

# Zoogeography and Speciation of Australian Desert Lizards: An Ecological Perspective

ERIC R. PIANKA

Geographic distributions of 94 species of Australian desert lizards are compared and 72 of these ranges are classified into eight biogeographic categories: ubiquitous (7 species), northern (8 species), southern (10 species), eremaea (6 species), central relicts (6 or 7 species), sandridges (8 species), shrub-*Acacia* (16 species), and sandplain-*Triodia* (10 species). Habitat specificity in nearly half these species has been well documented. Sandridge, shrub-*Acacia*, and sandplain-*Triodia* habitats are three particularly important desert habitats to which lizards have become specialized. Various routes by which habitat-restricted lizards could disperse between subregions of the desert are described and discussed. One of these, a band of shrub habitat through the southern part of the Gibson Desert, the Warburton Ranges, and the southern part of the Northern Territory, is named "The Giles Corridor." Points of habitat juncture are described, and it is suggested that several fairly localized regions have played major roles in both the speciation and the movements of habitat-restricted Australian desert lizards. A model of speciation based upon habitats fluctuating in space and time is proposed and discussed.

## INTRODUCTION

CONSIDERABLE attention has been given to the phytogeography of Australia (Gardner, 1944; Crocker and Wood, 1947; Burbidge, 1960) and the zoogeography of Australian birds (Gentilli, 1949; Keast, 1959a, 1961; Serventy and Whittell, 1967; Kikkawa and Pearse, 1969; Ford, 1971) and frogs (Littlejohn, 1961, 1967; Main, Lee, and Littlejohn, 1958; Main, 1968; Moore, 1954, 1961). For these taxa, the central deserts usually constitute barriers to dispersal and have therefore been important in the isolation of plant and animal stocks leading to speciation. The distribution of reptiles within Australia has been variously treated (Keast, 1959b, 1960; Kluge, 1967; Rawlinson, 1966, 1967, 1969; Storr, 1964b), but few previous authors have attempted to interpret fine details of distribution within the deserts. In fact, the deserts are often considered a single zoogeographic entity, usually called "eremaea" or the "Eyrean subregion." In this paper, I show that certain patterns of lizard distribution occur repeatedly within the Australian deserts, and I propose explanations as to the origin of these patterns. In order to do this, a model is developed based upon habitats fluctuating in space and time which adequately explains the known geographic distributions of some

desert lizards and allows certain predictions about the ranges of other poorly known species.

Studies on the ecology of a variety of Australian desert lizards (Pianka, 1968, 1969a, b, c, 1970a, b, 1971a, b, c, d; Pianka and Pianka, 1970a) have shown that, within the deserts, many species are highly specific in their habitat requirements. Three especially important habitats to which Australian desert lizards have become restricted are sandridges, shrub-*Acacia* habitats, and sandplain-*Triodia* habitats.<sup>1</sup> Habitat specificity is much less prevalent in desert-dwelling birds than it is in lizards (Keast, 1961; Pianka, 1969a; Pianka and Pianka, 1970b; Ford, 1971); this fact, coupled with (and related to) the relative mobility of birds, makes it unlikely that the present paper has much bearing upon avian zoogeography. However, other less mobile and more terrestrial forms, such as some insects and mammals, might be expected to be affected by the same environmental features, and therefore to have distributional patterns similar to those described here.

Sandplain habitats are usually dominated by species of porcupine grasses of the perennial genus *Triodia*, most frequently *T.*

<sup>1</sup> In a previous paper (Pianka, 1969a), I referred to shrub-*Acacia* habitat as "mulga" and to sandplain-*Triodia* habitat as "spinifex."

*basedowi*. Clays, loams, and/or rocky or stony soils generally support shrubs, varying from small chenopods to stands of larger bushes and small trees of the genus *Acacia* (especially common is mulga, *Acacia aneura*). Sandplain-*Triodia* and shrub-*Acacia* habitats are almost always mutually exclusive, with the vast majority of areas being either predominantly one or the other (grassy or shrubby). Shrub habitats occur in wetter, more mesic, situations, while *Triodia* habitats usually occur under drier, more xeric, ones. Occasionally ecotonal areas where these two habitat types blend together are found, especially on fairly sandy soils. Infrequently such ecotones may span distances of up to several miles, with a canopy of *Acacia* and an understory of *Triodia*; however, such extensive ecotones are rare. Habitats with large boulders and rock outcroppings ("Tors"), often exfoliating granite, support lizard faunas similar to those found in shrub-*Acacia* (especially mulga) habitats. This is not surprising, since cracks and crevices in large rocks presumably offer protection from predators and the elements (as well as foods) which are somewhat similar to those of shrub-*Acacia* habitats (Pianka, 1969b). Also, rocky soils almost always support a shrub-*Acacia* vegetation. Such rocky habitats can be profitably grouped with shrub-*Acacia* habitats for zoogeographic purposes (only a few lizard species, such as the saxicolous *Amphibolurus caudicinctus*, appear to be restricted to one or the other). Sandridge habitats are quite distinct and readily recognized, consisting of stabilized, long, red sand sandridges which show up well on aerial photographs (sandridges have been included on most recent detailed governmental maps). Sandridge vegetation is variable, often consisting of annuals, woody shrubs (such as *Thryptomene* and *Grevillea*), and occasional trees (such as *Eucalyptus gongylocarpa* and *E. dichromophloia*). Because they contain woody shrubs and considerable open space, sandridges have many of the structural attributes of shrubby habitats, and hence support a few shrub-loving species, such as *Diplodactylus strophurus*. [Moreover, Pianka and Pianka (1970b) noted that certain species of "mulga" birds like robins also occur in sandridge habitats.] Depending upon the locality, soil type, and soil depth, interdunal flats between sandridges are occupied either by sandplain-*Triodia* habitats, ecotonal habitats, or shrub-*Acacia* habitats.

Although certain parts of the Australian deserts are a complex mosaic of all three habitat types, great areas support expanses of a single relatively pure habitat. Other extensive regions, especially in the sandy deserts, are composed of a mixture of only two habitat types; thus, over much of the Great Victoria Desert, sandridges alternate monotonously with sandplains, and shrub-*Acacia* habitats occur only infrequently in depressions and dry lakebeds.

