

DESERT LIZARD DIVERSITY: ADDITIONAL COMMENTS
AND SOME DATA

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Morton and James (1988) presented some interesting arguments relating a wide range of climatic, edaphic, and biotic factors to diversity and abundance of desert lizards in Australia. One way to confront the multiple-causality dilemma is to postulate causal networks or webs of ecological forces (Connell and Orias 1964). Morton and James bravely proposed an elaborate and comprehensive synthetic scheme invoking multiple causality, beginning with the abiotic factors of unpredictable precipitation and nutrient-poor soils. They envisioned that these two physical factors act in concert and result in scant and erratic primary productivity, favoring spinifex grasses (*Triodia* and *Plectrachne*). Morton and James further postulated that these grasses' unique tussock growth is poor in nitrogen, and hence relatively unusable fodder for most herbivores, but still able to support an abundant and diverse termite fauna. Isoptera are a food resource that these authors considered particularly well suited to exploitation by ectothermic lizards. Morton and James also speculated that aperiodic heavy rainfall promotes woody vegetation and therefore supports arboreal and litter-dwelling species of lizards.

Obviously, such an intricate theory is neither easily refuted nor confirmed, but some data can be brought to bear on certain assertions and links in the putative causal network. Here, I examine some of the postulates and tenets of this rather complex mega-hypothesis, subjecting pieces of it to a partial test by means of both intra- and intercontinental comparisons. Diets of lizard faunas at two chenopod shrub sites play a key role because Morton and James (1988) contended that such areas should be more productive and should have fewer termites. I also emphasize two crucially important phenomena largely relegated to the background in their paper: disturbance and history.

Earth's most diverse lizard faunas occur in the Great Victoria Desert of Western Australia. At least 39–42 different species, perhaps as many as 50, occur in sympatry there. In contrast, only 6–17 lizard species are found together at roughly comparable sites in North America and in the Kalahari semi-desert of southern Africa (Pianka 1986). In reviews of various factors that promote lizard diversity in

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Australia (Pianka 1981, 1986; Morton and James 1988), almost a dozen major factors have now been postulated: (1) unpredictable precipitation, (2) nutrient-poor soil, (3) the unique tussock life form and physical structure of spinifex grasses (*Triodia* and *Plectrachne*), including their low nutrient content, (4) abundant and diverse termite faunas, (5) nocturnality, (6) fossoriality, (7) arboreality, (8) habitat specificity, (9) usurpation of ecological roles occupied by other taxa elsewhere, (10) a complex fire-succession cycle that creates and maintains habitat heterogeneity via disturbance, and (11) biogeographic and historical factors. No factors are mutually exclusive, and some evidence has been marshaled for all of them. Each is considered in turn below.

LIZARD ABUNDANCES

Morton and James' (1988) valuable estimates of lizard abundance and biomass in central Australia are surprisingly high. However, it makes perfect sense that Australian deserts should have as many, or even more, lizards per unit of area than deserts in North America or the Kalahari. Indeed, it would be hard to imagine otherwise, for primary productivity is comparable or even slightly greater in the Australian deserts, which do harbor an abundant and diverse insect fauna. However, lizards in the Australian deserts are *much more cryptic* than those in North America or the Kalahari, where by walking slowly one can encounter virtually all species present. In Australia, one must adopt a wide variety of techniques, and be exceedingly persistent, to find even a single specimen of many species. Certain abundant and conspicuous species, particularly the agamid *Ctenophorus isolepis*, are comparable to lizards in North America and the Kalahari in every way. However, the vast majority of Australian desert lizards are relatively inconspicuous. In my collections, relative abundances of 55 of the 60 species are less than 5%; taken together, all 55 of these "rare" species are represented by fewer individuals than the other five common species, which sum to more than half the total (Pianka 1986). In the Great Victoria Desert, I, too, undertook limited pit trapping using drift fences (Banta 1957). Results were very disappointing in terms of active diurnal species; over about 6 mo, a dozen traps captured only a few agamids, a handful of *Ctenotus*, and one *Varanus*. However, fossorial *Lerista* proved to be fairly trappable; several dozen were collected. More-active, litter-dwelling *Menetia*, *Morethia*, and *Lerista muelleri* were present in low abundance but did not fall into pit traps.

UNPREDICTABLE PRECIPITATION

Among 24 study sites on three continents with climatic data, long-term average annual precipitation varies from a minimum of 93 mm at Pahrump in North America to a maximum of 312 mm at Red Sands in Australia (Pianka 1986). Standard deviation in total annual precipitation varies from 44 to 177 mm across these sites and is positively correlated with the mean ($r = 0.77$, $P < 0.001$). Annual precipitation is lowest and least variable in North America (average mean, 144 mm; average SD, 69), intermediate in the Kalahari (average mean, 201 mm;

average SD, 94), and greatest and most variable in Australia (average mean, 233 mm; average SD, 129). However, when standard deviation in precipitation is expressed as a fraction of the annual mean (i.e., as the coefficient of variation), the difference between continents is slight (average CV's, 0.51, 0.48, and 0.56, respectively). Although scatter is extensive and neither correlation necessarily has biological meaning, the number of lizard species is significantly correlated both with long-term mean annual precipitation ($r = 0.61$, $P < 0.001$) and with the standard deviation in annual precipitation ($r = 0.73$, $P < 0.001$). This trend is reversed within the Kalahari semi-desert, however, where the number of lizard species is negatively correlated with both long-term average annual precipitation ($r = -0.45$, $P < 0.15$) and standard deviation in precipitation ($r = -0.88$, $P < 0.01$).

As noted above, the long-term mean and the standard deviation in annual precipitation are themselves positively correlated. When the effects of long-term average annual precipitation are held constant by partial correlation, the number of lizard species and the standard deviation in precipitation remain significantly correlated ($r = 0.52$, $P < 0.01$). However, when standard deviation in precipitation is partialled out, the number of lizard species no longer correlates with long-term annual precipitation ($r = 0.11$). Hence, productivity alone may not foster diversity, but annual variability in productivity may (partial correlation does not separate variables unequivocally). Certainly, productive sites favor narrower diets and, as a result, should support more species of lizards than less-productive areas, but the mechanisms by which increased variability promotes diversity are less obvious. Temporal heterogeneity could facilitate coexistence, both by continually altering relative competitive abilities among members of a community and by periodically reducing population sizes, which would lower the intensity of competition (Hutchinson 1961). Such a disturbance mechanism could operate in desert lizard faunas. This link in the causal network proposed by Morton and James seems reasonably well established.

