecimlineatus*, *C. schomburgkii*, *Lerista bipes*, and *Diplodactylus conspicillatus*. Four species that appear to have decreased in abundance over that 25-year interval include *C. grandis*, *C. helenae*, *Gehyra purpurascens*, and *Rhynchoedura ornata*.

A detailed comparative analysis of relative abundances and patterns of resource utilization was undertaken for the L-area data sets of 1966–1968 and 1978–1979 (Pianka, 1986).² Patterns of resource utilization in 1978 were compared with comparable information gathered in 1967. Considerable species-specificity and substantial fidelity in the use of food types and microhabitats was evident among many of these Australian desert lizards. For example, some species are termite specialists, whereas others virtually never touch termites. The ant specialist *Moloch horridus* consumed nothing but ants during both 1967 and 1978. Diets of saurophagous species such as the pygmy monitor *Varanus eremius* also varied little. Diet and microhabitat utilization patterns of most species, even those of generalists such as the gecko *Gehyra variegata*, proved to be fairly consistent in time, too. Overall estimates of resource utilization based upon all specimens of each species varied relatively little between 1967 and 1978. Also, site-to-site comparisons show that each species is typically its own closest neighbor in niche space. A few shifts in resource utilization were evident in certain species, however (see Pianka, 1986, for details).

On the L-area, 530 lizard specimens representing 29 species were collected in 1967 (Table I). Tracks of the wary and large monitors *Varanus gouldi* and *V. giganteus* were regularly noted, although no specimens of these very wary lizards were actually sighted. Specimens of the elusive spinifex gecko *Diplodactylus elderi* were not collected either, but this species was listed as “highly expected on the basis of geographic range, habitat, autecology, and micro-

²Unfortunately, due to lack of funds I have not yet been able to finish such an analysis for lizards collected during 1989–1992.

TABLE 1 Relative Abundance (Percentages) of Lizard Species on the L-Area in 1966–1968, 1978–1979, 1989–1992, and 1966–1992

	1966–1968	1978–1979	1989–1992	1966–1992
<i>Ctenophorus inermis</i>	1.69	0.32	0.20	0.44
<i>Ctenophorus isolepis</i>	10.34	33.82	12.37	20.31
<i>Moloch horridus</i>	1.69	0.57	0.25	0.56
<i>Pogona minor</i>	1.50	0.77	0.20	0.59
<i>Varanus eremius</i>	0.56	0.83	0.50	0.64
<i>Varanus giganteus</i>	tracks	tracks	tracks	tracks
<i>Varanus gouldi</i>	tracks	0.26	0.60	0.42
<i>Varanus tristis</i>	1.13	1.15	0.20	0.68
<i>Ctenotus ariadnae</i>	0.94	0.70	1.80	1.27
<i>Ctenotus calurus</i>	2.07	9.38	15.02	11.18
<i>Ctenotus grandis</i>	8.46	2.49	0.85	2.47
<i>Ctenotus helenae</i>	9.96	1.98	1.05	2.56
<i>Ctenotus pantherinus</i>	1.50	1.34	2.25	1.81
<i>Ctenotus piankai</i>	0.38	0.19	2.40	1.29
<i>Ctenotus quattuordecimlineatus</i>	8.65	11.68	20.78	15.72
<i>Ctenotus schomburgkii</i>	1.32	2.55	4.21	3.20
<i>Cryptoblepharus plagiocephalus</i>	5.08	3.38	3.21	3.52
<i>Egernia inornata</i>	0.38	0.13	0.15	0.17
<i>Egernia kintorei</i>	0.19	0.0	0.0	0.02
<i>Egernia striata</i>	6.96	4.34	4.11	4.57
<i>Lerista bipes</i>	1.13	3.38	8.06	5.37
<i>Lerista muelleri</i>	0.0	0.38	1.05	0.66
<i>Menetia greyi</i>	0.56	0.26	4.06	2.15
<i>Morethia butleri</i>	0.0	0.06	0.10	0.07
<i>Tiliqua occipitalis</i>	0.0	0.0	0.10	0.05
<i>Delma butleri</i>	0.0	0.26	0.35	0.27
<i>Delma nasuta</i>	0.0	0.0	0.05	0.02
<i>Lialis burtonis</i>	0.38	0.13	0.25	0.22
<i>Pygopus nigriceps</i>	1.50	0.19	0.20	0.37
<i>Diplodactylus conspicillatus</i>	1.13	1.72	3.11	2.32
<i>Diplodactylus elderi</i>	0.0	0.26	0.15	0.17
<i>Diplodactylus stenodactylus</i>	0.0	0.13	0.05	0.07
<i>Gehyra purpurascens</i>	19.43	11.89	5.86	10.57
<i>Gehyra variegata</i>	2.0	1.00	0.50	0.24
<i>Heteronotia binoei</i>	0.19	0.06	0.10	0.10
<i>Nephurus levis</i>	1.13	0.26	2.90	1.66
<i>Rhynchoedura ornata</i>	9.40	4.08	2.85	4.18
Total number of lizards	530	1565	1997	4092
Lizard species diversity	9.9	6.2	9.9	9.8
Lizard species richness	30	34	36	37

habitat" (Pianka, 1969). During 1978, some 1565 new lizard specimens representing 34 species were captured on the L-area (Table I). Only 1 species collected in 1967 was not encountered in 1978 (the large nocturnal skink *Egernia kintorei* mentioned previously); 5 new species were recorded in 1978, including *Varanus gouldi* and *Diplodactylus elderi*, both of which were expected in 1967 as explained above. Tracks of the enormous *Varanus giganteus* were seen again, but these exceedingly intelligent lizards evaded sighting and eluded capture. During 1989–1992 (hereafter referred to as 1990), 36 species were observed (Table I).