Lizard species invariably found either on or closely associated with sandridges in the desert include *Amphibolurus fordii*, *Diporiphora winneckeii*, *Physignathus longirostris*, *Ctenotus brooksi*, *C. colletti*, *C. dux*, *C. leae*, *Diplodactylus stenodactylus*, and *Nephruerus laevis*. Species occurring only in shrub-*Acacia* habitats are *Amphibolurus reticulatus*, *A. scutulatus*, *Varanus caudolineatus*, *Diporiphora amphiboluroides*, *Ctenotus leonhardii*, *Egernia depressa*, *Sphenomorphus richardsoni*, *Diplodactylus pulcher*, and *Nephruerus vertebralis*. Other species found, for the most part, on sandplains vegetated with *Triodia* are *Varanus eremius*, *Moloch horridus*, *Ctenotus calurus*, *C. grandis*, *C. helenae*, *C. pantherinus*, *C. piankai*, *C. quattuordecimlineatus*, *Egernia striata*, *Pygopus nigriceps*, and *Nephruerus levis*. The precise reasons why various species prefer or are confined to one habitat or another are largely unknown, although they may be guessed at in some cases. For example, *Egernia depressa* seems to rely upon crevices in mulga trees and exfoliating granitic outcrops for cover, and several species of *Ctenotus* (*grandis*, *helenae*, *pantherinus*, *piankai*, and *quattuordecimlineatus*) are all very adept at moving in and out of, and within, *Triodia* tussocks, which are used both as places in which to forage as well as safe sites for escape from potential predators (Pianka, 1969c). This evidence of pronounced habitat specificity, coupled with extremely high species densities of lizards (Pianka, 1969a), suggests that considerable speciation must have taken place within the Australian deserts.

Over two thirds of the Australian continent is classified as desert climatologically. Usually the limits of the "desert" proper are given in terms of long-term average annual precipitation, with the 250 mm isohyet forming the approximate southern, and the 500 mm isohyet the approximate northern, boundary. Within this extensive region, soils and vegetation vary considerably.

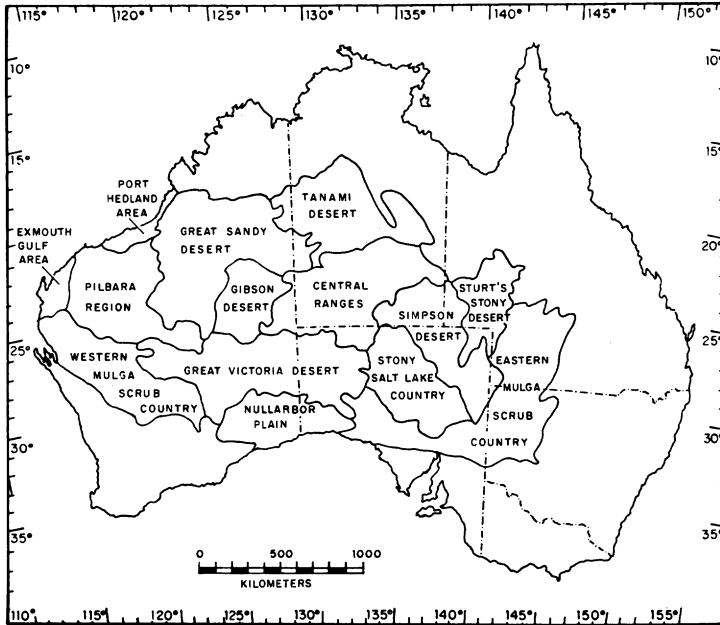


Fig. 1. Various subregions of the Australian desert. This map is based on a wide variety of sources, especially Beard (1969), Gardner (1942), Madigan (1936), and Prescott (1944). Note the southeasterly arm of the Pilbara Region, called the Carnegie Salient, which contains shrub habitats and Lake Carnegie. The southwestern finger of the Central Ranges, protruding into the Gibson Desert, is the Warburton Ranges (shrub *Acacia* habitat). See text for further description of habitats and Fig. 2 for their approximate distributions.

Different authors have recognized and named at least a dozen more or less distinct subregions, heterogeneous within and among themselves (Fig. 1). Boundaries between these are sometimes quite sharp, as is generally the case at the borders of the sandridge deserts, but at other places they are often somewhat vague. Beard (1969) defined certain subregions in Western Australia, and Madigan (1936), Gardner (1942), Prescott (1944), Crocker and Wood (1947), Wood and Williams (1960), Stephans (1956), Perry and Lazarides (1962), Speck (1963), Serventy and Whittell (1967), Leigh and Noble (1969), and Ford (1971) have delineated others.

Five of the subregions shown in Fig. 1 are characterized by relatively sandy soils and considerable amounts of *Triodia*. These are the Exmouth Gulf Area, the Tanami Desert, and the three major sandridge deserts: the Great Victoria Desert, the Simpson Desert, and the Great Sandy Desert. Sandridges occur in all five areas, but are especially widespread in the latter three. A little known, isolated, sandridge area exists in the middle of the Tanami Desert. All five sandy

subregions typically support a vegetation classified as "desert grassland" or "grass steppe" which is usually a *Triodia*-dominated habitat. Within these regions, however, scattered dry lakebeds and "breakaways" (rocky cliffs) support shrub habitats with some *Acacia*. In some places, especially in the Simpson Desert and in the South Australian sector of the Great Victoria Desert, sandridges alternate with interdunes of mulga and shrubby habitats.

The Pilbara Region and the Central Ranges, at higher elevations than the sand deserts, are characterized by greater topographic relief (and hence greater heterogeneity of soils and vegetation) and generally harder soils. Large areas of the Pilbara Region consists of rocky hills covered with species of *Triodia* other than *T. basedowi*. In the Central Ranges, tracts of sand desert frequently interrupt harder country. Thus, the vegetation of both of these subregions, especially the latter, is extremely complex, consisting of intermixtures of both *Triodia* and mulga habitats. True sandplains and sandridges are almost totally absent from

