

THE DIVERSITY AND ABUNDANCE OF LIZARDS IN ARID AUSTRALIA: A NEW HYPOTHESIS

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Submitted May 12, 1987; Accepted November 12, 1987

The vertebrate fauna of arid Australia is characterized by an extraordinarily rich assemblage of lizards, an ecological phenomenon first recognized and described by Pianka (1969a,b, 1972, 1973, 1981, 1982, 1986; Pianka and Pianka 1976). The extent of the Australian lizard radiation remains a challenge to ecologists, because Pianka's (1975, 1986) careful comparisons of Australia, southern Africa, and North America demonstrate that individual arid ecosystems have disparate assemblages despite their superficially similar environments. Pianka recently concluded that "the differences in the ecologies of most lizard species among these three continental desert-lizard systems are much more striking than are the similarities" (1986, p. 23). Why are there so many species of lizards in local assemblages in arid Australia? Naturally, Pianka has devoted considerable thought to potential explanations, as have other workers (see, e.g., Milewski 1981a; Cogger 1984). We believe that the proposed explanations are not completely convincing; in addition, recent research suggests that some aspects of the Australian radiation are still not widely recognized. In this paper, we review the published hypotheses for the high local species diversity among lizards in Australia and then examine emerging concepts about edaphic, climatic, and biological characteristics of inland Australia that may assist in the search for a more complete explanation. Finally, we advance a set of predictions that allows the key segments of our hypothesis to be tested. Our principal interest lies in the diversity of lizards that may be found at one site. We consider beta diversity only briefly, because we believe that Pianka (1972) has provided an adequate historical explanation.

ABUNDANCE OF LIZARDS

We begin by looking at two aspects of the Australian lizard fauna that seem poorly appreciated: the abundance of lizards, and the prominence of subterranean species. Pianka's comments on the relative abundance of lizards (Pianka 1969a,b, 1972, 1973, 1986) are carefully written, but he sometimes gives the impression that

TABLE 1

MEAN ABUNDANCES OF ELEVEN SPECIES OF AUSTRALIAN LIZARDS IN A SPINIFEX GRASSLAND

Species	Estimated Abundance (no./ha)	Estimated Biomass (g/ha)
Scincidae		
<i>Ctenotus helena</i>	18	215
<i>C. leonhardii</i>	25	128
<i>C. pantherinus</i>	56	740
<i>C. quattuordecimlineatus</i>	68	306
Agamidae		
<i>Ctenophorus isolepis</i>	33	198
Gekkonidae		
<i>Diplodactylus ciliaris</i>	37	255
<i>D. conspicillatus</i>	39	160
<i>D. stenodactylus</i>	55	148
<i>Nephrurus levius</i>	34	384
<i>Rhynchoedura ornata</i>	48	67
Varanidae		
<i>Varanus brevicauda</i>	26	257
TOTAL	439	2858

NOTE.—Estimates of abundance based on mark-recapture studies during spring and summer, 1985–1986; study site is located in a spinifex dune field with *Triodia basedowii* and *T. pungens* 30 km south of Alice Springs, Northern Territory. Estimated abundances calculated using the Petersen method and averaged over 12 subsites.

most species are sparse: for example, “one must often work all day to collect just a few dozen animals” (1986, p. 150). Most Australian herpetologists probably share this opinion, but our current mark-recapture studies in a spinifex dune field in central Australia suggest that the abundance of lizards is greater than has been realized. Our work is based on an array of 200 pit traps at a 50-ha study site situated 30 km south of Alice Springs, Northern Territory (mean annual rainfall, 270 mm). The pit traps are grouped into 12 subsites, each covering 0.3 ha. Table 1 shows the mean density estimates for adults of 11 of the most common of the 41 species recorded, calculated from over 2000 records of individually marked lizards captured from September 1985 to November 1986.

The skinks *Ctenotus pantherinus* and *C. quattuordecimlineatus* were the most common species; two other *Ctenotus* species were also abundant. The most conspicuous species, *Ctenophorus isolepis*, was less abundant than many of the more cryptic skinks and geckos. One particularly cryptic species, *Varanus brevicauda*, is rarely or never seen by humans, but it is reasonably common, judging by our pit-trapping results. The only other published density estimate for arid Australian lizards is similar to that shown in table 1 (3110 g/ha; Heatwole and Butler 1981).

The abundance of many of the species at our study site was greater than, or comparable to, that of dominant species in North American flatland deserts (table 2). We attempted to include maximum estimates for all common species studied by Pianka (1967, 1986, p. 155) in the flatland deserts of North America. A comparison of the two tables suggests that the total biomass of lizards is far greater in Australia than in North America; a maximum of 10 species may be

TABLE 2

MAXIMUM ABUNDANCES OF SIX OF THE DOMINANT LIZARD SPECIES
IN NORTH AMERICAN FLATLAND DESERTS

Species	Maximum Abundance (no./ha)	Estimated Biomass (g/ha)	Source
Teiidae			
<i>Cnemidophorus tigris</i>	185	3700 ^a	Milstead 1965
	15	306	Turner et al. 1969b
	12	240 ^a	Pianka 1970
	36	720 ^a	Parker 1972
Iguanidae			
<i>Callisaurus draconoides</i>	2	10 ^a	Pianka & Parker 1972
	15	75 ^a	Tanner & Krogh 1975
<i>Crotaphytus wislizeni</i>	3	91	Turner et al. 1969a
<i>Phrynosoma platyrhinos</i>	5	120	Tanner & Krogh 1973
<i>Sceloporus magister</i>	7	210	Tinkle 1976
<i>Uta stansburiana</i>	31	100	Tinkle & Woodard 1967
	44	140	Turner et al. 1970
	26	83	Tanner & Hopkin 1972
	50	160	Parker 1974

NOTE.—The species considered are those occurring in the flatland-desert system studied by Pianka (1967).

