

HABITAT SPECIFICITY, SPECIATION, AND SPECIES DENSITY  
IN AUSTRALIAN DESERT LIZARDS

ERIC R. PIANKA

*Department of Biology, Princeton University, Princeton, New Jersey<sup>1</sup>*

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*Abstract.* From data demonstrating habitat specificity, it is concluded that Australian desert lizards recognize more habitats than North American desert lizards. The large amount of environmental heterogeneity and intimate mixing of habitats in Australia allow many more lizard species to coexist there than in North America. An interpretive hypothesis for lizard speciation by means of habitats fluctuating in time and space is proposed.

In terms of the number of lizard species they support, the Australian deserts<sup>2</sup> are the richest in the world. Here one can find as many as 40 different species of lizards occurring together. Such extraordinarily high species densities raise important ecological and evolutionary problems. For instance, how do so many different species coexist without competitive exclusion? And how has so much speciation been possible with so few geographical barriers? The present paper contains data and discussion relevant to both these questions.

The term "spinifex" is used in this paper to include all species of porcupine grass (genus *Triodia*), a plant life form unique to the Australian continent (Burbidge 1953). These perennial grasses form dense clumps, up to several feet in diameter, consisting of a central dense complex lattice-work and numerous outwardly directed needle-like spines. The term "mulga" is here used in the broadest sense of the word, and includes chenopodeaceous shrubbery as well as stands of any species of *Acacia*. This broad definition is useful because certain lizard species treat these environmental elements as a distinct habitat (documented later in this paper). Thus defined, "mulga" habitats usually consist of a chenopod shrub layer with small *Acacia* trees, while "spinifex" habitats almost always entirely lack chenopods and generally have a *Eucalyptus* upper story. Where the two habitats are adjacent, there are often broad ecotones, and at such places, clumps of *Acacia* trees may be scattered through an otherwise eucalypt-spinifex habitat. In such situations many "mulga" lizards can be found in close proximity to "spinifex" lizards, and vice versa. Rarely ecotonal areas consist largely of *Acacia* trees, but have an understory of spinifex instead chenopods (such areas are usually on fairly soft soils). In general, spinifex habitats occur on

sandy soils with good drainage and mulga habitats on desert loams, clays, and stony soils with poorer drainage.

A pure spinifex flat in the Great Victoria Desert supports at least 16 species of lizards; a nearby sandridge area has at least 39 species. A nearly treeless chenopodeaceous lakebed community a few miles away supports at least 15 different lizard species. Examination of the differences in lizard species composition of such censuses elucidates the ecological importance of the various constituent environmental elements. Some lizard species are ubiquitous in nearly all desert habitats; these can be subtracted from censuses to leave only those with varying degrees of habitat restriction. Then, by removing from the species remaining those that occur on a pure spinifex flat, the species which require still more complex habitats can be isolated. Similarly, a sandridge census may be compared to a sandplain census to determine which species are confined to one or the other. Thus a census of a mixed mulga-eucalypt-spinifex area can be reduced into its components. The autecologies of various component species have here been considered in establishing the ecological importance of various elements of habitat. These autecological studies are being prepared as separate publications.

Table 1 lists eight lizard censuses made between October 1966 and January 1968 in the Western Australian sector of the Great Victoria Desert. Table 2 gives the habitat elements and locations of these eight areas. The A and M areas are mixed acacia-eucalypt-spinifex (*Acacia-Eucalyptus-Triodia*) habitats on desert loams. These two areas thus constitute mixtures of the mulga and the spinifex habitats. The D and E areas are desert sandhill and sandridge habitats, respectively, with large eucalypt trees and spinifex plus a variety of other sandridge perennials. Extensive spinifex habitat occurs on the sand plains between sandridges, and these two areas therefore contain both spinifex and sandridge habitats. The L and G areas consist of sandplain habitats with large eucalypt trees, spinifex, and a few scattered bushes; these areas

<sup>1</sup> Present address: Department of Zoology, University of Texas, Austin, Texas.

<sup>2</sup> They are "deserts" only in a climatological sense, since the vegetation usually contains an important component of trees.