NUTRIENT-POOR SOIL

Soil fertility could differ fundamentally between Australia and southern Africa (Beadle 1954; Charley and Cowling 1968; Charley 1972; Buckley 1981; Milewski 1981; Morton and James 1988). Poorer Australian soils might, by virtue of lower productivity, favor ectotherms, thus tending to support a more diverse lizard fauna (Milewski 1981). Actual data on soil fertilities remain exceedingly scant, however, and putative intercontinental differences are far from firmly established.

Selected soil samples from the southern Kalahari were compared with those from central Australia by Buckley (1981, 1982), who noted somewhat lower percentages of organic materials in Australia but higher concentrations of calcium, potassium, and phosphorus. Such crude comparisons between continents are of dubious utility because nutrients vary considerably from inter-dunal streets to sand-ridge crests (Buckley 1981). More recently, Buckley et al. (1987) presented data from soil samples selected to be as comparable as possible. The surprising result was that Australian soils are at least three times as rich as

comparable Kalahari soils, at least in levels of citric-acid-extractable phosphorus and potassium.

Both the Kalahari and the Great Victoria deserts are characterized by summer rainfall regimes and stabilized red sand ridges. In topography and climatology, the two regions are so similar that, without recourse to their different biotas, the two continents are virtually indistinguishable. This great physical similarity is hardly surprising in view of their common origin in Gondwanaland and Pangaea, coupled with their similar present-day latitudinal positions. Major soil-fertility differences seem rather unlikely. Better data and more-detailed intercontinental comparisons are needed to evaluate this link in Morton and James' mega-hypothesis.

SPINIFEX GRASSES

The composition of lizard faunas is profoundly influenced by the physical structure of the vegetation. The mere existence of the hummock-grass life form in Australia is a major factor contributing to lizard diversity on that continent (Pianka 1981). A pure spinifex (*Triodia*) grass flat (Neale area) supports at least 16 species of lizards (perhaps as many as 20), including 6 or 7 species of *Ctenotus* skinks (Pianka 1969). These grass tussocks are extraordinarily well suited for lizard inhabitants, providing not only protection from predators and the elements but also a rich and diverse insect food supply (fig. 1, Neale area, *upper left*). Certain lizard species appear to spend almost all their lives within dense *Triodia* clumps, whereas other lizards exploit the clumps' edges. Still other species forage in the open spaces between tussocks but rely on spinifex clumps as escape shelters in emergencies.

Morton and James (1988) suggested that the spiky sclerophyllous structure of spinifex grasses is an adaptation to nutrient poverty under aridity, citing Winkworth (1967), Beard (1984), and Griffin (1984). Moreover, they argued that spinifex grasslands produce a high biomass of fodder that is nutritionally poor for most herbivores, but they postulated that termites are particularly able to exploit these nitrogen-poor but cellulose-rich foods. Indeed, they proposed that termite diversification and species richness in arid Australia have their bases in spinifex fodders. Why hasn't the hummock-grass growth form arisen in other parts of the world? Historical accident springs to mind. Moreover, evidence shows that termites are even more abundant in the Kalahari than they are in Australia (see the next section).

TERMITE ABUNDANCE AND DIVERSITY

Termites constitute a crucial link in Morton and James' mega-hypothesis. Isoptera of southern Africa are conspicuous and diverse; they have apparently facilitated the evolution of termite-specialized species of skinks, lacertids, and geckos (Pianka 1986). Indeed, termites make up a full 41% by volume of the diet of all Kalahari lizards but only about 16% of the overall diet of the entire saurian fauna in western North America and 18.5% in Western Australia. Nearly half the lizard species in the Kalahari have specialized on termites, as have approximately

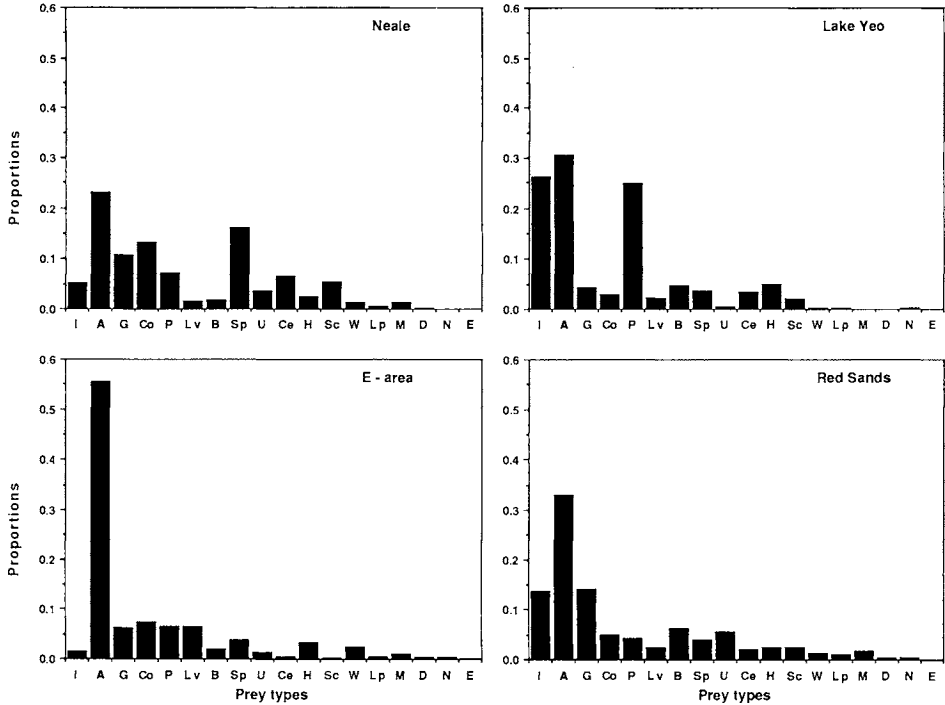


FIG. 1.—Proportional representation of various prey categories in the diets of lizards at four sites in the Great Victoria Desert of Western Australia. Neale is a recently burned, pure-spinifex flat, Lake Yeo is a chenopod shrubby area, and area E and Red Sands are complex sand-ridge sites. Prey are ranked according to their overall abundance in the diets of all Australian lizards collected at nine different study sites, excluding vertebrate foods, which are even more important by volume than are termites (see the text). Prey category: I, Isoptera; A, ants; G, grasshoppers and crickets; Co, Coleoptera; P, plants; Lv, insect larvae; B, blattids (roaches); Sp, spiders; U, unidentified miscellaneous insects; Ce, centipedes; H, Hemiptera and Homoptera; Sc, scorpions; W, wasps; Lp, Lepidoptera; M, mantids and phasmids; D, Diptera; N, Neuroptera; E, insect eggs.

one-quarter of the species in Australia (no North American lizard species can really be considered a termite specialist).