^a Our approximate calculations; all other estimates provided in the sources.

found together in North America, but the 11 Australian species listed in table 1 show abundances equivalent to or greater than the maximum densities recorded for dominant North American species. Further, inclusion of the 30 less common Australian species not shown in table 1 will significantly increase our final estimates when sufficient recapture data become available. Although we must be cautious because detailed estimates for Australia are available only from our site, it appears that both the diversity and the abundance of lizards are greater in spinifex grasslands than in North American deserts.

Another aspect of abundance concerns subterranean species, especially members of the species-rich scincid genus *Lerista*. Pianka's extensive surveys (1986, pp. 157–158) suggested that such animals were rarely captured, but we found large numbers of *Lerista bipes* during further pit-trapping studies conducted near The Granites, 500 km northwest of Alice Springs (mean annual rainfall, about 370 mm) (table 3). *Lerista bipes* dominated all samples, constituting 62% of the individuals captured; because individuals weigh only 0.7 g, on the average, the percentage of biomass was correspondingly less. At the Alice Springs site, *Lerista* species were less abundant (26% of individuals captured). In Pianka's (1986) sample, in contrast, *Lerista* species constituted a mere 1.4% of individuals captured by active searching. Pit trapping does not necessarily provide a more reliable measure of absolute abundance than does active searching, but compared with the latter method it is less biased against subterranean species. We conclude that subterranean Australian lizards are considerably more abundant at some places than has hitherto been recognized. Thus, arid Australia appears even more different from the North American deserts, where subterranean lizards do not occur, than

TABLE 3

RELATIVE PROPORTIONS OF VARIOUS GROUPS OF AUSTRALIAN REPTILES IN A SPINIFEX GRASSLAND

TAXONOMIC GROUP	NUMBERS OF INDIVIDUALS CAPTURED PER SAMPLING PERIOD			NO. OF INDIVIDUALS	ESTIMATED TOTAL BIOMASS (g)
	Mar-Apr 1985	Oct-Nov 1985	Mar-Apr 1986		
Scincidae					
<i>Lerista bipes</i>	123	341	202	666	466
Other species	37	90	24	151	903
Agamidae	4	12	3	19	132
Gekkonidae	9	145	49	203	356
Pygopodidae	—	2	2	4	36
Varanidae	3	3	7	13	279
Typhlopidae	4	10	8	22	44

NOTE.—Measured by pit trapping at eight sites within 50 km of each other on a spinifex sand plain with *Plectrachne schinzii*, 500 km northwest of Alice Springs, Northern Territory; trapping effort in the first sample was 720 pit-trap days, and in the other two 960 pit-trap days.

Pianka (1969a, 1973, 1986) has described. Subterranean species are prominent in the Kalahari (Huey et al. 1974; Pianka 1986), but quantitative comparison with Australia is not yet possible.

The Australian fauna has, therefore, two attributes in addition to those previously elucidated: abundance of individuals, and prominence of subterranean species. We begin our attempt to incorporate these features into an explanatory framework by re-examining previous hypotheses about the greater richness of lizard species in Australia.

PREVIOUS HYPOTHESES

Six hypotheses exist, some of which are interrelated. We believe that most have value but that they do not coalesce into a satisfactory whole. In discussing them, we highlight what we consider to be their more valuable attributes and later try to weld these aspects into a more comprehensive theory.

Usurpation by Lizards of Ecological Roles of Other Taxa

Pianka (1969a, 1973, 1975, 1981) suggested that some Australian lizards have usurped the ecological roles played by other taxa on other continents. As examples, he postulated that some *Lerista* (Scincidae) and *Aprasia* (Pygopodidae) are "worm-like," that some *Lerista* and *Menetia* (Scincidae) are "insect-like," that many pygopodids are "snake-like," that *Varanus* (Varanidae) are "mammal-like," and that, overall, the lizard fauna either competitively appropriated the resources used on other continents by birds or escaped competition with birds (Pianka 1969a, 1973).

The underlying difficulty with nearly all these postulates is that they are not explanations. We must still ask *why* usurpation has taken place. The concepts of

usurpation and inter-taxon competitive displacement imply that through evolutionary time one taxon obtained a greater proportion of available food resources, achieved better survival rates, reproduced more successfully, and radiated more rapidly than another. In order to arrive at a basic explanation, however, one must find out why one group was more successful at utilizing resources in that environment. Answers to this question must be of two general types.

One answer could be that past climatic events or geographical factors have allowed the development of high local species richness among lizards in arid Australia by reducing the ability of potentially competing taxa to inhabit the environment and to radiate within it (Pianka 1969a, 1972, 1973, 1986). The presumed outcome of these idiosyncratic factors would be that any groups not excluded could radiate with relatively little competitive restriction and might then appropriate the resources generally used by the excluded group. Pianka (1985, 1986) examined and rejected the possibility that more extreme Pleistocene glaciation restricted the diversity of lizards in North America compared with that in Australia and South Africa. The suggestion is not convincing for a variety of reasons, and, as Pianka expressed it, "it is overly facile, even glib, to assert that the Australian deserts are more diverse than other deserts simply by virtue of antiquity" (1985, p. 502).