TABLE 1. Data from 16 months of lizard censusing on 8 different study areas in Western Australia. The M and D areas were not sampled as extensively as the other study areas. (Table 2 gives the exact locations of these study areas)

Lizard species	A	M	D	E	L	G	N	Y
<i>Amphibolurus clayi</i>				x				
<i>Amphibolurus reticulatus</i>								x
<i>Amphibolurus inermis</i>	x	x	x	x	x	x	x	x
<i>Amphibolurus barbatus minor</i> <sup>a</sup>	x	x	x	x	x	x		
<i>Amphibolurus fordi</i>				x		x		
<i>Amphibolurus isolepis gularis</i>		x	x	x	x	x	x	x
<i>Amphibolurus scutulatus</i>	x	x						x
<i>Diporiphora amphiboluroides</i> <sup>a</sup>	x	e						
<i>Diporiphora winneckeii</i> <sup>a</sup>			x	x				
<i>Moloch horridus</i>	x	x	x	x	x	x		e
<i>Physignathus longirostris</i>			x	x				
<i>Varanus brevicauda</i>		x	x					
<i>Varanus caudolineatus</i> <sup>a</sup>	x	e						
<i>Varanus eremius</i>	x	x	x	x	x	x	x	
<i>Varanus gouldii</i>	x	t	x	x	t	x	t	x
<i>Varanus tristis</i> <sup>a</sup>	t	x	x	x	x	x		
<i>Ablepharus boutonii</i> <sup>b</sup>	x				x	x		
<i>Ablepharus butleri</i>	x			x		x		
<i>Ablepharus greyii</i>	x	e	e	x	x	e	x	e
<i>Ablepharus timidus</i>	x	e						e
<i>Egernia depressa</i> <sup>a</sup>	x							
<i>Egernia kintorei</i> <sup>b</sup>					x			
<i>Egernia inornata</i> <sup>b</sup>	x			x	x	x	x	x
<i>Egernia striolata</i> <sup>b</sup>		x	x	x	x	x	x	
<i>Omolepida melanops</i>						x		
<i>Rhodona bipes</i>			t	x	x	x		
<i>Rhodona macropisthopus</i>	x							
<i>Rhodona desertorum</i>				x				
<i>Sphenomorphus richardsonii</i> <sup>b</sup>								x
<i>Tiliqua multifasciata</i>				x				
<i>Ctenotus ariadnae</i>					x			
<i>Ctenotus allas</i>	x							
<i>Ctenotus brooksi</i>				x				
<i>Ctenotus calurus</i>		x	x	x	x	x	x	
<i>Ctenotus colletti nasutus</i>				x				
<i>Ctenotus duz</i>				x				
<i>Ctenotus grandis</i>	x	x	e	x	x	x	x	
<i>Ctenotus helenae</i>		x	x	x	x	x	x	
<i>Ctenotus leae</i>				x				
<i>Ctenotus leonhardii</i>	x	x						x
<i>Ctenotus pantherinus ocellifer</i>	x	x	x	x	x	x	x	
<i>Ctenotus piankai</i>			e	x	x	x	x	
<i>Ctenotus quattuordecimlineatus</i>				x	x	x	x	
<i>Ctenotus schomburgkii</i>	x	x	e	x	x	x	e	x
<i>Delma fraserii</i> <sup>b</sup>	x							
<i>Lialis burtonii</i> <sup>b</sup>	x	x	e	x	x	e	e	
<i>Pygopus nigriceps</i> <sup>b</sup>			x	e	x	e		
<i>Diplodactylus ciliaris</i> <sup>a,b</sup>		x		x				
<i>Diplodactylus conspicillatus</i> <sup>b</sup>		x	x	x	x	x	e	x
<i>Diplodactylus damaeus</i> <sup>b</sup>						x		
<i>Diplodactylus elleri</i> <sup>b</sup>	x	e	x	x	e	e	e	
<i>Diplodactylus pulcher</i> <sup>b</sup>	x							
<i>Diplodactylus stenodactylus</i> <sup>b</sup>			x	x				
<i>Diplodactylus strophurus</i> <sup>a,b</sup>	x		x	x				x
<i>Gehyra variegata</i> <sup>a,b</sup>	x	x	x	x	x	x		x
<i>Heteronota binoei</i> <sup>b</sup>	x	e	e	x	x	x	x	x
<i>Nephrurus levis</i> <sup>b</sup>					x	x	x	
<i>Nephrurus laevisimus</i> <sup>b</sup>			x	x				
<i>Nephrurus vertebralis</i> <sup>b</sup>	e	x						x
<i>Rhynchoedura ornata</i> <sup>b</sup>	x	x	x	x	x	x	x	x
Totals (x + t)	29	22	24	39	28	27	16	15
Totals (x + t + e)	30	28	30	40	29	31	20	18

<sup>a</sup>Arboreal  
<sup>b</sup>Nocturnal  
x = collected  
t = presence indicated by tracks  
e = highly expected on considerations of geographic range, habitat, autecology, and microhabitat.

are thus typical spinifex habitats with a eucalypt canopy. The N area is a "pure" spinifex flat (grass desert), while the Y area is a relatively pure shrub desert. The latter is a lakebed community consisting primarily of chenopodeaceous shrubbery. In addition to these eight study areas, supplementary investigations were made on a variety of other spinifex and mulga habitats in the Great Sandy Desert, the Tanami Desert, and the Simpson Desert.