Relative abundances of various species on the L-area, as reflected in the numbers actually collected, did not remain constant but fluctuated fairly substantially (Table I; Pianka, 1986). Abundances of some species shifted upwards or downwards by factors of 3 or more, but most species abundances varied to a lesser degree. Regardless of the direction (increase versus decrease), the average magnitude of change in relative abundance from 1967 to 1978 was 2.70 (SD = 1.55, $N = 28$). Average change in relative abundance from 1978 to 1990 was 3.01 (SD = 3.46, $N = 31$). Change in relative abundance from 1978 to 1990 is plotted against the change from 1967 to 1978 in Fig. 3. The two species that increased markedly in abundance over the second time interval are the tiny skink *Menetia greyi* and the knob-tailed gecko, *Nephurus levis*. Apparent changes in abundances of uncommon species could easily be artifacts and should not be taken too seriously.

Some 26 species are represented in Fig. 3. Under the null hypothesis that densities are changing randomly, the expectation would be 8.5 species in each of the four quadrants. Observed numbers of 9, 6, 3, and 8 do not differ significantly from expected ($\chi^2 = 4.35$, $df = 3$, $P = 0.25$). The presence of species in the northwest and southeast quadrants suggests density-dependent feedback that would confer community stability. However, species in the southwest and northeast quadrants pose a dilemma: why is it that species in the southwest quadrant (decreasing over both intervals) do not go extinct and those in the northeast quadrant (increasing over both intervals) do not take over? The proportion of species that increased over the 1967–1978 interval was only $9/26 = 0.35$, whereas over the 1978–1990 interval 15 out of 26 species (0.58) increased in abundance. The greatest disparities from expected in changing abundances were the 3 species that were increasing over the 1967–1978 interval but decreasing over the 1978–1990 interval (southeast quadrant).

From 1967 to 1978, at least two species increased markedly in abundance (*Ctenophorus isolepis* and *Ctenotus calurus*). Four other species declined during this period (*Ctenotus grandis*, *Ctenotus helenae*, *Gehyra variegata* and *Rhynchoedura ornata*). In the light of these apparent changes in relative abundance, patterns of resource utilization in both diets and microhabitats among eight abundant species were scrutinized closely (Pianka, 1986). Diets of five food specialists changed little, but proportional representation of various prey items

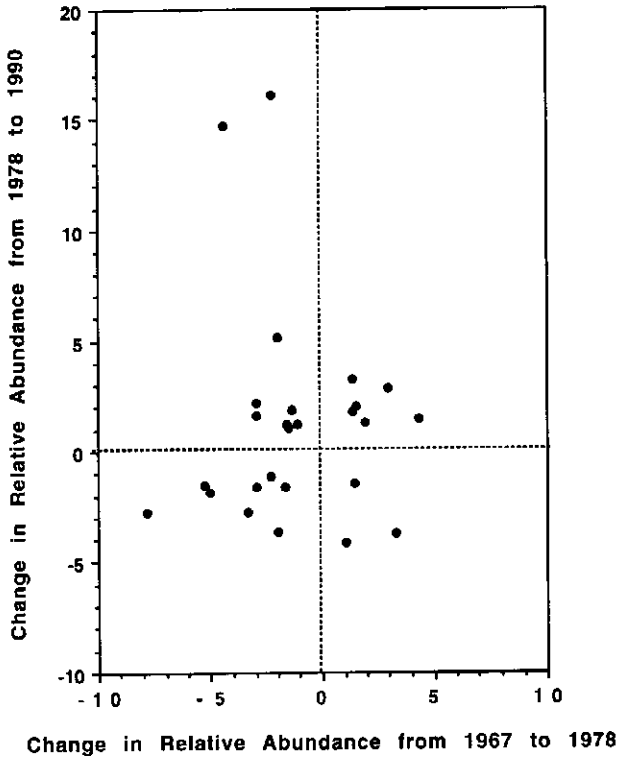


FIGURE 3. Change in relative abundance of L-area lizards between 1978-1979 and 1989-1992 plotted against the change in relative abundance from 1966-1968 to 1978-1979.

in the diets of three more generalized feeders shifted somewhat. Similarly, microhabitat utilizations varied little in five species (two arboreal plus three terrestrial), but changed in three other terrestrial species (for further details, see Pianka, 1986, and discussion following).

Foods available to these lizards, as reflected in what the animals actually ate, appeared to have undergone some changes between 1967 and 1978. Two observations suggested that the food supply available to lizards was diminished in 1978. First, average stomach volume decreased from 0.47 cc (1968) to 0.31 cc (1978). Second, prey diversity increased: the diversity of foods eaten by all lizards increased slightly from 3.48 to 4.28, partially due to the decrease in the importance of termites. The L-area is unusual among my Australian study areas in its very high values for termite consumption (Pianka, 1989). Percentage compositions of prey categories consumed by all species changed by less than an order of magnitude, so these changes may be deemed as relatively conservative.