Similarly, it is difficult to see how the evolutionary history of the lizards could have resulted in a more dramatic radiation in Australia than elsewhere. All modern families of lizards appear to have originated in the early Cretaceous or before; in particular, most of the families now present in North America are known to have been on that continent as early as the Cenozoic (Estes 1983). Thus, there appears to have been ample time for diversification to occur in North America. Further, it cannot be argued that lizards radiated more dramatically in Australia because of a paucity of birds and mammals. Large elements of the Australian gekkonid, pygopodid, scincid, and varanid radiations are probably of Gondwanan origin (Estes 1983; P. R. Baverstock, pers. comm.); hence, lizards, together with extensive faunas of birds, mammals, and many other animals, were present throughout the development of the Australian arid zone. Under these conditions, it is difficult to imagine purely geographical effects that gave lizards the upper hand.

We concur with Pianka (1986), therefore, that ecological factors are more likely to account for the high present-day diversity of Australian lizards. We recognize, however, that much could be learned from an analysis of the history of lizards on the various continents. Paleontological analysis is an important technique, but perhaps a more promising approach is biochemical analysis of present faunas using methods such as microcomplement fixation (Baverstock, pers. comm.). Such an approach may allow reconstruction of the timing and the rates of radiation on different continents, and thus it would provide a historical assessment of the ecological hypothesis advanced below.

A second possible explanation for the differential success of vertebrate groups in arid Australia is that they possess differing abilities to survive and reproduce in that environment because of the relative fitnesses of their physiologies for that

habitat. Lizards are relatively diverse in most arid areas of the globe, presumably because the costs of thermoregulation are lower in arid areas and because the ability to become inactive during periods of stress confers an advantage on ectotherms over endotherms in relatively unpredictable arid environments (Schall and Pianka 1978; Pianka 1986). Because lizards are universally successful in arid environments, we need to ask what attributes of arid Australia have resulted in greater species richness and high densities of individuals. In urging the necessity of examining the characteristics of available resources, we are establishing a theme to which we return continually below.

One aspect of the supply of resources in arid Australia is of primary importance. As Pianka (1973, 1981) pointed out, rainfall is relatively uncertain in arid Australia, and extended dry periods lasting unpredictably from months to years are characteristic (Gentilli 1971; Low 1978; Westoby 1980; Morton 1982; Griffin and Friedel 1985). Because of the difficulties faced by endotherms in withstanding substantial, unpredictable reductions in food supplies during extended dry periods, mammals are less diverse than they are in North American deserts; small mammals in particular are much less abundant (Newsome and Corbett 1975; Morton 1979; Morton and Baynes 1985). In general, birds experience the same difficulties; local populations fluctuate considerably, and nomadism is prominent (Schodde 1982). In contrast, lizards are much better equipped to persist through unproductive periods. One immediate consequence of these factors is that mammalian predators are scarce in arid Australia. Not only do they face severe difficulties in surviving long periods of adverse conditions, but during winter they may also find it difficult to subsist on lizards, which, in the main, remain inactive. Following Milewski (1981a), we suggest that reptiles themselves are the most effective predators under these conditions and that this is why varanid lizards are so prominent as predators and scavengers (for a summary of dietary studies, see Pianka 1982).

Some other suggestions of usurpation advanced by Pianka (1969a, 1973, 1975, 1986) may be misleading. As Cogger (1984) has pointed out, *Lerista* and *Aprasia* cannot be considered "worms" when they eat invertebrates, a diet most unlike that of earthworms. Pianka's (1969a) assertion that the local species richness of desert-dwelling snakes is lower in Australia than in North America is difficult to sustain, because the numbers of species listed in his table 4 do not differ significantly between continents (Mann-Whitney *U*-test, $P > 0.1$). Further, we have recorded eight species of snakes at our study site south of Alice Springs, a number greater than at any of Pianka's (1969a) Australian sites. Thus, it seems unnecessary to postulate usurpation by pygopodid lizards of the role of snakes.

In conclusion, the concepts of inter-taxon exclusion and usurpation by lizards do not explain the greater richness of lizard species in arid Australia because they merely restate the fact that one group is more successful than another in using available resources. One pattern of resource availability—highly uncertain production—does suggest why lizards should be more prominent in Australia, and we continue to focus on resource characteristics during the following examination of further hypotheses.

The Structure of Spinifex

Pianka (1969a, 1972, 1973) and Cogger (1974, 1984) emphasized the importance of spinifex grasses (*Triodia* and *Plectrachne*) to Australian lizards because the spinifex grasslands contain the richest assemblages of species. They suggested that spinifex is extraordinarily well suited to lizards because it provides extremely prickly and effective protection from predators, a microclimate considerably less harsh than the arid environment at large, and a horizontal structural diversity that encourages fine-scale partitioning of space (lizards may forage principally within hummocks, at their edges, or in spaces between them). Pianka (1981) also suggested that spinifex hummocks provide a rich insect supply.

These suggestions are only partly convincing because only lizards reach spectacular levels of species richness in spinifex grasslands. Each suggestion should apply to some degree to other vertebrate groups, but in important ways none does. There are few methodical studies of birds, but our current work suggests that the avifauna of spinifex grasslands is characterized by low diversity and scarcity (M. R. Fleming and Morton, unpubl. data). Spinifex appears to provide resources that are suitable more for reptiles than for birds. Birds seem less likely to partition space horizontally; rather, avian diversity tends to increase more with vertical heterogeneity (Cody 1985). Consequently, the principally horizontal nature of patchiness in spinifex may be disadvantageous to birds.