Widely foraging species of lizards, such as the North American teiid *Cnemidophorus*, Australian *Ctenotus* skinks, and certain Kalahari lacertids (*Eremias*), tend to consume more termites than do sympatric sit-and-wait, ambush-foraging species (Huey and Pianka 1981). Chenopod-shrub study sites in both the Kalahari and Australia support only two or three widely foraging lizard species, whereas non-chenopod sites have many more widely foraging species (Pianka 1981, 1986). These facts seem to fit Morton and James' predictions.

Morton and James (1988) made the legitimate point that large saurophagous (lizard-eating) varanids bias overall prey-resource spectra in Australia toward vertebrate foods. When vertebrates are excluded from consideration as a resource, the percentage by volume of termites in the overall diet of all Australian lizards rises

TABLE 1
TERMITES AS PERCENTAGE OF DIET FOR SAURIAN FAUNAS OF NINE
AUSTRALIAN AND TEN KALAHARI DESERT SITES

AUSTRALIA		KALAHARI	
Site	%	Site	%
Atley	31.5	Aarpan	31.9
Area E	1.5	Bloukrans	30.3
Great Victoria	21.4	Area D	30.4
Laverton, 1966-1968	53.2	Geselskop*	30.4
Laverton, 1978-1979	51.1	Kameel Sleep	40.5
Lorna Glen	3.2	Ludrille	62.2
Millrose	13.5	Mahlzeit	30.0
Neale	5.1	Rhigozum	71.1
Red Sands	13.7	Tsabong	58.3
Lake Yeo*	26.1	Farm X	26.3

NOTE.—Percentage of diet calculated by volume. For the Australian sites, the total diet excluded lizards as prey (see the text).

* Chenopodiaceous shrubby sites.

from 18.5% to 23.5%, still considerably below the Kalahari's 41%. Such "corrected" estimates are given for each of my nine Australian study sites in table 1, along with comparable site-by-site termite percentages for 10 Kalahari sites (values uncorrected since vertebrates constitute only 2.3% of the diet of all Kalahari lizards). Termite consumption varied considerably from site to site. At a chenopodiaceous shrubby site in the dry lake bed of Lake Yeo in Australia, lizards consumed 26% termites by volume (fig. 1, *upper right*); at eight other Australian spinifex sites (figs. 1, 2), these values ranged from 2% to 53% termites (mean, 21.6%). Termite consumption was actually lower than at Lake Yeo at all spinifex sites except two (Atley and Laverton). In the Kalahari, Geselskop was a chenopod-shrub site with 30% termite consumption (fig. 3); the termites eaten by all lizards at nine other Kalahari sites accounted for 26% to 71% of the diet (figs. 3, 4; mean, 42.3%). Termite consumption was below that at Geselskop at several non-shrub Kalahari sites but above it at several others. Table 2 summarizes termite-consumption patterns by all species of lizards at 10 Kalahari study sites. The chenopod-shrub site Geselskop had a moderate percentage of consumption but the highest diversity of termites of any Kalahari site. Further data on termite abundances are still needed, but these preliminary data do not seem to support this rather critical link in Morton and James' mega-hypothesis. Some amendments to modify the vital termite link in their scheme seem necessary.

NOCTURNALITY

An average Great Victoria Desert site supports 10 nocturnal lizard species, compared with only 5 in the Kalahari and 1 or 2 in North America. Nocturnal lizards in Australia include pygopodids, skinks, and geckos. 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 historical factors. (1)