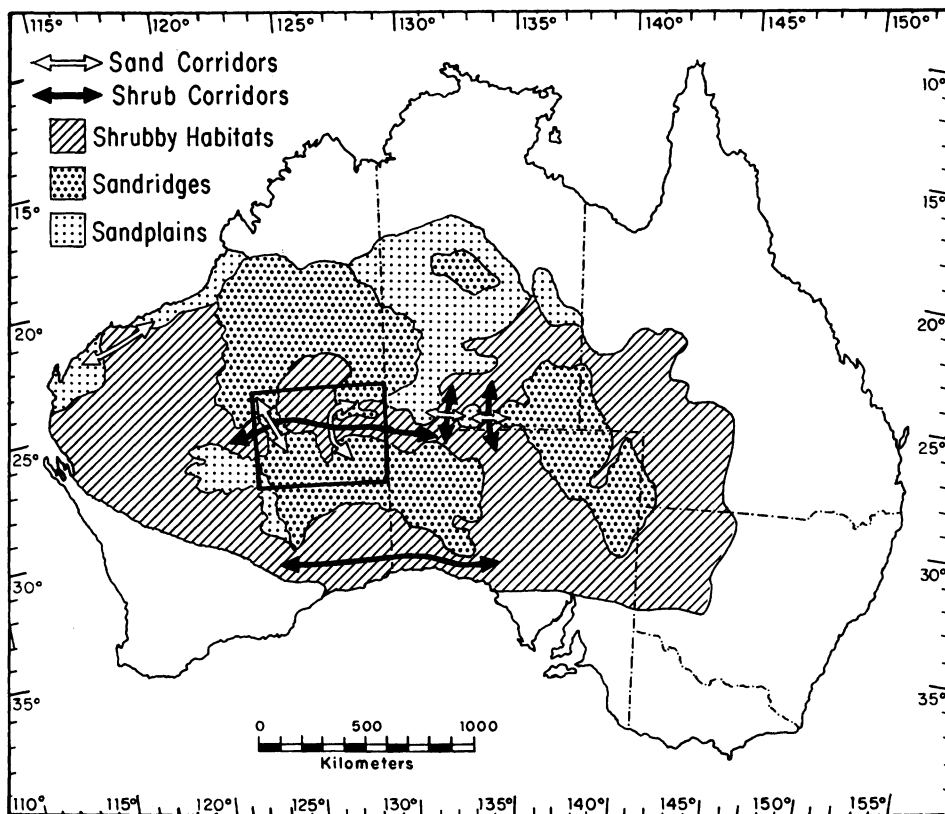


Fig. 2. Map showing the approximate extent of sandplains, sandridges, and shrub habitats. Shrub and sand corridors indicated by arrows. Note especially the two long east-west shrub corridors; the northern one is The Giles Corridor while the southern one runs through the Nullarbor Plain and its bordering zone of myall. Only the major habitat occurring in any given area is shown; small scale maps like this cannot show adequately the habitat heterogeneity within subregions, which in some cases is quite pronounced. The rectangular region in Western Australia, which includes most of The Giles Corridor, is enlarged in Fig. 10. See text.

the Pilbara Region, but both (especially sandplains) occur in patches throughout the Central Ranges.

The Western Mulga Scrub Country and the Eastern Mulga Scrub Country (inland Queensland, New South Wales, and South Australia) are connected by the shrubby habitats of the Nullarbor Plain and its bordering zone of myall (*Acacia sowdeni*), which is structurally similar to mulga.

Sturt's Stony Desert and the Stony Salt Lake Country of South Australia are rocky deserts with predominantly very open *Acacia* and shrubby vegetation. The latter subregion is broken up by numerous, often extensive, dry salt lakes (such as Lake Eyre).

The Gibson Desert is heterogeneous (Beard, 1968, 1969), with sandridges and sandplains interspersed with patches of rocky desert and

shrub-*Acacia* habitat reminiscent of the two stony deserts just described. The southern part of the Gibson Desert contains extensive patches of shrub and mulga habitat (Giles, 1889; Beard, 1968, 1969; Leigh and Noble, 1969). (See also Fig. 10.)

Sandridges have now been accurately mapped by aerial photography and their extent can easily be plotted. Sandplain-*Triodia* habitats and shrub-*Acacia* habitats are somewhat more difficult to delineate accurately, but can be approximated reasonably well by reference to the same sources as those for Fig. 1. [A crude, but fairly effective, means of detecting whether or not a given area supports shrubby or *Triodia* habitats is to use human population density as an indicator; shrub-*Acacia* habitats provide good sheep fodder and have been popu-

lated by pastoralists, whereas sandplain-*Triodia* habitats are relatively useless to man and are almost always completely uninhabited.] In Fig. 2, the approximate extent of each of the three habitats recognized by lizards are shown (note that this figure is highly diagrammatic, giving only the *major* habitat type occurring in any given region). Very frequently, where sandridges occur, there are sandplains between them. Several of the more important routes by which habitat-restricted lizards could disperse from one subregion to another are also marked on this figure.

Interpretation of finer patterns of desert lizard distribution has been hampered by inadequate collections from remote uninhabited inland areas, as well as by lack of knowledge of which species occur in the different desert habitats and subregions. During a 16-month field investigation on the ecology of Australian desert lizards, my wife and I observed and collected nearly 4,000 specimens of some 75 species.<sup>2</sup> Although our efforts were concentrated on sandy areas in the little known Great Victoria Desert, we also visited parts of all subregions depicted in Figure 1, except for Sturt's Stony Desert. We extended the known ranges of many species, collected specimens which allowed the taxonomic resolution of others, and were able to elucidate the habitat requirements of some 60-odd species (Pianka, 1969a). Information on the lizard faunas of different desert subregions was obtained both personally and by reference to Kinghorn (1945), Loveridge (1934, 1938), Thompson and Hosmer (1964), and Slater (1964).

Storr (1964a) estimated that there are about 250 species of lizards in Australia, distributed approximately as follows among the five families: Gekkonidae (50), Pygopodidae (11), Scincidae (about 130), Agamidae (41), and Varanidae (17). Around 125 species are known to occur in the desert; that is, roughly half the recognized species of Australian lizards are desert dwellers in at least a part of their geographic range.

## RESULTS

The basic raw data for this paper, other than the information presented in the introduction and contained in the various authorities on vegetation cited therein, are the

geographic distributions of some 94 desert lizard species in 22 genera (listed in Table 1). These distributional maps are the result of the labors of many people over the last two decades, especially Cogger (1957), Kluge (1967), Mitchell (1948, 1950, 1953, 1965), Pianka (1968, 1969b, 1969c, 1970a, 1971b, c, 1972), Pianka and Pianka (1970a), Rawlinson (1966), and Storr (1963a, 1963b, 1964b, 1965, 1966, 1967a, 1967b, 1968a, 1968b, 1969, 1971). In making these maps (26 of them are presented in Figs. 3, 4, 5, and 6; others have been published by the authors cited above), I not only drew on the literature and my own collection, but also visited all the Australian Museums and collated most of the available locality data for a number of taxonomically sound species. The final maps reflect the expected range of each species, using known habitat and microhabitat requirements, as well as actual localities of collection. About one-third of the total known Australian lizard fauna is represented, or approximately 75% of the estimated desert lizard fauna (94 out of 125 species).

Seventy-two of the 94 species ranges can be classified into eight reasonably distinct biogeographic categories, the first five of which were recognized by Keast (1959b):

(1) *Ubiquitous Species*. Seven species appear to be found virtually throughout Australia, both within and outside the deserts: they are *Varanus gouldi*, *V. tristis* (absent from the Nullarbor Plain and southeastern New South Wales), *Ablepharus boutoni*, *Ablepharus greyi*, *Gehyra variegata*, *Heteronotia binoei*, and *Lialis burtoni*. As would be expected, these lizards occur in all three of the major desert habitats.

(2) *Northern Species*. This group is somewhat less well defined, but nonetheless appears to be worth distinguishing. Eight species are distributed across northern Australia, southwards to varying degrees, but seldom much past the Tropic of Capricorn. These are *Varanus acanthurus* (Fig. 3), *V. breviceauda* (known only from the perimeter of the Great Sandy Desert, the Port Hedland Area, and the Exmouth Gulf Area—Pianka, 1970a), *Diporiphora bilineata*, *Ablepharus taeniopleurus* (which may also be an isolated "central relict"—see below), *Tiliqua multifasciata* (Fig. 3), *Diplodactylus conspicillatus*, *D. taeniatus*, and *Nephrurus asper*.