Nonetheless, consumption of grasshoppers and crickets and insect larvae dropped precipitously, whereas consumption of ants and vertebrates showed strong increases (the apparent change in vertebrate foods is an artifact to the extent that it reflects my own heightened effort to collect *Varanus*).

Although there is little reason to suspect that availabilities of microhabitats should have altered appreciably over the decade between my two visits, data on microhabitat utilization of the entire L-area saurofauna in 1967 versus 1978 did show some changes (Pianka, 1986). The fraction of lizards first sighted in the sunshine at the edge of porcupine grass tussocks increased 4-fold, whereas those observed in grass shade decreased. Overall diversity of microhabitats used by all individuals of all lizard species decreased from 6.36 to 5.37.

A simplistic first hypothesis might be that lizard abundances fluctuate directly with prey availability. If so, a doubling of the availability of ants would be expected to lead to a doubling of the density of myrmecophagous species. Likewise, abundances of termite specialists would be expected to "track" termite availabilities. Assuming that my estimates based on the diets of all lizards reflect real changes in prey availabilities (a sort of a "bioassay"), this hypothesis is easily tested and rejected: *Moloch horridus*, an obligate ant specialist, decreased by a factor of 3 even though ants actually increased more than 2-fold in the overall diet of all lizards. Also, although termites decreased slightly (from 50 to 42%) in the overall diet of all lizards (Pianka, 1986), the relative abundance of an obligate termite specialist, *Diplodactylus conspicillatus*, increased by 50%. Another termite specialist, *Rhynchoedura ornata*, fluctuated in the opposite direction, declining to less than half its former abundance. A related observation of interest can be made on *Ctenotus calurus*, the species that exhibited the most dramatic increase (4.5-fold, or 450%) from 1967 to 1978; this tiny blue-tailed skink almost doubled its consumption of termites (from 44.3 to 81.2%), despite the fact that termites decreased in the overall diet of all lizards. The fraction of insect larvae in its diet fell from 51.3 to only 2.0% while percentage representation of larvae in the overall diet of all lizards fell from 5.7 to 1.0%.

Yet another interesting, although unfortunately uncommon, species is the flap-footed legless lizard, *Pygopus nigriceps*, a nocturnal denizen of the open spaces with an unusually high consumption of scorpions and spiders (the diet of 16 individuals consisted of 34% scorpions and 26% spiders by volume). In the overall diet of all lizards, the importance of scorpions and spiders was trivial and did not change appreciably (only 1.5 to 1.7%, and 1.2 to 0.7%, respectively). Nonetheless, *Pygopus* relative abundance declined by almost an order of magnitude from 1.5 to a mere 0.2%.

Dietary and microhabitat niche breadths of L-area lizard species, and changes therein, were summarized by Pianka (1986, Table 10.6). The average magnitude of observed change in niche breadths (irrespective of sign) among

all species was similar for foods (1.51) and microhabitats (1.46). Average food niche breadths declined slightly (2.55 to 2.13), whereas average microhabitat niche breadths remained approximately constant (2.30 versus 2.32). Variances in niche breadths among species were lower in microhabitat than in diet (Pianka, 1986). Across species, dietary niche breadth is weakly but significantly positively correlated with microhabitat niche breadth ($r = 0.268$, $P < 0.02$), an indication that food specialists tend to be restricted to fewer microhabitats than food generalists.

Optimal foraging theory predicts that diets should contract when foods are abundant but expand when foods are scarce (MacArthur and Pianka, 1966). Relative abundances of consumers might also be expected to vary directly with prey abundance. Of the 7 species that increased in abundance, food niche breadths decreased as predicted in 4, increased in 2, and stayed constant in 1 (the termite specialist *Diploclactylus conspicillatus*). Abundances of 2 species changed little and their food niche breadths remained fairly constant. Of the 15 species that declined in abundance, diets expanded (as expected) in only 2, contracted in 6, and changed little among 7 others (the latter included both food specialists and food generalists).

The L-area 1967 and 1978 data sets were also exploited to test the hypotheses that abundances of ecologically similar species fluctuate either (1) in phase with one another, or (2) out of phase with one another, more so as compared with ecologically dissimilar species (Pianka, 1986). The first hypothesis emerges from a non-competition argument asserting only that species track available resources, whereas the second suggests interactions between species of the mutually detrimental class such as might arise from interspecific competition. Both hypotheses could easily be fatal oversimplifications if the majority of species experience diffuse competition and both positive as well as negative indirect effects on one another (see also the following discussion).

To perform such a test (Pianka, 1986), I computed the direction and magnitude of changes in relative abundances among all possible pairs of species. Using lumped data from both visits, overall ecological overlap was estimated as the product of dietary overlap times microhabitat overlap. The relative change in the abundances of each pair of species was expressed as the ratio of the change in each ($\Delta N_i / \Delta N_j$). No correlation emerged from comparison of this matrix of changes in abundance versus the above-mentioned matrix of overall ecological overlap, either among all 33 species ($r = -0.011$) or using just 11 species for which sample sizes were more adequate ($r = -0.001$). Nor did the elements in the matrix of changes in abundance correlate with dietary overlap ($r = +0.006$). Finally, the correlation between the elements in the above matrix of changes in abundance versus elements in the inverse of the matrix of overall ecological overlap was also negligible ($r = +0.005$). While these results are less than satisfying, at least they seem to support neither of

the above hypotheses. Rather, they suggest either that stochasticity in this system is considerable, or that abundances of each species vary more or less independently of those of other species. Alternatively, species abundances might vary in response to resources and to one another, but their interactions might be aligned along many niche dimensions with some direct competitors yielding positive density effects (indirect "competitive mutualisms"), whereas others yield net negative density effects; under such circumstances, the overall total effects might appear to be mere "noise."