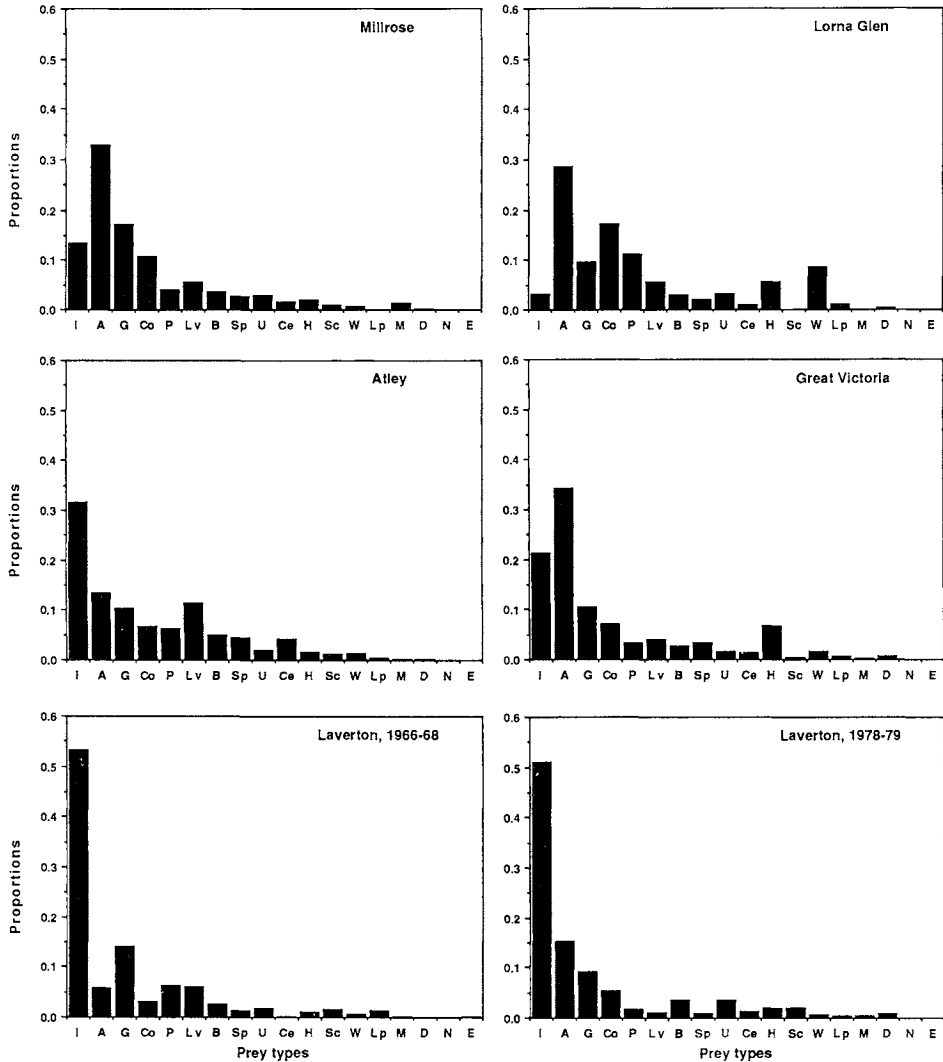


FIG. 2.—Proportional representation of various prey categories in the diets of lizards at five sites in the Great Victoria Desert of Western Australia, with prey ranked and coded as in figure 1. All these sites are spinifex areas, although Millrose and Atley are on ecotones with substantial amounts of mulga. Laverton and Great Victoria are spinifex sites nearing climax, not recently burned.

Various desert systems could differ in the diversity and abundance of resources available 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 and/or the 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

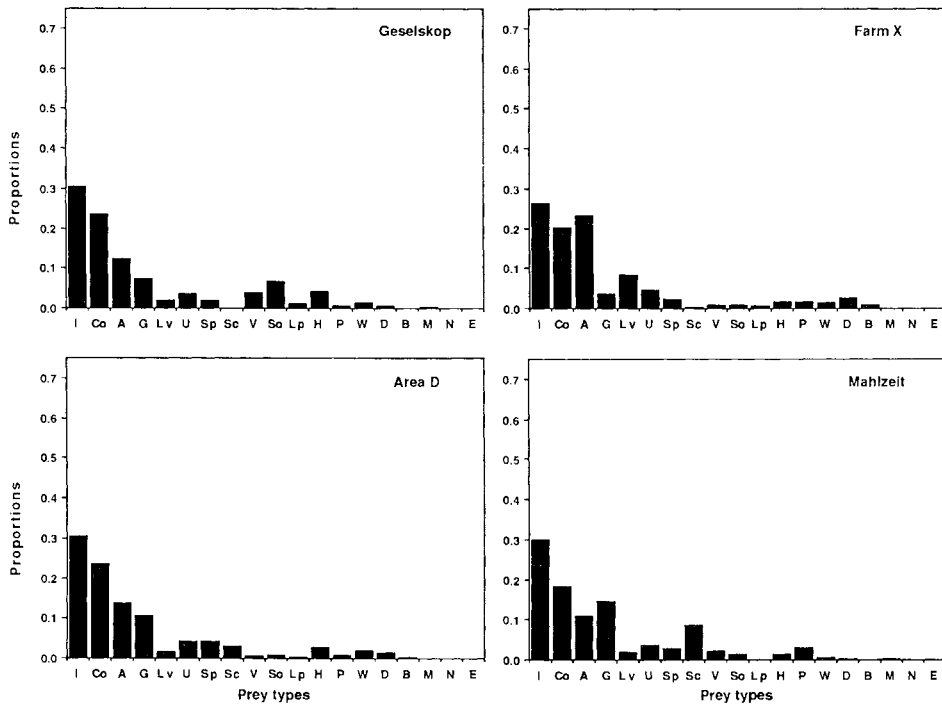


FIG. 3.—Proportional representation of various prey categories in the diets of lizards at four sites in the Kalahari semi-desert of southern Africa. Geselskop is a chenopod shrubby area. Mahlzeit and Farm X are sand-ridge sites in the sand veld. Prey categories are ranked from most abundant to least abundant in the overall diets of all Kalahari lizards at ten different sites. Prey category: I, Isoptera; Co, Coleoptera; A, ants; G, grasshoppers and crickets; Lv, insect larvae; U, unidentified miscellaneous insects; Sp, spiders; Sc, scorpions; V, vertebrates; So, solpugids; Lp, Lepidoptera; H, Hemiptera and Homoptera; P, plants; W, wasps; D, Diptera; B, blattids (roaches); M, mantids and phasmids; N, Neuroptera; E, insect eggs.

Northern Hemisphere, which must certainly have influenced the evolution of nocturnal lizards. However, present-day climates are easily adequate for nocturnal lizards in at least the southernmost parts of the Sonoran Desert of North America. The eublepharine gecko *Coleonyx* thrives as a nocturnal terrestrial lizard in the Sonoran and Mojave deserts, occurring as far north as latitude 37°. Some geckos reach comparable southern latitudes in Australia, and many Asiatic species occur at even higher latitudes (Szczerebak 1986; Szczerebak and Golubev 1986). As expressed so forcefully by Hutchinson in a slightly different context, “if one . . . species can [exist in the nocturnal terrestrial niche], why can’t more?” (1959, p. 150). Even though a native rock-dwelling, climbing gecko, *Phyllodactylus xanti*, occurs in the southern Sonoran Desert and several introduced Mediterranean climbing *Hemidactylus* occur nearby, no arboreal geckos have invaded the flatland deserts of North America. A successful tree- or shrub-climbing gecko species, such as an Australian *Gehyra*, might well be able to establish itself in this