(3) *Southern Species*. Ten species have southern distributions, often extending from southern coastal Queensland through eastern

<sup>2</sup> Our collection has been donated to the Los Angeles County Museum of Natural History.

TABLE 1. THE NINETY-FOUR SPECIES CONSIDERED IN THIS REPORT, WITH REFERENCES TO THE AUTHORITIES FOR LITERATURE RECORDS. Asterisks denote 26 species whose range maps are given in Figures 3, 4, 5, and 6.

<i>Amphibolurus</i>	<i>Egernia</i>
<i>adelaidensis</i>	* <i>depressa</i>
<i>caudicinctus</i> (Storr, 1967b)	<i>kintorei</i>
* <i>clayi</i> (Storr, 1966)	<i>inornata</i>
* <i>cristatus</i> (Pianka, 1971d)	<i>margaretae</i>
<i>femoralis</i> (Storr, 1965)	<i>slateri</i>
* <i>fordi</i> (Storr, 1965)	* <i>striata</i>
<i>inermis</i> (Storr, 1966)	* <i>stokesi</i>
<i>isolepis</i> (Pianka, 1971c)	
<i>pictus</i> (Storr, 1966)	<i>Omolepida</i>
<i>reticulatus</i> (Storr, 1966)	<i>melanops</i>
<i>rufescens</i> (Storr, 1967b)	<i>petersi</i>
* <i>scutulatus</i> (Pianka, 1971d)	
<i>Diporiphora</i>	<i>Lerista</i>
<i>amphiboluroides</i>	<i>desertorum</i>
<i>bilineata</i>	<i>frosti</i>
* <i>winneckei</i>	
<i>Moloch horridus</i> (Pianka & Pianka, 1970)	<i>Sphenomorphus</i>
<i>Physignathus longirostris</i>	<i>fasciatus</i>
<i>Tympanocryptis</i>	<i>richardsoni</i>
<i>cephala</i>	} (Storr, 1967)
<i>intima</i>	
<i>lineata</i>	
<i>parviceps</i>	
	<i>Tiliqua</i>
<i>Varanus</i>	* <i>multifasciata</i>
* <i>acanthurus</i>	* <i>occipitalis</i>
<i>brevicauda</i> (Pianka, 1970)	<i>rugosus</i>
<i>caudolineatus</i> (Pianka, 1969b)	<i>Lialis burtoni</i>
<i>eremius</i> (Pianka, 1968)	<i>Pygopus nigriceps</i>
<i>giganteus</i>	<i>Ophidiocephalus taeniatus</i>
<i>gilleni</i> (Pianka, 1969b)	
<i>gouldi</i>	<i>Diplodactylus</i>
<i>tristis</i>	<i>byrnei</i>
<i>Ablepharus</i>	<i>ciliaris</i>
<i>boutoni</i>	<i>conspicillatus</i>
<i>butleri</i> (Storr, 1963b)	<i>damaeus</i>
<i>greyi</i>	* <i>elderi</i>
<i>taeniopleurus</i>	<i>galeatus</i>
	<i>maini</i>
<i>Ctenotus</i>	* <i>pulcher</i>
<i>ariadnae</i>	<i>squarrosus</i>
<i>atlas</i>	<i>stenodactylus</i>
* <i>brooksi</i>	* <i>strophurus</i>
<i>calurus</i>	<i>taeniatus</i>
<i>colletti</i>	<i>tessellatus</i>
<i>dux</i>	<i>vittatus</i>
* <i>grandis</i>	<i>intermedius</i>
* <i>helenae</i>	} (Kluge, 1967)
* <i>leae</i>	
* <i>leonhardii</i>	
<i>pantherinus</i>	<i>Gehyra variegata</i>
<i>piankai</i>	* <i>Phyllurus milii</i>
* <i>quattuordecimlineatus</i>	<i>Heteronotia binoei</i>
<i>schomburgkii</i>	<i>Oedura marmorata</i> (Cogger, 1957)
<i>mimetes</i>	* <i>Rhynchoedura ornata</i>
<i>severus</i>	
<i>uber</i>	<i>Nephruerus</i>
	<i>asper</i>
	* <i>laevissimus</i>
	* <i>levis</i>
	* <i>vertebralis</i>
	<i>wheeleri</i>