Such an explanation cannot apply to small mammals, however. In North American deserts, small mammals partition horizontal space extensively and exhibit high species richness (Price and Brown 1983). Yet, few species of Australian rodents occur in spinifex grasslands; indeed, they are usually uncommon or rare (Morton 1982; Morton and Baynes 1985). The resource supply for herbivorous and granivorous small mammals must be so poor that they have generally been unable to make use of the beneficial attributes of spinifex outlined by Pianka and Cogger. In contrast, about ten species of insectivorous dasyurid marsupials, nearly half the arid Australian fauna, occur in spinifex (although they are usually uncommon), and specialization has proceeded to the generic level (*Ningaui*; see Kitchener et al. 1983). Consequently, insectivorous mammals seem to have radiated in concert with lizards, although nowhere near as dramatically. These considerations lead us to argue that explanations of the greater species richness of lizards are to be found principally in the food web built up on this unusual grass and not solely in its structure. The argument, which is fully developed below, is that termites are especially abundant in spinifex grasslands and that they are particularly suitable prey for lizards.

Nocturnality

Relatively large numbers of species of nocturnal lizards occur in arid Australia (Pianka 1969a; Pianka and Pianka 1976). Cogger (1984) was not inclined to believe that the phenomenon has ecological significance; instead, he suggested that the prominence of nocturnality simply reflects fortuitous early colonization by nocturnal groups. We do not agree with Cogger; instead, we agree with Pianka (1973,

1986), who has argued persuasively that far fewer nocturnal lizards have arisen in other deserts despite the presence of appropriate colonizing stock. Nocturnal lizards may not have succeeded in North America for two reasons: the presence of a diverse fauna of nocturnal mammals (Milewski 1981a), or a paucity of nocturnal invertebrate prey (Pianka 1973, 1981, 1986).

Milewski (1981a) argued that in arid North America and southern Africa predatory mammals are sustained by the high densities of granivorous small mammals, thereby implying that nocturnal lizards experienced constantly high predation pressure over evolutionary time. In Australia, however, nocturnal lizards are preyed on mainly by other reptiles; thus, lizards may have radiated more dramatically. The suggestion has merit, but some of its ramifications are difficult to assess. It assumes that predatory mammals exert stronger evolutionary pressure than do reptiles, a postulate virtually impossible to test. Further, it is difficult to reconcile with the fact that no nocturnal or diurnal insectivorous vertebrate group is as diverse in North American deserts as in arid Australia, which indicates that North American insectivores in general have experienced limited evolutionary opportunities. Thus, it seems likely that the paucity of nocturnal lizards reflects to some extent a more widespread phenomenon, namely, a less abundant invertebrate fauna. As discussed below, we believe that Pianka's (1973, 1981, 1986) emphasis on invertebrates warrants further attention.

Arboreal Habitats

Arboreal species are frequently present in arid Australia; they are less frequent in the Kalahari and rare in North America (Pianka 1969a, 1973, 1986). This important segment of the arid Australian lizard fauna reflects the presence of tall shrubs or trees (principally *Acacia* and *Eucalyptus*) in acacia shrublands and spinifex grasslands, the two dominant vegetational formations. Dominance by tall shrubs and the presence of trees result first from climatic factors causing sporadic heavy rainfalls, often decades apart, which allow long-lived plants to become established (Westoby 1980; Milewski 1981b; Griffin and Friedel 1985), and second from infertility, which may reduce competition from ephemeral plants during the rare establishment opportunities (Coley et al. 1985). We believe Pianka's (1969a, 1973, 1986) explanation of the use of arboreal habitats to be sufficient; we merely observe that terrestrial lizards inhabiting dense litter may also be more widespread and diverse because of the abundance of trees and shrubs. As Pianka has shown, however, the greater use of arboreal habitats cannot, by itself, account for the greater diversity of Australian lizards.

Habitat Specificity

Lizards appear to recognize more habitats in Australia than elsewhere (Pianka 1969a, 1972, 1973, 1986). Historical factors are probably important in the development of high beta diversity, although Pianka does not rule out ecological factors. He has convincingly depicted modes by which broad habitat selection may have evolved (Pianka 1972), but the selective forces favoring fine-scale microhabitat partitioning remain obscure.

Pianka (1986) also suggested that fire-driven succession in spinifex grasslands might help maintain diversity. Successional change is reflected by the changing specific composition of lizard assemblages (Morton and M. W. Gillam, unpubl. data), but this relationship cannot by itself explain why so many species occur together in any one successional state.

Nutrient Limitation

Milewski (1981a) postulated that because inland Australian soils are generally less fertile than the soils of arid North America and southern Africa, the production of resources suitable for vertebrates is less and is more sporadic. Hence, lizards are favored because they can forgo food for long periods, whereas birds and mammals require regular sources of food. Milewski (1981a) also made the connection between infertility and the structure of perennial vegetation such as spinifex, thereby suggesting that nutrient limitation had produced a type of plant cover particularly suitable for lizards. We feel that Milewski (1981a) made an important conceptual advance but that his argument was not fully developed. The linkage between infertility and food resources deserves closer examination.