Another study site, Red Sands, located about 100 km to the east of the L-area (8 km west of new Yamarna Homestead), was chosen as a study site because it contains large stable sandridges. Interdunal flats at Red Sands have a complex vegetation similar to that of the L-area consisting of scattered marble gum trees, mallees, and various shrubs with an understory of spinifex. Slopes and crests of sandridges support relatively less spinifex but more woody shrubs. The saurofauna of Red Sands (Table II) was first censused in 1978–1979 when 42 species were observed (diversity = 8.0). Much of the Red Sands area burned in 1982, but some extensive patches of old spinifex escaped the fire. A subsequent, more complete census undertaken in 1989–1992 demonstrated a sharp increase in species diversity (12.0) plus marked changes in the relative abundances of about a dozen species (Table II). Abundances changed more drastically at Red Sands than they did on the L-area, and changes were much more variable; average change in relative abundance from 1978 to 1990 at Red Sands was 8.26 (SD = 15.26, $N = 39$), as compared to the L-area changes of 2.70 (SD = 1.55) and 3.01 (SD = 3.46) for 1967–1978 and 1978–1990, respectively. A total of 47 species of lizards have now been collected at Red Sands (see Appendix), several of which may be accidental transients since they were collected only once or twice [these include *Ctenophorus fordi*, which appears to have undergone a local extinction on the study area, and *Nephurus vertebralis* and *Varanus gilleni*, both of which are shrub-*Acacia* species (Pianka, 1969, 1986)]. Ten species that appear to have increased in abundance at Red Sands are *Ctenophorus clayi*, *Ctenotus ariadnae*, *Ctenotus brooksi*, *Ctenotus colletti*, *Ctenotus piankai*, *Egernia inornata*, *Lerista bipes*, *Lerista desertorum*, *Menetia greyi*, and *Diplodactylus conspicillatus*. Five species that appear to have decreased in abundance include *Ctenophorus isolepis*, *Moloch horridus*, *Diplodactylus ciliaris*, *Gehyra purpurascens*, and *Rhynchoedura ornata*.

Two other study sites on flat sandplains support pure stands of spinifex, with no trees and just a very few scattered shrubs. An informative comparison can be made between these two sites, one of which was newly burned and the other long unburned (Table III). The newly burned site, known as the N-area (supporting 16 species of lizards with a diversity of 8.5), is located about 100 km to the east (8 km west of Neale Junction) and was censused during 1967. A comparable, but long-unburned, flat sandplain site, the B-area, located about 4

TABLE II Relative Abundances (Percentages) of Lizard Species at Red Sands in 1978-1979, 1989-1992, and 1978-1992 (see Appendix)

	1978-1979	1989-1992	1978-1992
<i>Ctenophorus clayi</i>	1.11	4.22	3.26
<i>Ctenophorus fordi</i>	0.07	0.00	0.02
<i>Ctenophorus inermis</i>	1.04	1.50	1.36
<i>Ctenophorus isolepis</i>	14.55	1.63	5.64
<i>Gemmatophora longirostris</i>	1.81	0.22	0.71
<i>Moloch horridus</i>	4.87	0.78	2.05
<i>Pogona minor</i>	0.70	1.13	0.99
<i>Varanus brevicauda</i>	0.00	0.13	0.09
<i>Varanus eremius</i>	0.49	0.25	0.32
<i>Varanus giganteus</i>	0.07	0.13	0.11
<i>Varanus gilleni</i>	0.07	0.00	0.02
<i>Varanus gouldi</i>	0.35	0.84	0.69
<i>Varanus tristis</i>	2.65	0.34	1.06
<i>Ctenotus ariadnae</i>	0.07	0.63	0.45
<i>Ctenotus brooksi</i>	0.28	3.91	2.79
<i>Ctenotus calurus</i>	0.97	0.91	0.93
<i>Ctenotus colletti</i>	0.56	3.54	2.61
<i>Ctenotus dux</i>	7.80	8.89	8.55
<i>Ctenotus grandis</i>	0.35	0.34	0.35
<i>Ctenotus helenae</i>	1.81	0.97	1.23
<i>Ctenotus pantherinus</i>	1.74	0.38	0.80
<i>Ctenotus piankai</i>	0.56	6.54	4.69
<i>Ctenotus quattuordecimlineatus</i>	6.27	9.20	8.29
<i>Ctenotus schomburgkii</i>	0.00	0.13	0.09
<i>Cyclodomorphus branchialis</i>	0.21	0.06	0.11
<i>Egernia inornata</i>	0.63	3.57	2.66
<i>Egernia striata</i>	0.91	0.66	0.73
<i>Eremiascincus richardsoni</i>	0.14	0.03	0.07
<i>Lerista bipes</i>	0.35	19.65	13.66
<i>Lerista desertorum</i>	0.07	1.44	1.02
<i>Menetia greyi</i>	0.07	5.69	3.95
<i>Morethia butleri</i>	0.07	0.34	0.26
<i>Delma fraseri</i>	0.21	0.00	0.07
<i>Delma nasuta</i>	0.00	0.03	0.02
<i>Lialis burtonis</i>	0.14	0.13	0.13
<i>Pygopus nigriceps</i>	0.21	0.28	0.26
<i>Diplodactylus ciliaris</i>	2.99	0.69	1.40
<i>Diplodactylus conspicillatus</i>	0.70	3.97	2.96
<i>Diplodactylus damaeus</i>	1.39	1.85	1.71
<i>Diplodactylus elderi</i>	0.91	0.16	0.39
<i>Diplodactylus strophurus</i>	0.84	0.06	0.30
<i>Gehyra purpurascens</i>	26.32	3.04	10.26
<i>Gehyra variegata</i>	0.00	0.16	0.11
<i>Heteronotia binoei</i>	0.07	0.03	0.04