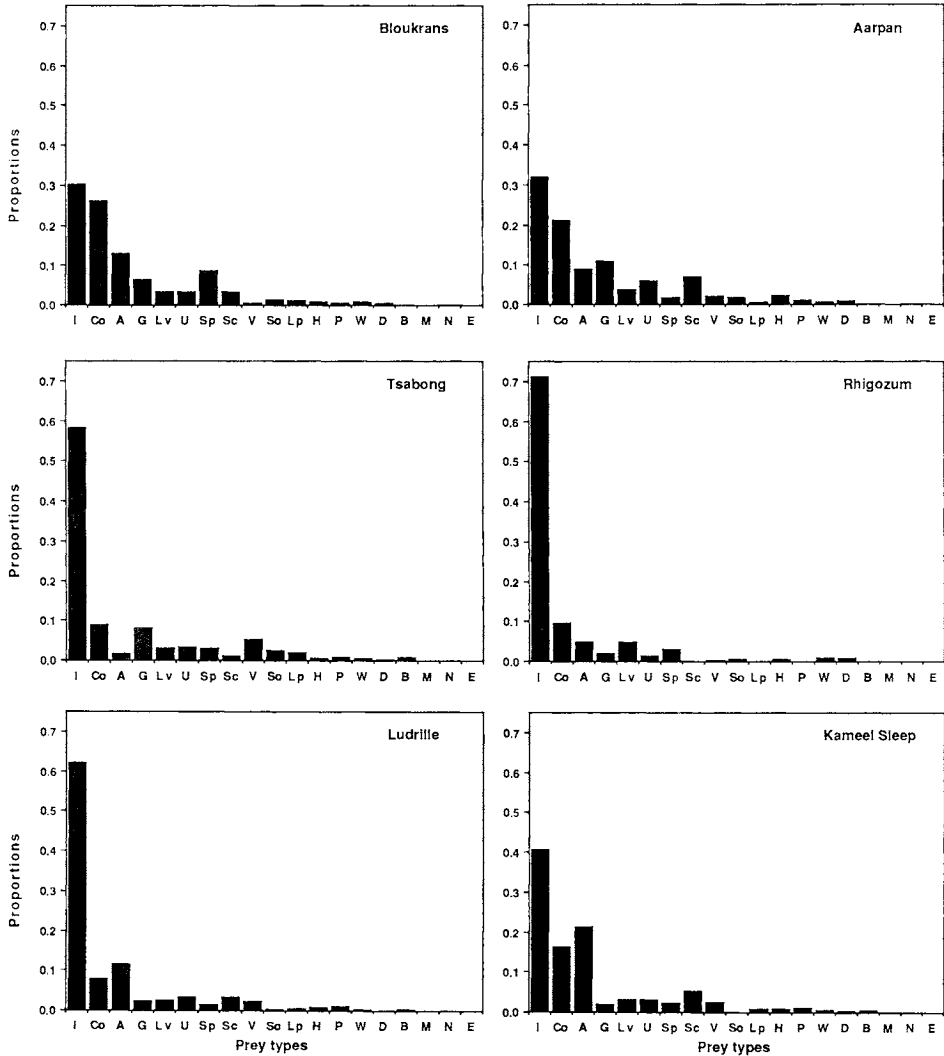


FIG. 4.—Proportional representation of various prey categories in the diets of lizards at six sites in the Kalahari semi-desert of southern Africa, with prey ranked and coded as in figure 3. Tsabong is a sand-plain site in southern Botswana, Rhigozum is a shrub site (non-chenopodiaceous), and the other four areas are sand-ridge sites in the sand veld.

desert region if given an opportunity. Unfortunately, without such an introduction, either accidental or deliberate, such interpretations must remain speculative.

I concur with Morton and James that rich termite faunas should foster nocturnality in lizard consumers, but one cannot downplay the importance of history. An ancient historical component to the diversity of nocturnal lizards is clear. All habitats in the New World exhibit low diversities of such lizards compared with similar Old World habitats (Cogger 1987; Duellman and Pianka 1990). Even the

TABLE 2
 TERMITES AS PERCENTAGE OF DIET FOR ALL LIZARDS AT TEN STUDY SITES IN THE KALAHARI SEMI-DESERT (BY VOLUME)

TERMITE TYPE	STUDY AREA									
	Aarpan	Bloukrans	Area D	Geselskop	Kameel	Ludrille	Mahlzeit	Rhigozum	Tsabong	Farm X
<i>Allodotermes</i> major workers	33	28	32	28	5	27	38	5	27	32
<i>Allodotermes</i> minor workers	6	6	6	6	1	3	5	1	4	6
<i>Allodotermes</i> (others)	0	0	1	0	0	0	0	0	0	1
<i>Hodotermes mossambicus</i>	32	23	38	24	62	27	29	48	29	31
<i>Psammotermes</i> workers	2	4	1	0	1	1	3	0	1	3
<i>Psammotermes</i> soldiers	1	2	1	0	0	0	1	0	1	1
<i>Trinervitermes</i>	19	19	15	15	23	23	13	41	16	22
Termite sp. K	0	0	0	0	0	0	1	0	0	0
Termite sp. M	2	2	0	0	0	0	0	0	0	0
Termite sp. N	0	0	2	0	0	8	0	0	0	0
Termite sp. O	0	0	0	0	0	1	3	0	16	0
Termite sp. P	0	13	0	19	3	2	0	0	1	0
Termite sp. R	0	0	0	0	0	0	1	0	0	0
Other Isoptera	4	2	3	8	5	7	5	4	6	3
Termite diversity	3.92	1.91	3.68	4.95	2.30	4.70	3.88	2.46	4.70	3.94

NOTE.—Termite diversity is estimated from the proportions in the table using the Simpson index of diversity, $1/\sum p_i^2$, where p_i is the proportion of prey type i in the diet.

cold deserts of Asia support a moderate diversity of gekkonid lizards (Szczerbak 1986; Szczerbak and Golubev 1986; Bauer 1987). A well-corroborated gekkonid phylogeny is necessary to decipher biogeographic trends.

FOSSORIALITY

It is hardly surprising that pit traps capture many fossorial *Lerista*, but this sort of sampling is as biased as any other collecting technique and seriously underestimates the relative abundances of active, alert lizard species. When I referred to Australian *Lerista* as "worm-like" (1981), I never intended for anyone to compare them with earthworms. I was using the term "worm" in its broadest sense to refer to their elongate vermiform body shape and seeming lack of legs. The major point I intended to make was simply that fossorial lizards *do not occur* in the North American deserts. In the Kalahari and Australia, subterranean lizards are sand-swimming skinks that specialize on termites. The absence of such fossorial lizards in North American deserts could arise as a result of reduced termite availability on that continent; alternatively, the lack of a suitable scincid phyletic lineage could be invoked. Two sand-swimming lizards are present on the North American continent on coastal sand dunes (the Florida sand skink *Neoseps* and the California legless lizard *Anniella*, a derived anguid), one of which does eat termites. In any case, this intercontinental difference seems largely historical.

ARBOREALITY

In the Great Victoria Desert, an average site supports from 1 to 9.5 species of lizards that live exclusively or to a large extent in trees (mean, 5.4). Comparable numbers for the Kalahari are from 2 to 5 (mean, 3.5); for North America, from 0 to 3 (mean, 0.9). When expressed as a percentage of the total number of species in the saurian fauna, arboreal species represent 18% (Australia), 24% (Kalahari), and 12% (North America). While there are indeed more species of arboreal lizards in Australia, there are not proportionately more. As noted by Morton and James (1988), the widespread distribution of *Eucalyptus* and *Acacia* is a major factor in the adaptive radiation of arboreal lizards in Australia.