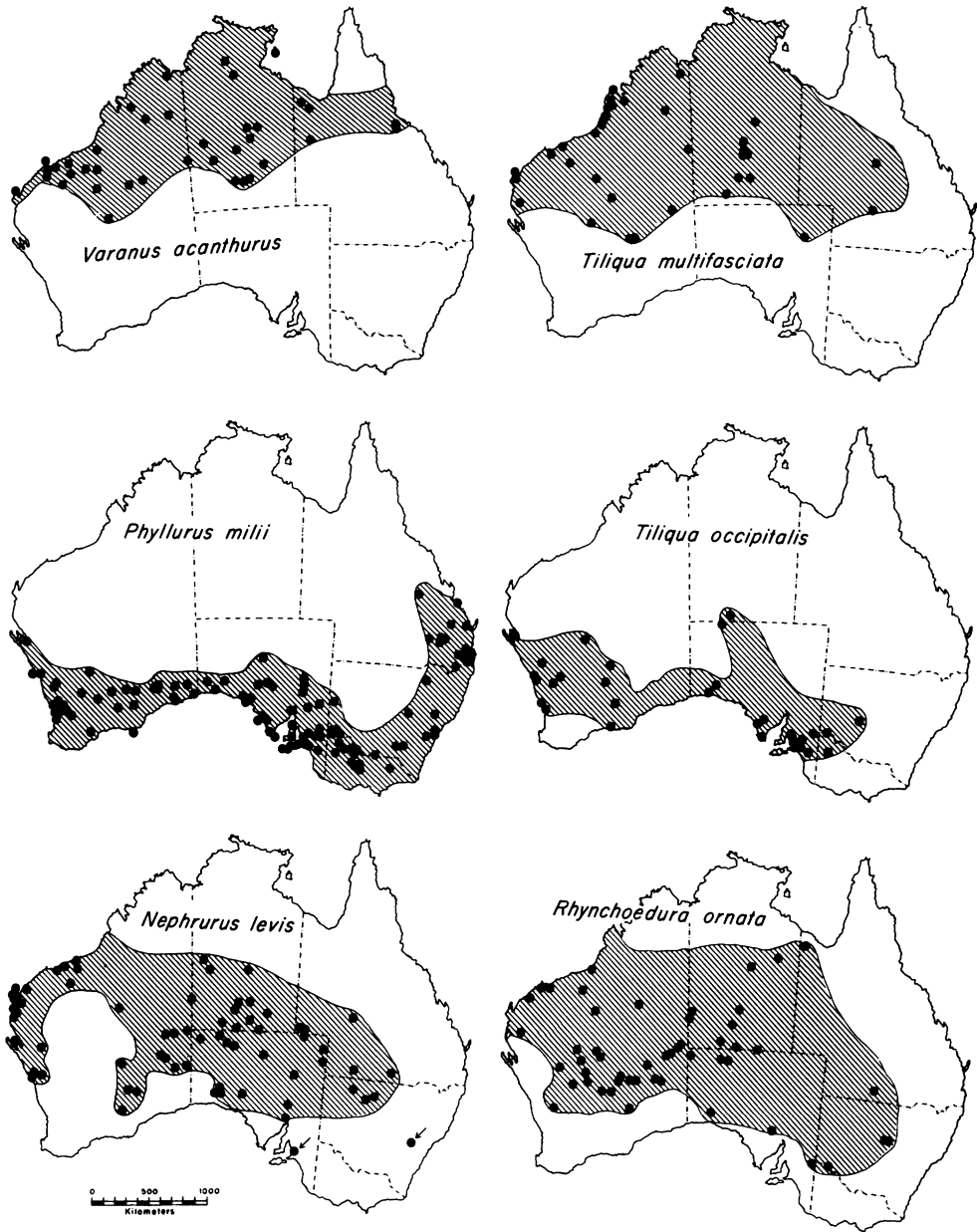


Fig. 3. Known localities of collection (solid symbols) and probable geographic distributions (cross-hatched) of two northern species (*Varanus acanthurus* and *Tiliqua multifasciata*), two southern species (*Phyllurus milii* and *Tiliqua occipitalis*), and two cremaen species (*Nephurus levis* and *Rhynchoedura ornata*).

New South Wales, Victoria, southern South Australia, and into southern and western Western Australia, sometimes as far north as Shark Bay (and occasionally to Exmouth Gulf). These are *Amphibolurus adelaidensis*, *A. cristatus* (Fig. 6), *A. pictus*, *Ablepharus*

*butleri*, *Egernia inornata*, *Tiliqua occipitalis* (Fig. 3), *T. rugosa*, *Diplodactylus vittatus*, *D. intermedius*, and *Phyllurus milii* (Fig. 3). It seems likely that the distributions of both the northern and southern species groups are strongly influenced by the thermal

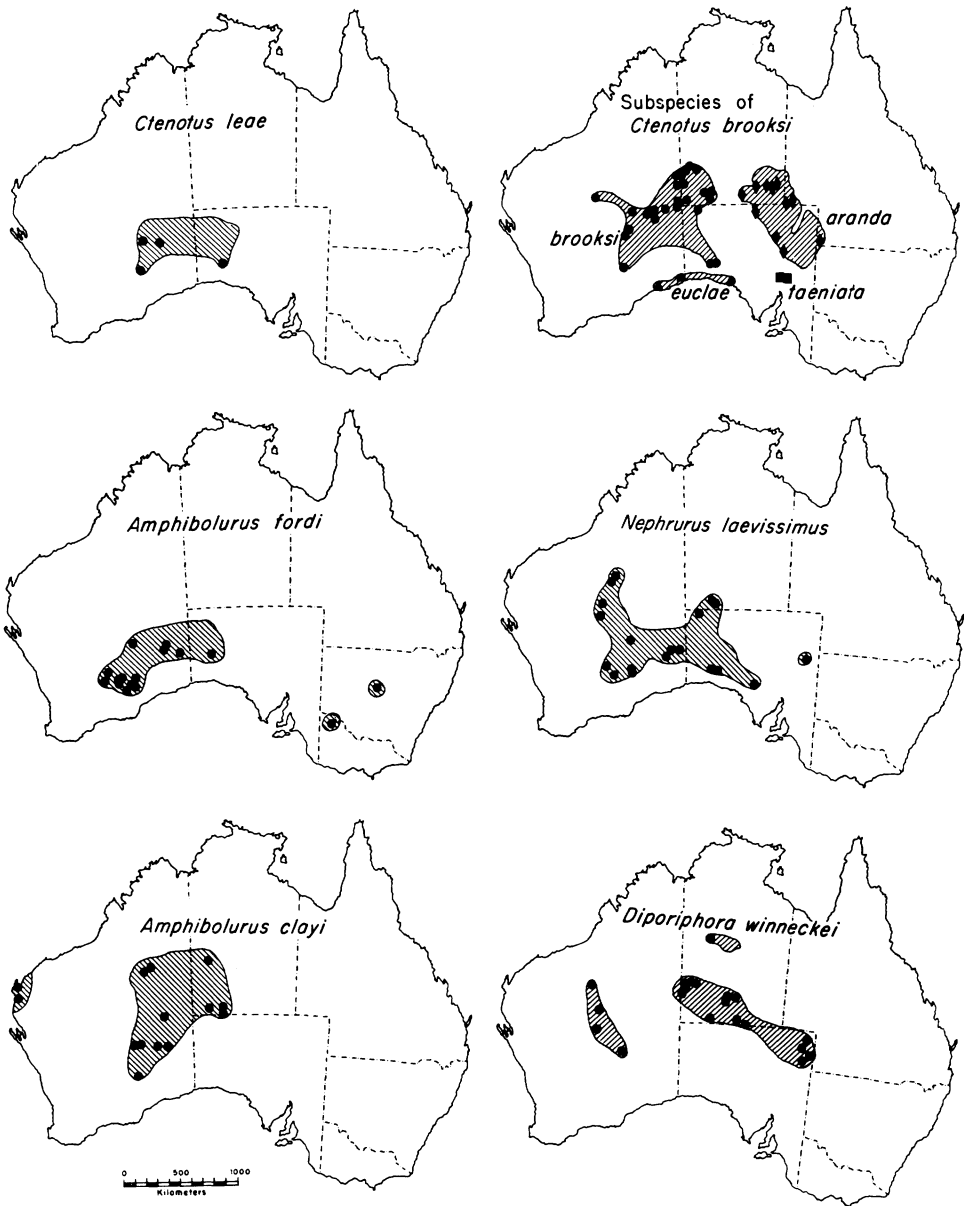


Fig. 4. Known localities of collection (solid symbols) and probable geographic distributions (cross-hatched) of six sandridge-specialized lizard species (*Ctenotus leae*, *C. brooksi*, *Amphibolurus fordii*, *Nephurus laevis*, *Amphibolurus clayi*, and *Diporiphora winneckei*).

climate, since the limits of their ranges often correspond to isotherms (which generally run east-west).