(continues)

TABLE II *continued*

	1978-1979	1989-1992	1978-1992
<i>Nephrurus laevisissimus</i>	13.44	10.29	11.27
<i>Nephrurus vertebralis</i>	0.00	0.06	0.04
<i>Rhynchoedura ornata</i>	2.16	1.25	1.53
Total number of lizards	1436	3196	4632
Lizard species diversity	8.0	12.0	14.4
Lizard species richness	42	44	47

km south of Red Sands (12 km west of new Yamarna Homestead), was censused during 1992-1993 and had a lizard species diversity of 7.7. This site contained old spinifex of two different ages, the oldest of which were probably about 40 years old (judged from counts of growth rings on an old mallee adjacent to the site). Some 29 species of lizards, including several probable "accidentals," were collected on the B-area (another species, *Varanus gouldi*, was also present as judged by numerous, very characteristic diggings). Although nearly twice as many lizard species were present at the B-area than at the N-area, species diversity was actually lower (7.7 versus 8.5). Two of the 30 species present at the B-area would appear to be accidentals, both because they were collected only once and because of their habitat requirements (*Ctenotus greeri* is a shrub-*Acacia* species and *Ctenotus leae* is a sandridge species). Four species of *Ctenotus* appear to increase in abundance as spinifex matures; these are *Ctenotus calurus*, *Ctenotus grandis*, *Ctenotus pantherinus*, and *Ctenotus pinkai*. Five lizard species that appear to decrease in abundance as spinifex matures are *Ctenophorus inermis*, *Ctenophorus isolepis*, *Egernia inornata*, *Heteronotia binoei*, and *Rhynchoedura ornata*. If the B-area does not burn naturally on its own accord, it will be burned experimentally in a controlled burn; lizard relative abundances will be monitored as often as possible over the next two decades in an effort to document how post-fire abundances change in time.

Percentages of lizards of 43 species that were captured at four different locations (flat, base, slope, and crest) on the two sandridge sites (the E-area and Red Sands) plus a nearby sandplain site (the B-area) are summarized in Table IV. Note that 7 species are virtually restricted to flats (*Varanus brevicauda*, *Ctenotus ariadnae*, *Ctenotus calurus*, *Ctenotus grandis*, *Ctenotus pantherinus*, *Delma butleri* and *Heteronotia binoei*), 4 other species occur on flats and/or near the bases of sandridges (*Ctenophorus isolepis*, *Ctenotus helena*, *Ctenotus schomburgki*, *Egernia striata*), whereas 8 other species are quite strongly associated with sandridges (*Ctenophorus fordii*, *Diporiphora winneckeii*, *Gemmatophora longirostris*, *Ctenotus brooksi*, *Ctenotus leae*, *Diplodactylus damaeus*, *Diplodactylus elderi* and *Nephrurus laevisissimus*). Fourteen other species have somewhat

TABLE III Relative Abundances (Percentages)
of Lizard Species at a Recently Burned Site
(N-Area) and a Long-Unburned Site (B-Area)

	N-area	B-area
<i>Ctenophorus clayi</i>		0.41
<i>Ctenophorus inermis</i>	2.74	0.41
<i>Ctenophorus isolepis</i>	24.66	11.26
<i>Pogona minor</i>		0.69
<i>Varanus breviceauda</i>		2.20
<i>Varanus eremius</i>	1.37	2.20
<i>Varanus gouldi</i>	1.37	diggings
<i>Ctenotus ariadnae</i>		8.38
<i>Ctenotus calurus</i>	6.85	19.78
<i>Ctenotus grandis</i>	4.11	21.02
<i>Ctenotus greeri</i>		0.14
<i>Ctenotus helenae</i>	1.37	0.41
<i>Ctenotus leae</i>		0.14
<i>Ctenotus pantherinus</i>	2.74	10.17
<i>Ctenotus piankai</i>	6.85	10.85
<i>Ctenotus quattuordecimlineatus</i>	1.37	2.20
<i>Ctenotus schomburgkii</i>		0.14
<i>Egernia inornata</i>	8.22	0.14
<i>Egernia striata</i>	5.48	2.06
<i>Lerista bipes</i>		0.55
<i>Menetia greyi</i>	4.11	3.71
<i>Tiliqua multifasciata</i>		0.14
<i>Delma butleri</i>		0.96
<i>Delma nasuta</i>		0.14
<i>Diplodactylus conspicillatus</i>		0.14
<i>Diplodactylus damueus</i>		0.28
<i>Gehyra variegata</i>		0.28
<i>Heteronotia binoei</i>	4.11	1.10
<i>Nephruus laevis</i>		0.14
<i>Nephruus levis</i>	10.96	
<i>Rhynchoedura ornata</i>	13.70	0.14
Total number of lizards	73	729
Lizard species diversity	8.5	7.7
Lizard species richness	16	29

broader habitat niche breadths, occurring with fairly high frequencies in all four habitats (these include *Ctenophorus clayi*, *Ctenophorus inermis*, *Moloch horridus*, *Pogona minor*, *Varanus eremius*, *Varanus gouldi*, *Varanus tristis*, *Ctenotus colletti*, *Ctenotus dux*, *Ctenotus quattuordecimlineatus*, *Egernia inornata*, *Lialis burtonis*, *Pygopus nigriceps*, and *Gehyra purpurascens*). The frequency distribution of habitat niche breadths is shown in Fig. 4. Across species,