HABITAT SPECIFICITY

Australian desert lizards clearly recognize more habitats than do lizards in the Kalahari. In the Great Victoria Desert, 10 lizard species are restricted to sand ridges, whereas only one Kalahari species is so specialized. Extensive habitat specificity contributes greatly to lizard diversity in Australia because most areas contain a mosaic of habitat elements. A perplexing question—why haven't Kalahari lizards evolved as great a degree of habitat specificity as Australian lizards?—remains unanswered. Historical factors, such as the ages of the two deserts and intercontinental differences in other taxa, including *Acacia*, *Eucalyptus*, and *Triodia*, are doubtlessly involved.

USURPATION OF NICHES OF OTHER TAXA

Various historical factors, such as the degree of isolation and available biotic stocks (particularly those of potential prey, predators, and competitors), have clearly shaped lizard faunas. Certain ecological roles occupied by non-lizard taxa in North America and the Kalahari have been usurped by Australian desert lizards. Australian pygopodid and varanid lizards clearly replace certain snakes and mammalian carnivores, taxa that are impoverished in Australia. Species densities of Australian "snakes" are similar to those in North America when adjusted by adding legless, snake-like pygopodid lizards to the real snakes. Just as pygopodids appear to replace snakes, varanid lizards in Australia are clearly ecological equivalents of such carnivorous mammals as the kit fox and coyote in North America. Mammal-like and snake-like lizards contribute from one to eight (usually only four) species at various Australian study sites, representing 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 desert lizards in Australia.

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. More species of ground-dwelling insectivorous birds occur in the Kalahari than in Australia, which could heighten competition between lizards and birds in the Kalahari (Pianka 1986). With increases in the total number of species of birds plus lizards, the number of lizard species increases faster than the number of bird species in Australia, whereas in North America and the Kalahari, bird species density increases faster than lizard species density. Reasons for these differences among continents remain obscure, but one factor may be that few birds migrate in Australia, because of both its isolation and the limited area at high latitude. In contrast, a fair number of migrant bird species periodically exploit the North American and African deserts; lizard faunas of these two desert systems could well be adversely influenced by competitive pressures from these insectivorous avian migrants.

Numerous more-elusive interactions between taxa doubtlessly occur. For instance, the Australian deserts might support such rich lizard faunas because of reduced predation pressures from snakes, raptors, and/or 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.

Even after removal of various non-lizard-like lizards, more species of rather typical (i.e., diurnal terrestrial) lizard-like lizards live in Australia than in other continental desert-lizard systems (Pianka 1986).

Morton and James raised a legitimate question: "Why have lizards usurped the

ecological roles of other taxa in arid Australia more than they have elsewhere?" (1988, p. 240). As they noted, answers to this interesting question are historical in nature.

FIRE-SUCCESSION CYCLE

Fires are a predictable event in arid Australia, particularly in spinifex grasslands (Burbidge 1943; Winkworth 1967; Griffin et al. 1988). Winkworth suggested that all spinifex communities are in a state of cyclic development from fire to fire. He estimated that, 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. Single fires in this region have covered 10,000 km² and 30,000 km², approximately 7% and 20% of the total area of spinifex habitat (Winkworth 1967; Griffin et al. 1988). With such exceedingly high levels of disturbance, one might expect a fairly rapid post-fire recovery rate. Within 4–5 yr, many areas will sustain another burn (Perry and Lazarides 1962). Burned plots converge on their original state quickly; after 7 yr, dry-weight production of spinifex totaled 823 kg per hectare, approximately one-quarter of the standing crop of mature stands at a nearby site (Winkworth 1967). The time required for a burned stand to reach maturity has not been directly estimated, but it is probably at least 20–25 yr, perhaps longer. The probability of a burn presumably increases sigmoidally with the time since the last burn.

Extensive analyses of spinifex fires in the Northern Territory have been undertaken by Griffin et al. (1983), Allan and Griffin (1986), and Griffin et al. (1988). Mapping every identifiable fire in the southern half of the Northern Territory between 1950 and 1984 (more than 5000 fires in some 750,000 km²), they discovered certain informative relationships between fire-patch dynamics and rainfall. At wetter, more productive areas, not only are fires more frequent and more numerous, but patches are more variable in size and tend to be younger. Following periods of low rainfall, fires are both less frequent and homogeneously smaller. Fuel-load recovery is a function of time and total rainfall, prompting these authors to devise a useful temporal-productivity metric against which to measure fires, cumulative millimeters of precipitation. They estimated that approximately 6300 mm of rainfall are needed for a site to accumulate sufficient fuel to burn again under extreme summer conditions.

The phenomenology of wild fires in the uninhabited Great Victoria Desert of remote interior Western Australia can be similarly examined over nearly a quarter of a century. Aerial photographs and satellite images can be used to study and quantify both the spatial pattern of burns and the dynamics of the recovery process. Data that can be collated for each fire include date, area, perimeter, compass direction (of burn and prevailing wind), fractal dimensionality, and the extent of reticulation. The geometry of burns is not only rich in detail but also exceedingly varied. In just 25 yr, some areas in the Great Victoria Desert have burned three times. Average time between fires is about a decade, and few areas escape burning for much longer than 25–30 yr.

In grasslands, fires burn along two fronts that are essentially unidimensional,

each aligned at an approximately right angle to prevailing winds. These fronts burn away from one another in opposite directions: the upwind front burns slowly into the wind, whereas the much hotter downwind front burns faster, racing with the wind. A fire along the upwind front typically dies out more easily than one along the downwind front. Airborne flaming materials, termed firebrands, may jump over unburned areas to rekindle new fires on the downwind side of a fire, sometimes establishing multiple fire fronts (these can extinguish one another when one runs into another's swath). Upon ignition, an isolated grass tussock generates an egg-shaped thermal field. At low wind velocities, isotherms for such fields are nearly spherical and close to the combustibles, but as wind speed increases, thermal fields become more ellipsoidal and extend farther out on the downwind side. If other tussocks are within such a field's threshold temperature for ignition, they too are lit and the fire spreads. Studies of thousands of forest fires have shown that the extent of such fires 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. Major factors that determine the frequency, extent, and geometry of grass fires include combustibility, plant biomass and spatial distribution, natural firebreaks, and, of course, winds, which are of paramount importance. If the density of combustible material is high and winds are not too strong, fire fronts can burn virtually everything in their path, leaving behind an almost completely burned swath (Griffin, pers. comm.). Strong winds, however, generate elongate tongues of fire, which promote reticulation (Griffin, pers. comm.; see also below). Bush fires are usually started by lightning, raging completely out of control for weeks on end across many square kilometers of desert, until they burn themselves out. Thunderstorms and lightning occur regularly during the summer (Griffin et al. 1983). In this part of the Great Victoria Desert, prevailing surface winds usually blow from west to east during most months (Maher and McRae 1964).