(4) *Eremaea* Species. Six species occur only in the desert region proper as outlined in Figs. 1 and 2, but they are found more or less everywhere in all the subregions of this extensive area; they are *Varanus giganteus*,

*Amphibolurus inermis*, *Ctenotus schomburgkii*, *Rhynchoedura ornata* (Fig. 3), *Pygopus nigriceps*, and *Nephurus levis* (Fig. 3). The gap in the range of *N. levis* in the Pilbara Region is probably related to the occurrence of *N. vertebralis*; see map in Fig. 6. Except for *N. levis*, which inhabits only sandplains in the western half of its range, these



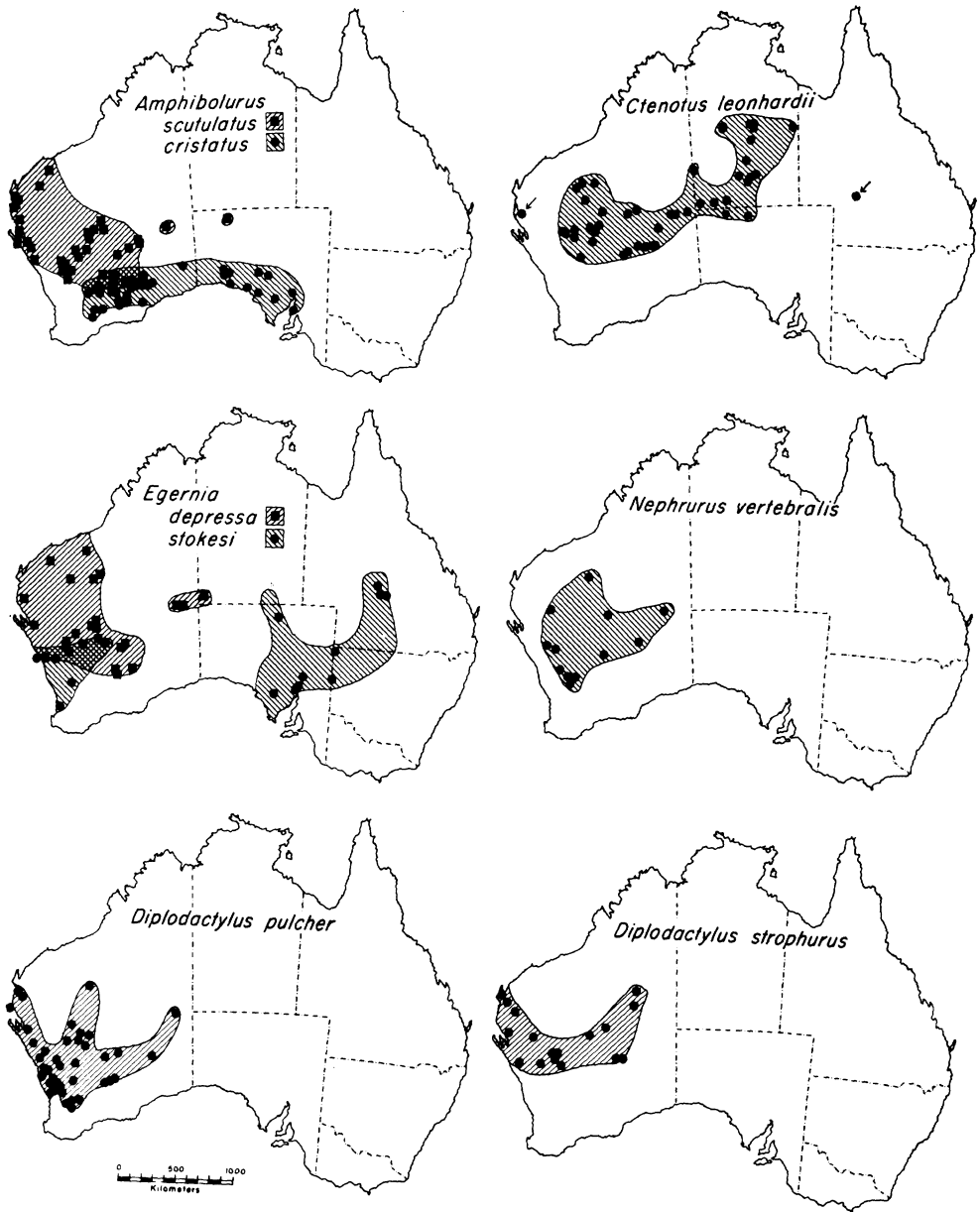


Fig. 5. Known localities of collection (solid symbols) and probable geographic distributions (cross-hatched) of seven shrub-Acacia species (*Amphibolurus scutulatus*, *Ctenotus leonhardii*, *Egernia depressa*, *E. stokesi*, *Nephurus vertebralis*, *Diplodactylus pulcher*, and *D. strophurus*). *Amphibolurus cristatus*, a "southern" species, is also included with *Amphibolurus scutulatus*.

species occur in all three of the major desert habitat types.

(5) *Central Relicts*. Six species have restricted distributions within the Central Ranges. The six central relicts are *Amphibolurus rufescens*, *Egernia margaretae*, *E. slateri*, *Omolepida petersi*, *Diplodactylus*

*galeatus*, and *Ophidiocephalus taeniatus* (known only from the holotype, collected at Charlotte Waters in 1896). It is probable that the ranges of this group were once more extensive and that they are now isolated "relict" populations (indeed, *Ophidiocephalus* could be extinct!). Two other species