TABLE IV Percentage of Lizards Captured at Four Different Habitat Locations, Total Number of Lizards, and Habitat Niche Breadth

	Flat	Base	Slope	Crest	Total	Niche breadth ^a
<i>Ctenophorus clayi</i>	26.7	34.0	15.8	23.5	143	3.74
<i>Ctenophorus fordi</i>	0.0	2.7	53.1	44.2	113	2.09
<i>Ctenophorus inermis</i>	44.9	24.7	18.0	12.4	89	3.22
<i>Ctenophorus isolepis</i>	61.3	19.8	15.1	3.8	450	2.28
<i>Diporiphora winneckeii</i>	0.0	0.0	16.7	83.3	18	1.38
<i>Gemmatophora longirostris</i>	12.0	16.3	16.3	55.4	46	2.67
<i>Moloch horridus</i>	19.8	16.6	43.6	20.0	174	3.37
<i>Pogona minor</i>	37.5	25.0	17.9	19.6	56	3.66
<i>Varanus brevicauda</i>	90.0	10.0	0.0	0.0	20	1.22
<i>Varanus eremius</i>	53.0	14.0	17.0	16.0	50	2.68
<i>Varanus giganteus</i>	27.3	18.2	9.1	45.5	6	3.10
<i>Varanus gouldi</i>	35.0	27.0	24.0	14.0	50	3.67
<i>Varanus tristis</i>	41.7	28.0	16.7	13.7	60	3.34
<i>Ctenotus ariadnae</i>	90.8	2.6	2.6	3.9	76	1.21
<i>Ctenotus brooksi</i>	0.0	3.1	16.0	80.8	159	1.47
<i>Ctenotus calurus</i>	92.5	6.4	0.8	0.3	194	1.16
<i>Ctenotus colletti</i>	10.5	38.3	25.8	25.4	105	3.46
<i>Ctenotus dux</i>	15.9	31.7	25.5	26.9	412	3.80
<i>Ctenotus grandis</i>	96.6	2.3	1.1	0.0	174	1.07
<i>Ctenotus helenae</i>	65.6	18.0	9.4	7.0	64	2.10
<i>Ctenotus leae</i>	4.0	0.0	32.0	64.0	25	1.95
<i>Ctenotus pantherinus</i>	87.9	5.5	4.3	2.3	128	1.29
<i>Ctenotus piankai</i>	46.1	32.9	13.0	8.0	257	2.91
<i>Ctenotus quattuordecimlineatus</i>	33.0	34.3	15.9	16.7	392	3.57
<i>Ctenotus schomburgkii</i>	67.9	21.4	3.6	7.1	14	1.95
<i>Egernia inornata</i>	13.5	45.8	28.0	12.7	174	3.10
<i>Egernia striata</i>	72.5	25.5	0.0	2.0	51	1.69
<i>Lerista bipes</i>	3.7	38.8	15.0	42.5	614	2.82
<i>Lerista desertorum</i>	1.3	42.3	10.3	46.2	39	2.48
<i>Menetia greyi</i>	22.3	49.8	8.3	19.7	211	2.92
<i>Morethia butleri</i>	0.0	66.7	13.3	20.0	15	1.99
<i>Delma butleri</i>	80.0	0.0	15.0	5.0	10	1.50
<i>Lialis burtonis</i>	18.8	31.2	25.0	25.0	8	3.88
<i>Pygopus nigriceps</i>	23.1	34.6	23.1	19.2	13	3.80
<i>Diplodactylus ciliaris</i>	7.6	17.1	25.9	49.4	85	2.89
<i>Diplodactylus conspicillatus</i>	24.9	53.0	9.6	12.4	125	2.72
<i>Diplodactylus damaeus</i>	7.2	17.8	17.1	57.9	76	2.49
<i>Diplodactylus elderi</i>	11.1	5.6	22.2	61.1	18	2.28
<i>Diplodactylus strophurus</i>	25.0	6.2	31.2	37.5	16	3.28
<i>Gehyra purpurascens</i>	40.3	14.0	22.0	23.7	513	3.49
<i>Heteronotia binoei</i>	91.7	4.2	4.2	0.0	12	1.19
<i>Nephrurus laevisimus</i>	2.9	20.3	20.9	55.9	599	2.51
<i>Rhynchoedura ornata</i>	50.7	21.7	8.6	19.1	76	2.88
Total number of lizards	1876	1461	1045	1548	5930	

Note. Niche breadth varies from 1 to 4 (based on all lizards captured on the B-area, the E-area, and Red Sands).