THE DIVERSITY AND ABUNDANCE OF LIZARDS: A SYNTHETIC THEORY

Any theory must account for the fact that spinifex grasslands contain the richest lizard assemblages (Pianka 1969a, 1986). Thus, this discussion begins with spinifex and then incorporates other arid Australian habitats.

Spinifex Grasslands

Spinifexes occur principally on well-drained, infertile, sandy soils, and their unique spiky sclerophyllous structure is thought to be an adaptation to nutrient poverty under aridity (Winkworth 1967; Beard 1984; Griffin 1984). Persistent, sclerophyllous aboveground tissue is a consistent adaptation to low nutrient levels in many parts of the world (Coley et al. 1985). In line with this relationship, the accumulation of aboveground tissue in spinifex grasslands ranges up to 8000 kg/ha (Winkworth 1967). This relatively high biomass is nevertheless of limited value to many herbivores because it is nutritionally poor (Mattson 1980); most grazing mammals virtually ignore spinifex (Newsome 1975; Kinnear and Main 1979). The accumulation of vegetational biomass does, however, provide food for detritivores, prominent among which are the termites. Many termites appear to prefer grasses and litter that contain little nitrogen, and they may even be disadvantaged by diets high in nitrogen (Spears and Ueckert 1976; Collins 1983). Consequently, spinifex grasslands contain enormous food supplies suitable for termites but not for most other herbivores. We suggest, in short, that the spinifex grasslands contain termite populations of enormous abundance and of considerable diversity.

Recognition of the general significance of Australian termites in the structuring of food webs has been slow to emerge. Matthews commented that "termites have a greater influence than any other single group of animals on the production, flow

and storage of energy . . . in arid Australia" (1976, p. 56) and suggested that this effect was particularly pronounced in spinifex grasslands and mulga shrublands, scrub thickets consisting primarily of *Acacia aneura*. Watson reported that "the fauna is surprisingly rich" (1982, p. 263), particularly among the dominant genera *Amitermes*, *Drepanotermes*, *Nasutitermes*, and *Tumulitermes*, which have speciated to a marked degree in the arid zone (Gay and Calaby 1970; Watson and Perry 1981; Watson 1982; Watson and Gay 1983).

In some areas of firmer soils, the remarkable densities of termite mounds makes the abundance of termites immediately evident (e.g., in the Tanami Desert, 800 mounds/ha; Morton, unpubl. data). Limited excavation suggests that foraging tunnels run from the nest within about 10 cm of the surface to virtually every spinifex hummock, opening from a vertical offshoot onto the surface beneath the center of the hummock (Watson 1969; Watson and Perry 1981). Thus, the termites can gather material from within each hummock, as well as emerge sporadically from tunnel openings between hummocks when it suits them. In addition, wood-eating termites and purely subterranean species are abundant; the genera *Amitermes*, *Nasutitermes*, *Tumulitermes*, *Heterotermes*, and *Microcerotermes* are particularly rich in species (Gay and Calaby 1970; Watson and Gay 1983; Watson, pers. comm.). The abundance of these termites almost certainly reflects an abundance of cellulose that cannot readily be used by other animals, as well as the presence of wood in the numerous shrubs and trees. Although data are sparse, we suggest that quantitative analysis of termite abundance and species richness will show them to be high in Australia relative to other arid ecosystems.

The impact of infertility on Australian plant communities has been recognized for 30 years (Beadle 1954), but there is still little appreciation that this factor must have profound consequences for consumers subsisting on such plants. We suggest that the food web based on infertile sandy soils, spinifex, and termites possesses inherent peculiarities. Although termites may be extraordinarily abundant, individually they are relatively small insects that spend most of their time below ground, emerging onto the surface only sporadically if at all. Animals subsisting on termites must therefore gain access to food that is almost always subterranean and consists of small items; under these conditions, predators almost certainly need to forage on the basis of low effort and low yield. Predators of such small items are, in general, relatively small themselves. An arid environment dominated by termites would, therefore, be expected to support a greater range of small, ectothermic predators than one dominated by mammalian and insect grazers dependent on aboveground green vegetation. The food chain in a termite-dominated environment might well ramify into a web of predatory invertebrates as well as vertebrates. In our opinion, reptiles make up the vertebrate group best able to exploit the termites and invertebrates constituting such a web. Birds and mammals most likely have difficulty feeding below ground because they cannot harvest small, dispersed items from the soil matrix efficiently enough to balance energy expenditure. Available information shows that termites are a highly important food source for lizards. Before turning to details of reptilian ecology, we examine the other major Australian vegetational formations apart from spinifex.

Acacia Shrublands, Chenopod Shrublands, and Tussock Grasslands

Acacia shrublands, especially those composed of mulga, are frequently found on infertile red earths and usually contain ephemeral or perennial grasses (Williams and Calaby 1984). The soils are not as poor as those on which spinifex grows (Jackson 1962; Slatyer 1975). The diversity and abundance of termites appear to be even greater than in spinifex grasslands (Watson et al. 1978), probably because dead wood and litter from shrubs provide a greater range of resources, and colonies of some harvesters reach densities of 1000/ha (Watson et al. 1973). Lizards are also diverse in mulga, although to a slightly lesser degree than in spinifex (Pianka 1969a, 1972, 1973). The presence of rich assemblages of termites and lizards supports our hypothesis that a connection exists between the two groups.