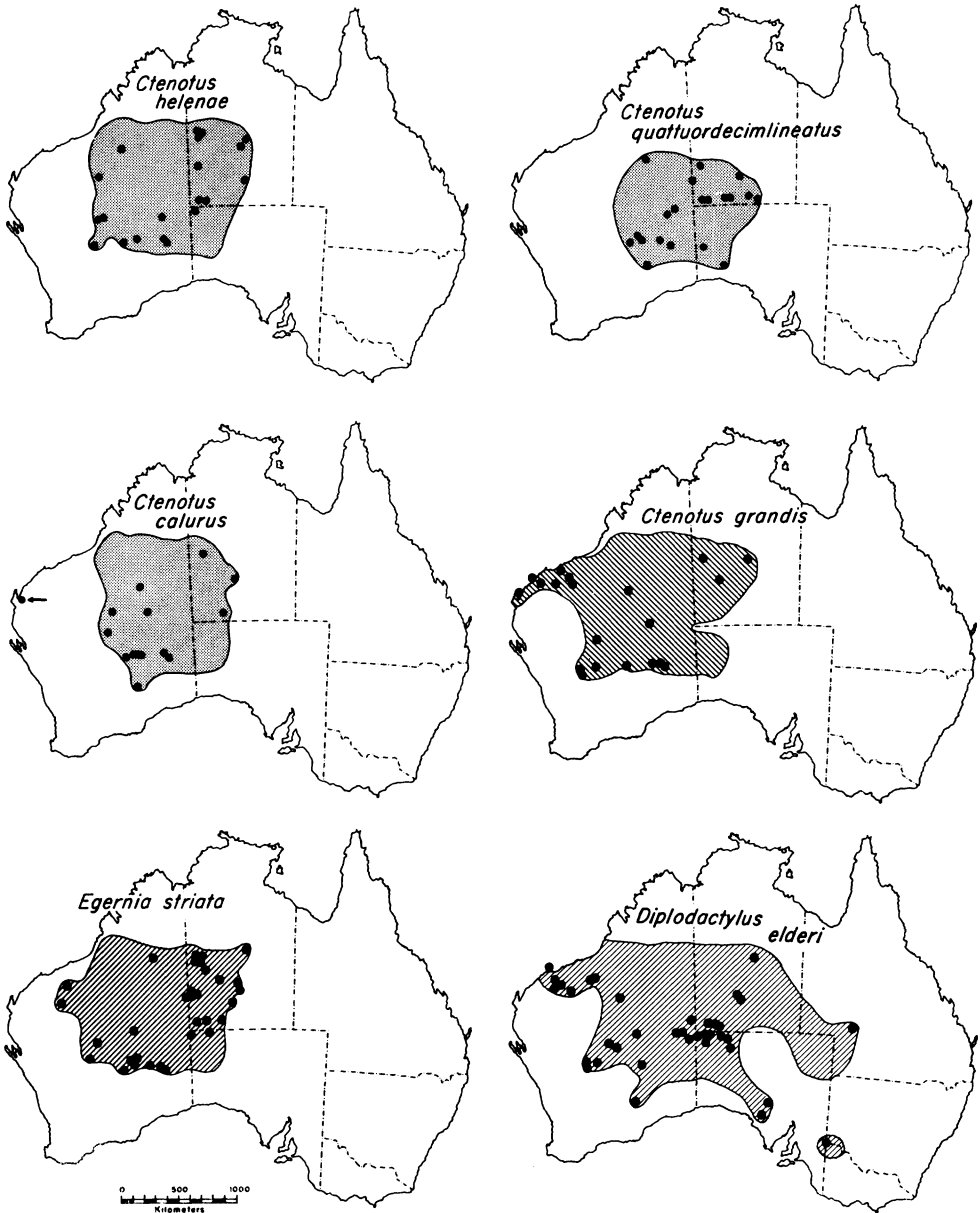


Fig. 6. Known localities of collection (solid symbols) and probable geographic distributions (stippled and cross-hatched) of six sandplain-Triodia species (*Ctenotus helenae*, *C. quattuordecimlineatus*, *C. calurus*, *C. grandis*, *Egernia striata*, and *Diplodactylus elderi*).

are distributed outside the Central Ranges but also appear to have central isolates; these are *Lerista frosti* (also southern) and *Ablepharus taeniopleurus* (also northern).

(6) *Sandridge Species*. Distributions of six of the eight species restricted to the sandridge habitat are shown in Fig. 4. These eight species are *Amphibolurus clayi* (also found

on sandplains), *A. fordi*, *Diporiphora winneckeii*, *Ctenotus brooksi*, *C. colletti*, *C. dux*, *C. leae*, and *Nephrurus laevisissimus*. *Phrygnathus longirostris* and *Diplodactylus stenodactylus* can be added to this list at a local level, but since both these species also occur in other habitats outside the sandridge country, I do not include them here. Move-

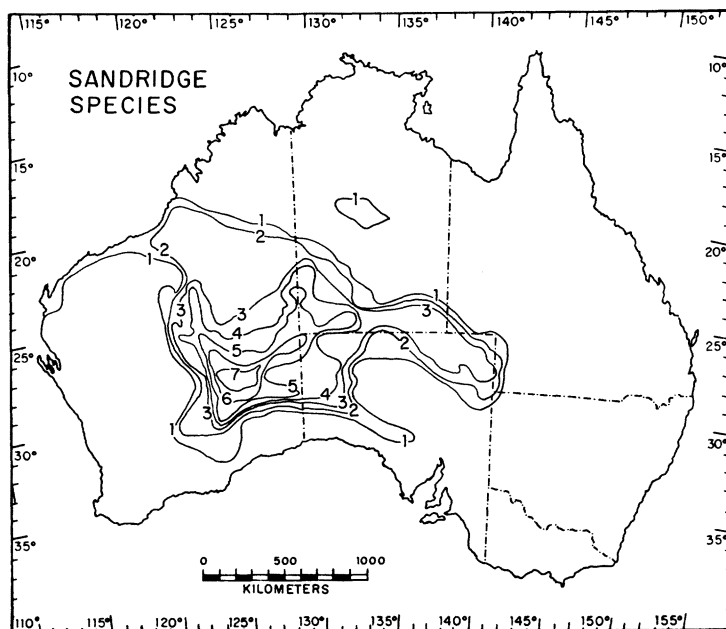


Fig. 7. Species density map for the eight sandridge-specialized species. Isopleths represent equal numbers of species.

ments and speciation of sandridge species are further discussed later in this paper.

(7) *Shrub-Acacia Species*. At least 16 species are either known to have habitat requirements appropriate to this category, or have distributions which strongly suggest that they are restricted to shrub-*Acacia* habitats; these are *Amphibolurus reticulatus*, *A. scutellatus*, *Diporiphora amphiboluroides*, *Varanus caudolineatus*, *Ctenotus leonhardii*, *C. mimites*, *C. severus*, *C. uber*, *Egernia depressa*, *E. stokesi*, *Sphenomorphus richardsoni*, *Diplodactylus pulcher*, *D. squarrosus*, *D. strophurus*, *Nephruroides vertebralis*, and *N. wheeleri*. The ranges of 7 species are shown in Fig. 5 (*Amphibolurus cristatus*, a "southern" species, is also included). Movements and speciation in shrub-*Acacia* species are treated in the discussion section of this paper.

(8) *Sandplain-Triodia Species*. Ten species have distributions corresponding to that of the sandplain-*Triodia* habitat; ranges of six of these are given in Fig. 6. The ten sandplain species are *Amphibolurus isolepis*, *Varanus eremius*, *Ctenotus calurus*, *C. grandis*, *C. helenae*, *C. piankai*, *C. quattuordecimlineatus*, *Egernia hintorei*, *E. striata*, and *Diplodactylus elderi*. At a local level within the Great Victoria Desert, several other species (*Moloch horridus*, *Ctenotus pantherinus*,

*Nephruroides levis* and *Pygopus nigriceps*) could be added to this list; however, they are not included because they occur in habitats other than sandplain habitats outside the Great Victoria Desert. Probable movements and speciation patterns of sandplain-*Triodia* species are considered further below.