Bush fires generate a spatial mosaic of patches of habitat at various stages of post-fire succession (Recher 1981). As a regular agent of disturbance, fires contribute substantially to maintaining spatial heterogeneity and hence diversity in Australian desert lizards (Pianka 1986). Fires vary considerably in intensity and extent. *Eucalyptus* trees are fire-resistant (Gardner 1957), often surviving a hot but brief ground fire carried by the exceedingly combustible spinifex (*Triodia* and *Plectrachne*). Indeed, spinifex tussocks are perfectly designed for combustion, consisting of hemispherical clumps of numerous match-stick-sized blades of dry, curled grass filled with flammable resins; the blades loosely interpenetrate one another and are laced with ample air spaces.

Fires frequently reticulate, missing an occasional isolated grass tussock or even large tracts embedded in, or immediately adjacent to, burns. Previously burned areas have sparser vegetation and act as gigantic firebreaks. Sand ridges and the bare surfaces above termitaria create smaller areas without vegetation, which also act as local firebreaks but with fundamentally different geometries and at different spatial scales. "Sleepers," created from burning hardwood embers of *Eucalyptus*, lie dormant in burned areas; some of these hot coals at the edges re-ignite days or even weeks later when new strong winds come up. New secondary bush fires take

TABLE 3
LIZARD CENSUSES AND DIVERSITY AT THREE STUDY SITES
IN THE GREAT VICTORIA DESERT

LIZARD SPECIES	AREA		
	N	L	G
Agamidae			
<i>Ctenophorus inermis</i>	2	14	6
<i>Ctenophorus isolepis</i>	18	585	113
<i>Moloch horridus</i>		18	1
<i>Pogona minor</i> *		20	3
Varanidae			
<i>Varanus eremius</i>	1	16	3
<i>Varanus gouldi</i>	1	4	1
<i>Varanus tristis</i> *		24	2
Scincidae			
<i>Ctenotus ariadnae</i>		16	
<i>Ctenotus calurus</i>	5	158	3
<i>Ctenotus grandis</i>	3	84	2
<i>Ctenotus helenae</i>	1	84	2
<i>Ctenotus pantherinus</i>	2	29	17
<i>Ctenotus piankai</i>	5	5	2
<i>Ctenotus quattuordecimlineatus</i>	1	229	31
<i>Ctenotus schomburgkii</i>		47	6
<i>Cryptoblepharus plagiocephalus</i> *		80	2
<i>Egernia inornata</i>	6	4	7
<i>Egernia kintorei</i>		1	
<i>Egernia striata</i>	4	105	10
<i>Lerista bipes</i>		59	2
<i>Lerista muelleri</i> *		6	
<i>Menetia greyi</i>	3	7	e
<i>Morethia butleri</i> *		1	1
<i>Omolepida branchiale</i>		e	2
Pygopodidae			
<i>Delma fraseri</i>		4	e
<i>Lialis burtonis</i>		4	e
<i>Pygopus nigriceps</i>		11	e
Gekkonidae			
<i>Diplodactylus conspicillatus</i>		33	9
<i>Diplodactylus elderi</i>		4	e
<i>Diplodactylus stenodactylus</i>		2	1
<i>Gehyra variegata</i> *		316	48
<i>Heteronotia binoei</i>	3	2	1
<i>Nephruurus levis</i>	8	10	2
<i>Rhynchoedura ornata</i>	10	114	28
Total number of individuals	73	2095	309
Total number of species	16	32	26
Species diversity	8.5	6.2, 9.9†	5.5

* Arboreal or litter-dwelling, associated with *Eucalyptus* trees.

† 1966–1968, 1978–1979.

e, Highly expected but not collected.

off at an angle to the primary burn, resulting in an interesting reticulating pattern that generates a qualitatively and spatially different sort of habitat refuge for various animals.

The extent to which grass fires reticulate appears to vary from region to region with the structure of the vegetation. In the savanna woodland of the Kalahari semi-desert in Botswana, southern Africa, for example, fires are frequent but do not seem to reticulate nearly as much (Short et al. 1976, p. 377, plate 342) as do fires in Australian spinifex habitats. Because spinifex habitats are relatively more open and contain various natural firebreaks, fires may reticulate more than they do in more homogeneous areas (this supposition can be tested by comparing fire geometries in different geographical regions using satellite imagery).

Combined effects of these forces on lizards and lizard microhabitats are drastic, yet exceedingly heterogeneous in space. Certain lizard species are arboreal or associated with trees. Many, even most, individual lizards survive such burns (Greer, pers. comm., cited in Recher 1981), although survival rates of some species are doubtlessly reduced for some time afterwards. Many lizards may become inactive, staying underground for a month or more until the vegetation and insect fauna recover. Population densities of certain open-dwelling lizard species, such as *Ctenophorus fordi* and *C. isolepis*, are actually greater on recently burned areas (Cogger 1969, 1972; Griffin et al. 1988). Many other desert lizard species, including *Ctenophorus inermis* and *Ctenotus calurus*, presumably reinvade burned areas, quickly reaching high densities in their preferred open habitat. Such species persist, but at extremely low densities, even in mature stands of dense, closed-in spinifex. Other lizard species, such as *Delma fraseri*, *Omolepida branchiale*, and *Diplodactylus elderi*, require large spinifex tussocks for microhabitats and presumably nearly vanish over extensive open areas following a burn. However, such climax species continue to exist as relicts in the isolated pockets and patches of habitat that escaped burning.