Chenopod shrublands support fewer species of lizards than do spinifex grasslands or acacia shrublands (Pianka 1969a, 1981, 1986; Brooker and Wombey 1978; Milewski 1981a), but we can find no information on their termite fauna. Soils in such areas are more fertile than those of spinifex grasslands or acacia shrublands (Graetz and Wilson 1984). If there is an inverse correlation between fertility and termite abundance or diversity, then the observed reduction in lizard diversity is consistent with our hypothesis.

Termites are depauperate in tussock grasslands, possibly because cracking clays (the principal soil) make it difficult for termites to construct permanent galleries (Gay 1970). The lizards of tussock grasslands have not been systematically investigated, but available information suggests that they are neither abundant nor diverse (Cogger 1986; Gillam, pers. comm.).

Synthesis

We suggest that a major cause of the lizard radiation in arid Australia is the presence of abundant and diverse termite assemblages, which in turn have developed because soil infertility, and therefore vegetation, favors termites over other grazing and detritivorous animals (fig. 1). Abundant termites may provide food directly for lizards, which can harvest them more efficiently than can other vertebrates, and they may indirectly increase food resources available to lizards because many other invertebrate groups may have increased in diversity and abundance by preying on termites. As termite abundance and diversity decline from infertile to more-fertile vegetational formations, lizard diversity declines.

Three other physical attributes of arid Australia mentioned previously may have enhanced the radiation of lizards (fig. 1). The unpredictable rainfall causes sporadic production, thereby favoring lizards but not birds. Nevertheless, aridity is mild on a global scale and perennial vegetation cover is relatively dense, especially on the infertile soils supporting spinifex grasslands and acacia shrublands. This factor presumably enhances the abundance of termites. In addition, the occasional heavy rains allow persistence of trees and tall shrubs, thereby providing structural diversity of significance to lizard assemblages and also increasing the abundance of wood-eating termites.

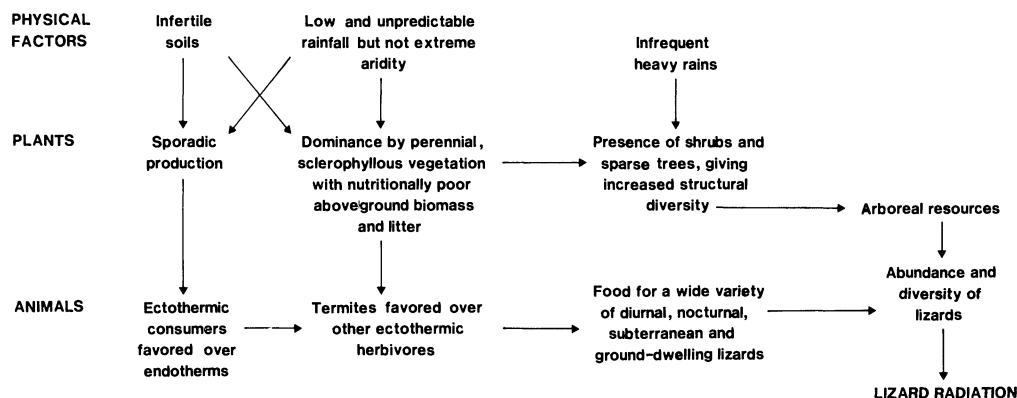


FIG. 1.—A summary of the web of ecological forces that forms the core of our hypothesis for the high diversity of lizard species in arid Australia. The diagram shows a series of postulated connections between physical factors, plants, and animals that has resulted in the evolution of a fauna dominated by ectothermic vertebrates (lizards). It represents the situation in spinifex grasslands and acacia shrublands; we suggest that the web is constructed differently in other arid Australian vegetational formations such as tussock grasslands and chenopod shrublands. We argue that the web of forces in North American deserts, where rainfall is more dependable and soils are more fertile, differs considerably and results in a greater diversity of alternative consumers.

This hypothesis potentially accounts for several unique attributes of Australian lizards. It suggests that the lizard body plan is particularly effective for exploiting the food resources of arid Australia. It suggests that the physical structure of spinifex is of lesser importance and that spinifex is a center of lizard diversity primarily because of the sheer abundance of termites and the relative ease with which lizards can exploit that food supply. It suggests that nocturnality is prominent among Australian lizards because many termites, and the invertebrates that prey on them, forage nocturnally. We now examine how closely our interpretations match detailed knowledge of reptilian ecology, both in Australia and on other continents.

COMPARISON OF HYPOTHESIS AND DATA

Intercontinental Comparisons

Pianka (1973, 1986) showed that termites constitute a major prey grouping in all desert saurian faunas, a result in broad agreement with our suggestion that termites are particularly suitable prey for lizards. However, Pianka and his co-authors suggested that termites are a more important food resource in the Kalahari Desert than in Australia (Pianka 1973, 1986; Huey et al. 1974; Pianka et al. 1979). Consequently, they argued that specialization for a diet of termites is prominent among Kalahari lizards and that "the Kalahari termite fauna is very rich" (Huey et al. 1974, p. 310), a judgment based on work by Coaton (1963). Coaton recorded 14 genera of termites in the Kalahari but did not estimate the

numbers of species present. Comparison with arid Australia is difficult because of a lack of comparable published data; the only regional survey is of the Alice Springs district in central Australia, which found 48 species in 12 genera (Watson et al. 1978). Most of these species occurred in acacia shrublands, whereas the fertile tussock grasslands and riparian habitats supported only three or four species each. It is clear that some parts of arid Australia and southern Africa have rich termite assemblages; until further data are available, however, it will be difficult to determine whether the greater richness of lizards in Australia directly reflects a greater abundance or a greater richness of termites.