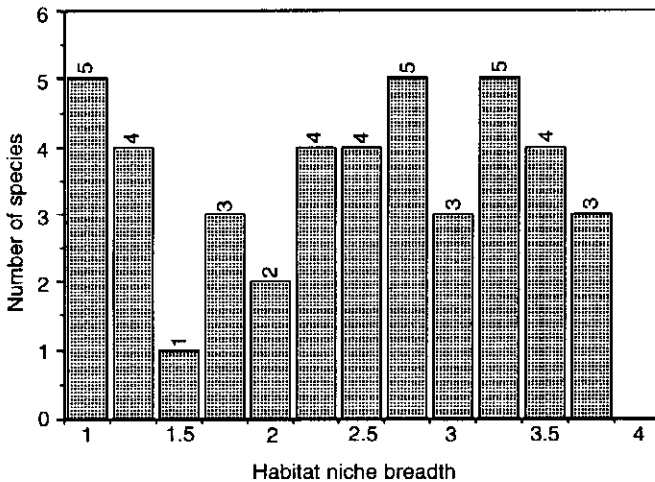


FIGURE 4. Histogram of habitat niche breadths among 43 species of Australian desert lizards (data from Table IV). Note that about 10 species are habitat specialists (niche breadths ≤ 1.5), while many other species are habitat generalists (niche breadths > 1.5).

neither dietary niche breadth nor microhabitat niche breadth is correlated with habitat niche breadth.

Macrohabitat and microhabitat relationships among lizards at a sandridge site in the eastern Simpson Desert in southwestern Queensland were reported by Downey and Dickman (1993). Interestingly, most of the species they captured (30 out of 36) were species that were also present at my own study sites halfway across Australia in the western Great Victoria Desert of Western Australia. Macrohabitat usage by these wide-ranging lizard species is generally quite similar in both regions (*Varanus brevicauda* is an exception). Some species are habitat specialists closely associated with the crests of sandridges, whereas many other species have broader macrohabitat niche breadths and are found in swales (flat sandplains), slopes, as well as on the crests of sandridges.

Lizards were also censused 40 km south of Alice Springs in central Australia by James (1994). He recorded 39 species, 31 of which occurred at my study sites in the Great Victoria Desert, about 1000 km to the west. He found that lizard faunas varied seasonally and that sandridge saurofaunas differed from those on flat sandplains. Moreover, he interpreted the unusual lizard composition on one subsite (his site 1) to be the result of a long period of shelter from fire as compared to other subsites. James (1994) also suggested that saurofaunas change over the long term as spinifex habitats regenerate after fires. Apparently, saurofaunas of sandy spinifex/sandridge habitats are very similar across arid Australia from the eastern Simpson Desert in Queensland to some 1500 kilometers to the west in the western Great Victoria Desert.

Population densities of certain species of lizards, such as *Ctenophorus fordi* and *Ctenophorus isolepis*, are actually greater on recently burned areas (Cogger, 1969, 1972; Griffin *et al.*, 1988). Some species of burrowing lizards such as *Lerista* spp. are also more abundant on recently burned areas than they are on nearby unburned sites. Many other desert lizard species with open habitat requirements, including *Ctenophorus inermis*, presumably invade and/or repopulate burned areas rapidly, quickly reaching high densities in their "preferred" open habitat (such species usually persist at very low densities even in mature stands of dense, closed-in spinifex). Other lizard species, such as *Delma butleri*, *Delma nasuta*, *Cyclodomorphus branchialis*, and *Diplodactylus elderi* require large spinifex tussocks for microhabitats and nearly vanish over extensive open areas following a burn. However, such "climax" species can continue to exist as relicts in the inevitable isolated, unburned pockets and patches of habitat that escaped burning.

Species present on recently burned areas represent a subset of those present on more mature climax sites, both in lizards (Pianka, 1989) and in birds (Pianka and Pianka, 1970). As noted above, relative abundances fluctuate substantially through succession, with some common species becoming quite rare as succession progresses (compare N- and B-areas in Table III). Rare species do not always remain rare and may be vitally important to hold an ecosystem together (Main, 1982), allowing the system to respond to changing environmental conditions. In the Great Victoria Desert, there are, quite literally, waves of lizards constantly moving about the landscape.

Evidence for metapopulation structure can be gleaned from comparison of the saurofaunas of two nearby sandridge study sites separated by a region of shrub-*Acacia* habitat. Eight sandridge-specialized species were present at one of these sandridge study sites, the E-area 30 km east of Red Sands, censused during 1966–1968. However, three of these eight species were not present 30 km west at Red Sands, where ample appropriate habitat was available. During 1978, one newly hatched juvenile of one of the three missing species was present (*Ctenophorus fordi*), but none was encountered despite concerted efforts in several subsequent years of sampling thousands of lizards during 1978–1979 and 1989–1992. A solitary individual, *Ctenotus leae*, also a missing sandridge species, was pit-trapped on the B-area 4 km south of Red Sands in 1993. Such missing species can be considered to be temporarily extinct locally—given enough time, presumably such species will eventually invade and reestablish viable populations. Likewise, populations of such habitat-specialized species could dwindle to precariously low levels during droughts and go temporarily extinct locally.