Table 3 indicates the species which are (1) restricted to mulga, (2) restricted to spinifex, (3) restricted to areas with loose sand (sandhills and sandridges), and (4) ubiquitous or nearly ubiquitous. The column "Unaccounted for" gives the species which are not listed in the first four, i.e. those species whose presence or absence cannot be easily explained by habitat considerations alone. Six of these 18 are arboreal and may be found on a variety of large shrubs and many different tree species; 9 others were collected on only one area and little can therefore be said concerning their habitat preferences. The remaining three species, *Ablepharus butleri*, *Egernia inornata*, and *Varanus brevicauda*, are forms whose geographical distributions prevent them from occurring on certain of the areas examined. The relative importance of vertical structural complexity in each of the habitat elements can be assessed by considering the proportion of arboreal to total species. These figures are: ubiquitous 0%, spinifex 0%, mulga 30%, sandridges 20%, unaccounted for 33%. Lizards in the last category are directly dependent upon the presence of eucalypt trees and/or large shrubs for a place to live. The overall percentage of arboreal species to all species in Australia is 18.3%.

Some interesting patterns of habitat specificity are evident in Table 3. For instance, among each of the genera *Ctenotus*, *Diplodactylus*, and *Nephrurus*, there are species which are specialized to mulga, spinifex, and sandridges. It is noteworthy that there are no spinifex-specialized agamids, but that six different *Ctenotus* species apparently are dependent upon spinifex. This fact can be compared with the situation in mulga- and sandridge-dwelling species, which have, respectively, three and four agamids and one and four *Ctenotus* species. The reasons for these patterns are obvious. Most skinks are wary and nervous, almost snake-like lizards, whereas the majority of agamids have longer limbs and are better suited to exploit large bushes and more open situations. Skinks, particularly *Ctenotus*, literally "swim" through spinifex, while agamids are generally clumsy, noisy, and slow to work their way through it. However, mulga and sandridge habitats provide considerable tracts of open space, as well as a variety of large woody bushes, and thus afford greater opportunities for agamid diversification. Mulga habitats are too open to support many species of *Ctenotus*,<sup>3</sup> whereas the dense perennials on sandridges are used much like spinifex by some of the dune-dwelling *Ctenotus*.

Ten species are ubiquitous to all habitats (or very nearly so), 10 are confined to mulga habitats, 12 to spinifex, and 10 to sandridges (Table 3). On the E area most of the ubiquitous, spinifex, and sandridge species occur together, along with several of those that are arboreal or otherwise unaccounted for, to give an overall list of some 40 species. This is four times the maximum number of species of lizards known to occur together in North American deserts (Pianka 1967).

<sup>3</sup>Two *Ctenotus* species which have been able to invade the mulga habitat forage in the open; both have proportionately longer legs than other *Ctenotus*.

TABLE 2. The total number of lizard species, existence of various habitat elements and the locations of the eight study areas. M = mulga Sp = spinifex S = sand E = eucalypts

Area	No.	M	Sp	S	E	Location of study area	Latitude° S	Longitude° E
A.....	30	+	+		+	17 miles S of Atley homestead, W.A.	28° 27'	119° 05'
M.....	28	+	+		+	9 miles NNE of Millrose homestead, W.A.	26° 17'	121° 00'
D.....	30		+	+	+	21 miles W of Lorna Glen HS, W.A.	26° 14'	121° 13'
E.....	40		+	+	+	5 miles NE of Dunges Table Hill, W.A.	28° 08'	123° 55'
L.....	29		+		+	24 miles E of Laverton, W.A.	28° 31'	122° 45'
G.....	31		+		+	17 miles S of Neale Junction, W.A.	28° 30'	125° 50'
N.....	20		+			8 miles W of Neale Junction, W.A.	28° 17'	125° 40'
Y.....	18	+				3-4 miles E of Stony Point, W.A.	28° 05'	124° 15'