A comparison with the North American case is more clear-cut. Only 10 species in two genera of termites occur in arid North America (Snyder 1954). Haverty and Nutting (1975) reported only 4 species of sympatric subterranean termites in the Sonoran Desert, and only 2 occur regularly on a watershed in the Chihuahuan Desert (Whitford et al. 1982). The relative lack of termites might reflect the fact that grasses are less important in North American deserts, that comparatively fertile soils favor other herbivores and detritivores, or that the North American deserts lie too far from the tropics for occupation by diverse assemblages of termites. Again, quantitative analysis of our hypothesis is necessary, but there is substantial evidence that termites are less diverse in arid North America.

Thus, the richest arid-zone lizard faunas occur on the two continents where termites are also richest, although the difference in lizard diversity between the Kalahari Desert and arid Australia is less clearly consistent with the hypothesis. One critical question is how increased richness and abundance might give rise to a greater diversity of lizards. The higher richness of termites may allow some lizard species to specialize by feeding on a small number of termite species, but it is also possible that a few abundant species of termites could provide food for a considerable number of lizard species using different foraging strategies to specialize on different segments of the foraging populations of one or a few termite species. This and several other unanswered questions concerning our hypothesis are mentioned in the Conclusion.

Australian Lizards and Termites

As noted above, Pianka (1973, 1986) stated that termites are a major group of prey for lizards in arid Australia. His trophic summaries, however, argue that vertebrates are the dominant food type of Australian lizards. In our opinion, he overemphasized the importance of vertebrates. First, Pianka's (1973, 1986) method of summarizing the diet of an entire saurian fauna appears to be biased toward large prey items such as vertebrates. His calculation that 27% of the volume of Australian prey were vertebrates (Pianka 1986) was a simple proportion of the total volume of prey recorded in his study, and it contained no factor to adjust for the vastly different sizes of lizards included in the analysis. Because vertebrate-eating lizards are much larger than the average, the contribution of vertebrates to overall prey is exaggerated and that of invertebrates underemphasized. Second, few of the 61 species at Pianka's study sites ate substantial amounts of vertebrate prey; vertebrates accounted for more than 50% of the diets, by volume, of only 5 species and for more than 25% of the diets of only 8 species

(1986, pp. 170–173). In arid Australia as a whole, only 12 species (principally varanids) out of about 200 (Cogger 1986) are likely to feed regularly on vertebrates. Third, the vertebrates being eaten are primarily lizards, and the very presence of these lizards must directly reflect some other food; thus, the trophic phenomenon of real interest is obscured to some extent by Pianka's method of summarizing his dietary data. In terms of the overall diversity of lizards, therefore, vertebrate prey play a minor role.

A consideration of the number of species that consume termites reveals the relative importance of this food type. Termites accounted for more than 50% of the diets of 16 of the species at Pianka's study sites and more than 25% of the diets of 26 species (1986, pp. 170–173). No other dietary category identified by Pianka occurred at such substantial levels in so many species. Further, Pianka's (1973, 1986) method of summarizing his dietary data was not biased toward termites, as it was toward vertebrate prey. Thus, termites constituted the most important food resource for lizards both in terms of the whole assemblage and in terms of the extensive range of foraging modes and morphological types exhibited by the species using that resource.

Three additional factors suggest that further work will strengthen our perception of termites as a major prey type. Pianka's (1973, 1986) analyses were conducted in the southern Australian arid zone, where termite diversity and abundance are almost certainly less than in the hotter northerly areas, where more biomass is produced during the summer (Wood and Lee 1971). It is possible, therefore, that the proportions of termites in the diets of lizards in the northern arid zone are even higher or that termite specialists dominate the lizard assemblages to a greater degree. Second, we emphasized earlier the abundance of subterranean lizards, particularly *Lerista* species (table 3). The diets of some *Lerista* are known to contain high proportions of termites (Pianka 1986; Morton, K. R. Jones, and L. R. Miller, unpubl. data), and it is likely that the dietary proportions of termites increase as species become more fossorial (P. Kendrick, pers. comm.). The biomass of lizards supported directly by termites may therefore be considerably higher than is indicated by simple listings of diets.

Finally, the two scincid genera that have speciated dramatically in the arid zone—*Ctenotus* and *Lerista*—appear to depend heavily on termites. Pianka (1969b) showed that the diets of 9 of the 14 *Ctenotus* species at his sites consisted of more than 50% termites by volume; these results may help explain the explosive radiation (Matthews 1976). Similarly, we suggest that the abundance of termites in certain habitats may have been a major driving force in the radiation of *Lerista*.

Australian Lizards and Non-Termite Prey

This discussion of dietary habits has focused on termites, but an abundance of termites may have a downstream effect by favoring a variety and abundance of predatory insects. This potential effect is difficult to test because the invertebrate fauna of arid Australia is so poorly known (Greenslade and Greenslade 1983, 1984). One taxon known to be particularly diverse and abundant in arid Australia

is ants (Greenslade and Greenslade 1983, 1984), but the richness of ants does not seem directly attributable to an abundant fauna of termites (although it may ultimately result in some way from edaphic infertility). However, it is notable that of the 61 species of lizards for which dietary data are available, ants account for more than 50% of the diets, by volume, of only 2 (*Moloch horridus* and *Ctenophorus isolepis*, both agamids) and for more than 25% of the diets of only 6 (Pianka 1986, pp. 170–173). Consequently, the relatively large volume of ants taken by the fauna as a whole (Pianka 1973, 1986) results from the ingestion of relatively small volumes by most species, suggesting that the high ratio of sclerotized chitin to digestible biomass of ants (Redford and Dorea 1984) has hindered predatory specialization on them. The possibility exists, however, that many subterranean species subsist on the eggs and larvae of ants, which are less chitinous and highly aggregated prey. Sparse data on the rich and probably abundant fauna of blind snakes (Typhlopidae: *Ramphotyphlops*) point to this conclusion (R. W. Braithwaite, J. C. Wombey, and R. Shine, pers. comm.).