During four years of field work in arid Australia over a quarter of a century, I have personally witnessed several instances of potential dispersal propagules—lizards wandering through inappropriate habitats where that species normally does not occur. Two were sandridge species, *Ctenophorus fordi* and

Ctenotus leae, both of which were a kilometer or more away from the nearest sandridge, well out into flat sandplain habitat. At a sandplain-sandridge site (Red Sands), I found two individuals of the shrub-*Acacia* species, *Nephrurus vertebralis*, one on the crest of a sandridge, the other at the base of a sandridge. Both individuals were in open areas with little plant cover, reminiscent of conditions within their preferred shrub-*Acacia* habitat, patches of which occurred about a kilometer away. On another occasion, at Red Sands, I collected a large male *Varanus gilleni*, which I strongly suspect is also a shrub-*Acacia* species, as I have captured 50 *Varanus tristis* at this site and never encountered another *V. gilleni*. Even though all five of these individual lizards were far away from appropriate habitat, they were in good physical condition and could easily have survived to reach another patch of appropriate habitat. Such a dispersal episode by a gravid female could start a new local population and result in windfall reproductive success (although there would be a genetic founder effect). Modern molecular techniques, such as DNA fingerprinting via restriction fragment length polymorphisms (RFLPs), offer a powerful new methodology for determination of relatedness, which might allow inference of such past genetic bottlenecks.

Empirical study of lizard metapopulations in the Great Victoria Desert is exceedingly difficult due to the long temporal and extensive spatial scales of this dynamic habitat mosaic, as well as to the infrequency of local extinction and dispersal-colonization events. Detailed analyses of satellite imagery in progress should enable us to describe the actual spatial-temporal phasing of the fire-succession cycle, which will then be used as a realistic habitat mosaic background in computer simulation studies of metapopulation dynamics. To what extent do such landscape dynamics impose particular biological attributes on component species? Given various degrees of extinction proneness, I plan to explore on computers what reproductive capacities and dispersal abilities are required in order for various habitat specialists to persist in this ever-changing landscape. For example, one would predict that habitat specialists must have higher powers of dispersal than habitat generalists. Moreover, due to the dynamic habitat mosaic and local extinctions, populations will be below their respective carrying capacities to varying degrees that will depend upon their relative abilities to track their preferred habitats in this ever-changing habitat mosaic.

What constitutes a "long-term" study? Some would say a year, others decades, but even millennia pale against the geological record. Humans live such short lives that it becomes an absurd anthropocentrism even to contemplate the long term. The desert-lizard/spatial-temporal habitat mosaic described here clearly fluctuates over decades and very probably even over centuries—although I amassed what appears to be a considerable amount of data during 28 years, a great deal more information will be required before a reasonable degree of understanding of this very complex system can be reached. I intend

to devote the remainder of my life to the continuation of this challenging study.

V. SUMMARY

Australian desert lizards have evolved a high degree of habitat specificity. Some species are restricted to flat spinifex sandplains, others to shrub-*Acacia* (mulga) habitats, and still others to sandridges. Lightning sets hundreds of wildfires annually in inland arid Australia, generating an ever-changing spatial-temporal patchwork of habitats that differ in their state of post-fire recovery. Different species of desert lizards have differing post-fire habitat requirements. Species that require open areas increase in abundance immediately following fire. Other species that require long-unburned spinifex tussocks disappear after fire. However, fires frequently reticulate, leaving behind refuges that allow the latter species to persist in isolated pockets of suitable old spinifex habitat. Sandridges and mulga habitats add two more important phases to this complex mosaic of habitats. Lizard populations in this region form metapopulations, temporarily going extinct within some isolated patches of habitat, but periodically re-invading from others. Such regional processes foster local diversity. Waves of lizards are constantly moving about this landscape. Long-term studies at two sites document changing relative abundances. Comparisons between sites in different stages of post-fire recovery suggest that some lizard species decrease in abundance following fire, whereas other species increase in abundance. Further long-term studies are needed to document changing relative abundances during this dynamic fire succession cycle.

Acknowledgments

My research has been financed by grants from the National Geographic Society, the John Simon Guggenheim Memorial Foundation, a senior Fulbright Research Scholarship, the Australian-American Educational Foundation, the University Research Institute of the Graduate School at the University of Texas at Austin, the Denton A. Cooley Centennial Professorship in Zoology at the University of Texas at Austin, the U.S. National Science Foundation, the U.S. National Aeronautics and Space Administration, as well as my own pocketbook. For logistic support, I am indebted to the staffs of the Department of Zoology at the University of Western Australia and the Western Australian Museum plus the staffs of Conservation and Land Management, both at Kalgoorlie and at the Western Australian Wildlife Centre at Woodvale. Aussies who gave generously of their time and greatly assisted in this research effort include June Anderson, Ken Aplin, Jean Bannister, Andrew Burbidge, Andy Chapman, Ian Keally, Bert Main, Lee Ann Miller, David Pearson, Nancy Scade, Laurie Smith, and the late Glen Storr. For much assistance in the field, I thank Helen Dunlap, Karen Pianka, Gretchen Pianka, François Odendaal, William Giles, Rand Dybdahl, the late Wayne Sanders, Daniel Bennett, and Magnus Peterson.

Appendix

As of April 1996, six additional species have been trapped at the Red Sands site bringing the total species richness for this site to 53 species of lizards. Two of these were expected at this site (*Ctenotus leae* and *Tiliqua multifasciata*) and two are "accidentals" from nearby mulga habitats (*Ctenotus leonhardii* and *Ctenophorus scutulatus*). The remaining two species are cryptic and were previously confused with others at the site.

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