Following a fire caused by lightning, sands are frequently wetted by thunder-showers. This facilitates rapid regeneration of spinifex, from both live roots and seedling establishment (Burbidge 1943). Newly burned areas are quite open, with lots of 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 the gaps between tussocks. Both factors increase the probability that a fire will be carried. Throughout this process, lizard microhabitats and associated food resources gradually change. Lizard species on recently burned areas constitute a subset of those present at more-mature climax sites (table 3). However, even though diversity is reduced, the overall abundance of lizards may actually remain as great (Griffin et al. 1988). The prey spectrum for a recently burned area (fig. 1, Neale) differs from that of a less recently burned area (fig. 2, Laverton, Great Victoria), with fewer termites but more spiders. Before a 1982 fire in the Laverton area, the fairly mature unburned site had an exceptionally high abundance of termites, which did not change appreciably between 1968 and 1978 (excluding lizards as food, the percentage of termites by volume in the overall diet of all lizard

species was 53.2% in 1968 and 51.1% in 1978). Comparing the prey-resource spectrum known before most of the areas burned with the post-fire spectrum would be exceedingly interesting.

The elements described above can be exploited to develop dynamic models of fire succession incorporating disturbance probabilities, flammabilities, fuel-load recovery curves, and various firebreak geometries, as well as the resulting spatial heterogeneity of microhabitats. Species-specific habitat requirements and colonization abilities of various lizards should also be incorporated into models. Models should generate testable predictions, such as expected frequency distributions of ages and sizes of fire scars, changes in relative abundances of insects, and colonizing versus climax species of lizards.

Further fieldwork is needed to document vegetational structure and the closure rates of spinifex. In addition, more information should be collected on exactly which lizard species are present, and in what abundance, at various stages following burns. Termite abundances and diversities should be estimated for sites at different stages of post-fire regeneration. Low-level aerial photography needs to be undertaken to make detailed maps of vegetational structure. Lizard faunas and foods eaten by lizards should be compared at several sites, recently burned and at various stages of post-fire recovery, to collect data for more-precise modeling of the dynamics of the fire-succession cycle. Exploiting controlled burns to test some aspects of such fire-succession models might well prove feasible. Morton and James' scheme (1988, p. 248, fig. 1) is easily modified to incorporate the fire-succession cycle, simply by adding fires to the list of physical factors. Spatial heterogeneity of habitats, which leads to lizard diversity, should also be added with an additional arrow leading to lizard diversity.

BIOGEOGRAPHIC AND HISTORICAL FACTORS

It is overly facile, even glib, to assert that one area has more species than another simply by virtue of antiquity. Ecological factors allowing coexistence of species and maintenance of diversity are essential. Nevertheless, one clearly cannot ignore history. Historical factors were invoked in more than half of the preceding sections.

Effects of historical variables such as plate tectonics and the Pleistocene glaciations are doubtlessly considerable but exceedingly difficult to evaluate. Higher taxonomic levels contribute little to differences in diversity since exactly five lizard families are represented in each continental desert-lizard system, although their identities differ (Pianka 1986). Different stocks of lizards interact differently with desert environments.

North American deserts are generally acknowledged to be of relatively recent geologic origin (Axelrod 1950), although sub-desert conditions probably prevailed in the general region long before the origin of true deserts. During the Upper Tertiary period, American deserts expanded but, with the onset of the Pleistocene glaciations, became restricted to northern Mexico and the extreme southwestern United States. Presumably, these deserts expanded rapidly to their present boundaries with the retreat of the glaciers about 10,000 yr ago.

The sands of the Kalahari were formed largely by the wind and originally distributed during the Tertiary, then redistributed in the Pleistocene by both wind and water. Kalahari sand ridges probably assumed roughly their present distribution during drier periods over the last 10,000 yr; the subsequent stabilization of the sand ridges by vegetation suggests a slight amelioration of the climate in more recent times (Lancaster 1979). So-called "Kalahari" sands are widespread in southern Africa, occurring well beyond the confines of the currently recognized Kalahari semi-desert. Dry to very dry conditions have prevailed in the area since the middle to the end of the Tertiary (Lancaster 1984).

Views on the age and history of the Australian deserts are varied and conflicting. Crocker and Wood (1947) postulated a "great aridity" following the last glaciation during the Pleistocene epoch, but others have argued for a much greater antiquity for at least portions of the continent (Bowler 1976; Bowler et al. 1976; Galloway and Kemp 1981). Certainly, Australian sand ridges appear exceedingly ancient (Bowler 1976).

The very arid Namib Desert of southwestern Africa is also quite ancient (Ward et al. 1983) and supports an extremely rich beetle fauna; yet it has only a moderate diversity of endemic lizard species (particularly geckos and lacertids). Most of these species have restricted geographical distributions, and diversity at any one spot is invariably low (Haacke 1976; Werner 1977; Robinson and Cunningham 1978). Hence, antiquity alone is insufficient to generate high lizard diversity.

Application of powerful new molecular techniques in phylogenetic systematics (Hillis 1987) certainly promises to decrease our ignorance of biotic historical factors. Intercontinental differences in the phylogenies of termites will be as crucial to our understanding as the differences among the various lizard groups. Cladistics can even be used to infer more-elusive non-biotic biogeographic events. As community ecologists race to catch up with other disciplines in biology before pristine natural systems vanish forever, we must discover better ways of dealing with the complex effects of biogeographic phenomena and historical constraints on community structure and organization (Duellman and Pianka 1990).

SUMMARY

A complex mega-hypothesis invoking multiple causality was recently proposed to explain the high diversity of lizards in arid Australia (Morton and James 1988). Putative causal links in its intricate scheme are evaluated, and some data are presented that can be brought to bear on the problem. Although many links in the causal network appear fairly well established, some are weak. Evidence that Australian soils are infertile is less than compelling. Chenopod-shrub sites do not necessarily support impoverished termite faunas, as had been predicted; a chenopod site in the Kalahari had the highest termite diversity of 10 study areas. Moreover, termites dominate the diets of Kalahari lizards and appear to be more abundant in the Kalahari semi-desert than in Australian deserts. A greater percentage of lizard species specialize on termites in the Kalahari than in Australia. A fire-succession cycle is quite important in spinifex habitats in Australia, generating a mosaic of habitats with differing degrees of openness at various post-fire

ages; this greatly enhances lizard diversity. Fires may reticulate more in inland Australia than in grassland regions in other parts of the world. Satellite imagery can be used to examine and quantify fire geometry. Fires, and fire-generated spatial heterogeneity, should be added to the list of physical factors driving the desert-lizard system. Historical and biogeographic phenomena must be better integrated into attempts to explain differences in diversity between geographical regions.

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