TABLE 3. Listings of ubiquitous species and those which are various restricted to particular habitats or habitat elements (see text)

Ubiquitous	Spinifex	Mulga	Sandridges	Unaccounted for
<i>Amphibolurus inermis</i>	<i>Varanus eremius</i>	<i>Amphibolurus scutulatus</i>	<i>Amphibolurus clayi</i>	<i>Amphibolurus barbatus minor</i> <sup>a</sup>
<i>Varanus gouldi</i>	<i>Ctenotus calurus</i>	<i>Amphibolurus reticulatus</i>	<i>Amphibolurus fordi</i>	<i>Ablepharus boutoni</i> <sup>a</sup>
<i>Ablepharus greyi</i>	<i>Ctenotus grandis</i>	<i>Diporiphora amphiboluroides</i> <sup>a</sup>	<i>Diporiphora winneckeii</i> <sup>a</sup>	<i>Varanus tristis</i> <sup>a</sup>
<i>Ctenotus schomburgkii</i>	<i>Ctenotus helenae</i>	<i>Varanus caudolineatus</i> <sup>a</sup>	<i>Physignathus longirostris</i> <sup>a</sup>	<i>Gehyra variegata</i> <sup>a</sup>
<i>Heteronota binoei</i> <sup>c</sup>	<i>Ctenotus pantherinus</i>	<i>Ablepharus timidus</i>	<i>Ctenotus brooksi</i>	<i>Diplodactylus ciliaris</i> <sup>a</sup>
<i>Rhynchoedura ornata</i> <sup>c</sup>	<i>Ctenotus piankai</i>	<i>Ctenotus leonhardii</i>	<i>Ctenotus colletti</i>	<i>Diplodactylus strophurus</i> <sup>a</sup>
(Nearly ubiquitous)	<i>Ctenotus quattuordecimlineatus</i>	<i>Egernia depressa</i> <sup>a</sup>	<i>Ctenotus dux</i>	<i>Ctenotus ariadnae</i> <sup>b</sup>
	<i>Egernia striata</i> <sup>c</sup>	<i>Sphenomorphus richardsoni</i> <sup>c</sup>	<i>Ctenotus leae</i>	<i>Ctenotus atlas</i> <sup>b</sup>
	<i>Rhodona bipes</i>	<i>Diplodactylus pulcher</i> <sup>c</sup>	<i>Diplodactylus stenodactylus</i> <sup>c</sup>	<i>Egernia kintorei</i> <sup>b</sup>
<i>Amphibolurus isolepis</i>	<i>Pygopus nigriceps</i> <sup>c</sup>	<i>Nephrurus vertebralis</i> <sup>c</sup>	<i>Nephrurus laevis</i> <sup>c</sup>	<i>Omolepida melanops</i> <sup>b</sup>
<i>Moloch horridus</i>	<i>Diplodactylus elderi</i> <sup>c</sup>			<i>Rhodona desortorum</i> <sup>b</sup>
<i>Lialis burtoni</i> <sup>c</sup>	<i>Nephrurus levis</i> <sup>c</sup>			<i>Rhodona macropisthopus</i> <sup>b</sup>
<i>Diplodactylus conspicillatus</i> <sup>c</sup>				<i>Tiliqua multifasciata</i> <sup>b</sup>
				<i>Delma fraseri</i> <sup>b</sup>
				<i>Diplodactylus damaeus</i> <sup>b</sup>
				<i>Ablepharus butleri</i>
				<i>Egernia inornata</i> <sup>c</sup>
				<i>Varanus brevicauda</i>

<sup>a</sup>Arboreal species  
<sup>b</sup>Collected on only one area  
<sup>c</sup>Nocturnal

TABLE 4. Numbers of species in several different vertebrate taxa on various study areas in North American and Australian desert habitats

Area	North America				Area	Australia			
	Lizards	Birds	Snakes	Small mammals		Lizards	Birds	Snakes	Small mammals
I.....	4	3	3?	4	Y	17	11	1-2	1-2
L.....	5	6+	4	6	N	20	22	3-4	1-2
G.....	5	3	2	4	G	31	30	4	1
V.....	6	4	4	8	L	29	33	4	3
P.....	7	7	3	6	E	40	35	3	2
S.....	6	6	5	5	D	30	32	3	1
M.....	8	9+	5	7	M	28	32	4	3
T.....	9	11+	3	4	A	30	35	6	1
W.....	9	13	7	6					
C.....	10	16	9	5					

The increase in total number of species can be traced to several different factors. (1) In Australian deserts, lizards usurp the ecological roles played by other taxa in North America. There are insect-like, worm-like, snake-like, and mammal-like lizards in Australia. Furthermore, Australia's desert snake and mammal faunas are comparatively impoverished (Table 4). When the number of snake-like lizard species (pygopodids) are

added to the number of snake species, Australian and North American "snake" species densities are closely comparable: the North American counts vary from three to nine and the Australian ones from three to eight. Because of introductions and extinctions, the situation is more difficult to analyze in mammals, but it is fairly safe to assert that the large monitor lizard *Varanus gouldi* is an ecological analogue of the North American kit fox.