CONCLUSION

Figure 1 summarizes our view of the driving forces behind the high lizard diversity in arid Australia. Several elements of our overall hypothesis have been succinctly stated by Pianka (1969a, 1973, 1975, 1981, 1986), but the proposed linkage of edaphic and climatic factors is new. If there is to be any advance in understanding, however, testing key components of the hypothesis is essential. Here, several critical questions are mentioned.

First, study of the molecular systematics of lizard faunas could reveal the age and taxonomic range of the radiations on different continents. If such work, in association with paleontological interpretation, showed that the Australian radiation was considerably older than those on other continents, it would cast doubt on the explanatory value of our ecological hypothesis.

Second, it is necessary to establish whether the species richness and abundance of termites differ among the continents. It is important to determine the relative abundances of termites, but because of the difficulties in quantifying subterranean biomass (Baroni-Urbani et al. 1978), this aspect will lag behind the study of diversity.

Third, a comparison of the abundance and diversity of lizards and termites in the four major Australian vegetational formations (spinifex grasslands, acacia shrublands, tussock grasslands, and chenopod shrublands) would show whether our postulation of trends is correct.

Fourth, we suggest that termites become more diverse and abundant within a vegetational formation as one proceeds from the southern to the northern Australian arid zone. The prediction that termite-eating lizards become more abundant along that gradient requires testing.

Fifth, further investigation of the ecology of subterranean *Lerista* species in Australia is necessary to test our assertion that termites constitute the dietary basis for this significant segment of the lizard radiation.

Sixth, our argument assumes that increased richness and abundance of termites allow greater diversity of lizards. It is not clear whether greater richness or increased abundance of termites provides discrete resources for a larger number of lizard species. Closer ecological examination of termite-eating lizards (particularly *Ctenotus* spp.) is necessary to establish whether different foraging behaviors allow lizard species to specialize on one of a range of species of termites or on different segments of the foraging populations of one termite species.

SUMMARY

We attempt to integrate previous partial explanations for the greater diversity and abundance of lizard species in arid Australia with new ideas concerning spinifex grasslands, the habitat with the most startling lizard diversity, in order to present a more comprehensive and testable theory than has hitherto been provided. Our synthesis focuses on the factors allowing diversification in local assemblages, not on between-habitat diversity. Our argument has four major components.

1. Spinifex grasses grow on unusually infertile soils, and spinifex is nutritionally very poor. Thus, herbivorous animals are relatively uncommon, whereas termites are exceedingly common and diverse. *Acacia* shrubs grow on firm soils that are only slightly more fertile than sands; and termites are probably even more abundant here than in the grasslands. Chenopod shrubs and tussock grasses, which grow on relatively fertile soils, probably have considerably fewer termites.

2. The diversity of lizards increases from fertile vegetational formations to infertile spinifex grasslands and acacia shrublands. We suggest that termites, being individually small but abundant, provide a food resource particularly suitable for lizards. Consequently, lizards have been able to diversify, especially where sandy soils allow subterranean activity.

3. Four contributory factors appear to have enhanced the abundance and diversity of Australian lizard species. Vegetational production in arid Australia is uncertain because the variability in rainfall is high and droughts may be lengthy; hence, ectothermic lizards are favored over birds and mammals. Nevertheless, aridity is mild and vegetational cover is usually high, thereby providing abundant food for termites. Because many termites forage nocturnally, abundant resources are available for exploitation by nocturnal lizards. Finally, arboreal lizards are prominent because climatic peculiarities allow trees to grow sparsely throughout arid Australia; the added structural complexity allows further diversification of termites and lizards.

4. Our interpretation is broadly consistent with available literature on lizard and termite faunas in arid Australia, North American deserts, and the Kalahari Desert, although important gaps remain.

Our hypothesis consists of a web of forces rooted in the edaphic and climatic characteristics of arid Australia. It suggests that lizards are better suited than other vertebrates to infertile and arid environments because of their morphological and physiological characteristics; this phenomenon reaches its climax in Australia.

ACKNOWLEDGMENTS

We dedicate this paper to E. R. Pianka. We salute him for his painstaking yet imaginative studies of desert-dwelling lizards and for his obvious affection for the biota and landscapes of outback Australia. G. F. Griffin, R. Shine, and D. M. Stafford Smith provided indispensable stimulation and support, and we are also indebted to others who have added vital sparks to our attempts at synthesis, especially R. W. Braithwaite, M. W. Gillam, J. A. L. Watson, M. Westoby, W. G. Whitford, S. Cairns, G. Caughey, M. R. Fleming, K. R. Jones, P. R. Baverstock, and T. C. Burton. C.D.J. acknowledges financial support from a Commonwealth Postgraduate Research Award, the Northern Territory University Planning Authority, the North Australia Research Unit of the Australian National University, and the Australian Museum's Postgraduate Research Trust Fund.

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