It is not possible from my data to determine whether there is a corresponding impoverishment in the Australian insect and worm faunas.

(2) Probably as a direct consequence of the milder and more constant climate, Australian desert lizards have been able in their adaptive radiation to partition environmental resources temporally as well as spatially. Whereas most North American desert habitats support no nocturnal lizards, and those that do support no more than two species (Pianka 1967), nocturnality is much more prevalent in Australian desert lizards, where between 32 and 44% of the total lizard fauna on a given area are nocturnal. Twenty-two nocturnal species are listed in Table 1; of these, between 8 and 13 may occur on any particular study area. There are nocturnal counterparts in Australia of most of the diurnal American species (see Pianka 1966), with widely foraging and sit-and-wait types, open-area and edge foragers, terrestrial and arboreal types, and even specialized secondary carnivores which prey upon the other species.

(3) Some groups of Australian desert lizards are more narrowly specialized than their North American ecological equivalent. In particular, this is true of the skincid genus *Ctenotus*; in this group as many as 11 species may occur sympatrically. Ecological coexistence of so many congeners is accomplished by differences in body size, time of foraging, microhabitat and habitat. The detailed comparative ecology of this genus is currently under preparation.

(4) The desert environment in Australia is spatially more heterogeneous than it is in North America. Because of greater horizontal environmental heterogeneity (i.e., the existence of more "habitats"), Australian desert lizards have been able to develop habitat differences to an extent unparalleled in North American desert lizards. There is, however, little difference in the degree of vertical subdivision of biotope space between the continents; 11 out of the 60 Australian species are arboreal (18.3%), while 2 out of 12 North American species are arboreal (16.7%).

A major difference between the American and Australian desert environments is the unique and exceedingly complex structure of spinifex itself. A pure stand of this grass supports 20 species of lizards (see N area census in Table 1). This is double the maximal lizard species density possible on structurally complex sites in North America. However, even a chenopod flat (Y area, Table 1), which is structurally nearly identical to a North American Great Basin desert flat, supports 18 species. This strongly suggests that the total number of lizard species is determined not by the structure of the environment alone, but by climate and history (within the structural limitations of the environment).

Finer comparison of the Australian chenopod flat lizard census with a census from the Great Basin desert is illuminating. There are only five lizard species in the latter list: *Cnemidophorus tigris*, *Uta stansburiana*, *Phrynosoma platyrhinos*, *Crotaphytus wislizeni*, and *Callisaurus draconoides*. Table 1 gives the Australian census of 18 species (Y area). Two species of *Ctenotus* (a small one and a larger one) replace *Cnemidophorus*, *Amphibolurus isolepis* is a rough analogue of *Uta*, *Moloch* replaces *Phrynosoma*, *Amphibolurus inermis* and *Amphibolurus reticulatus*, although partially herbivorous, appear to be crude counterparts of *Crotaphytus* in the northern parts of its range, and *Amphibolurus scutulatus* replaces *Callisaurus*. If these 7 species are then removed from con-

sideration, of the remaining 11, one is ecologically a mammal (*Varanus gouldi*), one is an "insect" (*Ablepharus greyi*), one is a "worm" (*Ablepharus timidus*), and the other 8 species are nocturnal. Thus the nearly fourfold difference is explicable in terms of climate, history, and narrower specializations.

There are about twice as many bird species on study areas in the Australian deserts as there are on comparable areas in the North American desert (Table 4). Habitat selection in Australian desert birds occurs to a limited extent, but is not nearly so pronounced as in desert lizards. There are several bird species specialized to mulga and several restricted to spinifex habitats. However, Australian bird species do not treat sandridges as distinct habitats for there are no avian dune specialists. The number of birds species versus the number of lizard species were compared for a wide range of desert habitats in the United States and in Australia (Fig. 1). As total diversity increases, bird species are added faster than

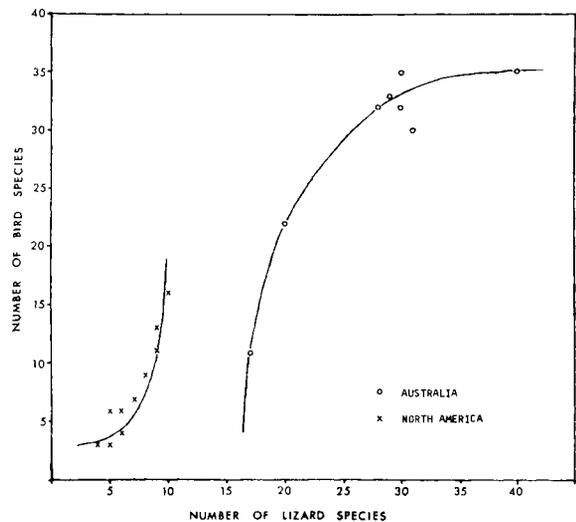


FIG. 1. A plot of the number of species of lizards versus the number of bird species occurring together for a range of North American and Australian desert habitats. Data for North America from Pianka (1965). Australian bird censuses from Pianka and Pianka (1970). Due to the mobility of birds, the two lowest Australian points somewhat overestimate the number of bird species (via influx from adjacent more diverse habitats). However, the effect of this error is to lessen, rather than heighten, the difference between the two continents. The richest Australian area (35 bird species and 40 lizard species) represents an exceptionally complicated mixture of 2 different habitats and is therefore not strictly comparable with the other plotted points.

lizard species in North America, while the reverse is true in Australia, where lizards increase faster than birds. The graph thus reflects the difference in degree of habitat specificity between taxa and continents.

The problem of speciation of desert lizards in Australia can be profitably considered in terms of this evidence for strong habitat specificity. If, over geologic time, large enough areas of "spinifex" habitats were surrounded and separated by tracts of "mulga" habitats (and perhaps vice versa), and if, during the course of long-term climatic changes, these two phases alternatively made and

broke contact,<sup>4</sup> the system would approximate an archipelago in its capacity to produce new species. Indeed, theory suggests that this system could form new species even more rapidly than an archipelago since *both* phases carry species specific to them. Such a mechanism for the generation of new species, given an environment complex enough to allow the ecological coexistence of many species, could quite conceivably have given rise to the very diverse lizard fauna existent today.

Simultaneous with the above hypothetical processes, sandridges were almost certainly formed and windblown, resulting in the alternate separation and merging of various sandridge lizard stocks. It is even possible that these shifting sands could have served to alter the boundaries and junctions between the mulga and spinifex phases alluded to above. The capacity of extensive areas of windblown sand to produce groups of sand-specialized lizard species has been examined by Norris (1958) in the iguanid genus *Uma*.

There are conflicting views as to the age and history of the Australian deserts. Crocker and Wood (1947) postulated that the Australian continent has become very arid only during relatively recent times. They proposed a "Great Aridity" during the Pleistocene following the last glaciation. Axelrod (1950) has also suggested that the Australian deserts are of late Tertiary origin. Darlington (1965), Keast (1959), Littlejohn (1961), and Main (1968) have argued for relative antiquity of at least a portion of the deserts. To date, only Kluge (1967) has been concerned with speciation taking place within the deserts. There has been a substantial amount of work on birds (Gentilli 1949, Keast 1961, Serventy and Whittell 1967) and frogs (Main, Lee, and Littlejohn 1958, Littlejohn 1961, Main 1968), but in these taxa the deserts serve as a barrier to dispersal, rather than as a source area.

If the Pleistocene "Great Aridity" concept has any validity, and the Australian deserts actually are among the youngest on earth, then it would seem imperative to invoke an extraordinarily efficient process of speciation to account for the phenomenal species densities now present. Some support for a relatively recent origin of many of the lizard species considered here derives from their morphology and is reflected in their taxonomy (Kluge 1967, Storr 1965, 1966, 1968). The size of the genera *Amphibolurus*, *Diplodactylus*, and *Ctenotus* alone suggests a recent origin for these groups. Alternatively, if the Australian deserts are much older than Crocker and Wood suggest, the lack of geographic barriers to the movement of desert lizard species lends credence to the hypothesis of speciation proposed here.

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<sup>4</sup> Although I have been able to locate no direct evidence that either spinifex or mulga are at present encroaching upon each other, it seems reasonable to assume that this is happening, especially in places where sandy soils are being transported by either wind or rain.

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