The last three biogeographic categories, corresponding to the major habitat elements of the desert (sandridge, shrub-*Acacia*, and sandplain-*Triodia* habitats) together contain some 34 species. In addition, the geographic distributions of at least seven of the 22 remaining species can be satisfactorily explained on the basis of their habitat requirements, as follows:

SPECIES	HABITAT
<i>Amphibolurus caudicinctus</i>	Rocky or hilly country with large rocks
<i>Amphibolurus femoralis</i>	Exmouth sands in north-west Western Australia
<i>Moloch horridus</i>	Sandplains and sandy soils
<i>Tympanocryptis cephalo</i>	Rocky and stony desert regions of Western Australia
<i>Tympanocryptis lineata</i>	Gibson Desert, Nullarbor
<i>Diplodactylus byrnei</i>	Plain and rocky deserts
<i>Oedura marmorata</i>	Exfoliating granitic outcrops in deserts

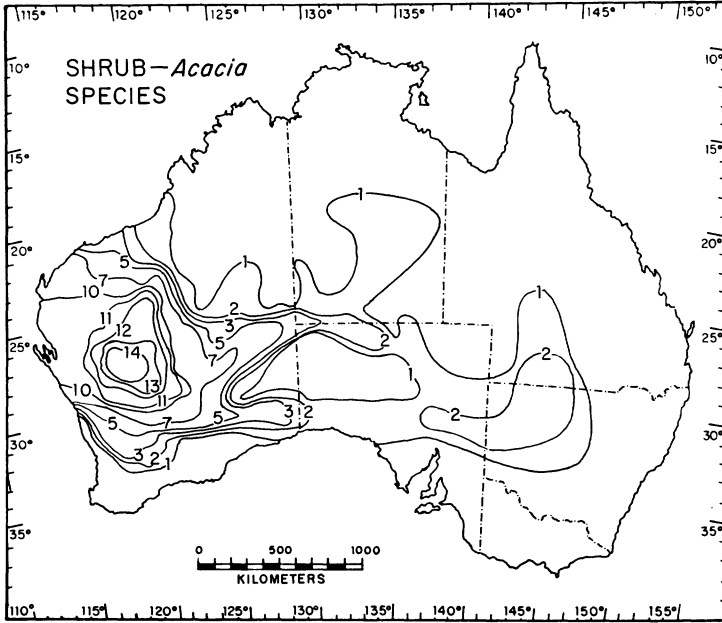


Fig. 8. Species density map for the sixteen shrub-*Acacia* species. Isopleths represent equal numbers of species.

Thus nearly one-half the lizards surveyed (41 out of the 94 species) show some degree of habitat restriction. As indicated above, detailed ecological studies in sandridge,

shrub-*Acacia*, and sandplain-*Triodia* habitats have shown that habitat specificity is even more pronounced on a local level. Figs. 7, 8, and 9 present overall species density

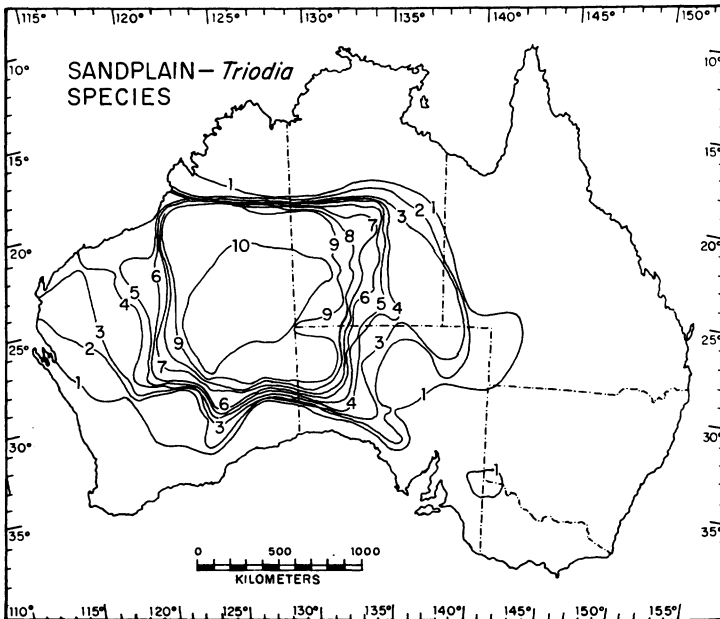


Fig. 9. Species density map for the ten sandplain-*Triodia* species. Isopleths represent equal numbers of species.

maps for those species apparently restricted to sandridge, shrub-*Acacia*, and sandplain-*Triodia* habitats, respectively.

#### DISCUSSION AND CONCLUSIONS

##### Sandridge Species

That there has been some movement between the three major sandridge deserts is evidenced by the occurrence of certain sandridge-specialized forms in two or more of the deserts. *Amphibolurus clayi*, *Diporiphora winneckei*, *Ctenotus colletti*, and *Nephrurus laevis* have all been recorded from both the Great Sandy Desert and the Great Victoria Desert (the first two species also occur in the Tanami Desert). *Diporiphora winneckei*, *Nephrurus laevis*, and *Ctenotus brooksi* are known both from the Great Victoria Desert and the Simpson Desert, as well as from sandy parts of the Central Ranges (see Fig. 4). However, there is also substantial evidence that there have been restrictions on the movements of sandridge-specialized lizard stocks. Storr (1969) considers *Ctenotus brooksi* of the Simpson Desert subspecifically distinct from those occurring in the Great Victoria Desert and the Central Ranges (Fig. 4). Thus it seems quite likely that the narrow stretch of shrub-*Acacia* habitat in the south-central part of the Northern Territory is effectively isolating eastern and western races of this species. A pale southern race, *Ctenotus brooksi euclae*, is apparently restricted to the white coastal sands and sand dunes. Races of this species may thus offer an example of incipient speciation in a sandridge-specialized lizard stock. *Nephrurus laevis* appears to be similarly distributed with a Simpson Desert isolate. Another, apparent, disjunctly distributed sandridge species is *Diporiphora winneckei* (Fig. 4), which occurs in the Great Victoria Desert, the Great Sandy Desert, the Simpson Desert, the sandy parts of the Central Ranges, and on the isolated sandridges of the Tanami Desert (Slater, 1964). To date, *Amphibolurus fordii*<sup>3</sup> and *Ctenotus leae* appear to be restricted to the Great Victoria Desert. In Fig. 2 several sand corridors connecting the three major sandridge deserts are shown. At the present time, there is little or no geographic barrier to movements of sandridge-specialized

lizards between the Great Sandy Desert and the Great Victoria Desert, whereas the sandridges of the Tanami Desert and the Simpson Desert are clearly more remote and isolated (Figs. 1 and 2).

A number of lizard species (*Amphibolurus clayi*, *A. isolepis*, *Diporiphora bilineata*, *Varanus breviceps*, *Ctenotus calurus*, *C. grandis*, *Sphenomorphus fasciolatus*, *Nephrurus levis*, and *Diplodactylus taeniatus*) occur both in the Great Sandy Desert and on the Exmouth Gulf Area sands. Although it is impossible to be certain as to which direction a species has moved solely from information on present-day distributions, it is often assumed that such movements occur most frequently from high species density centers towards lower ones and from extensive distributional areas toward more restricted ones. If this is the case, the nine species listed above may have followed light brown sandy soils and/or coastal sands from the northwestern edge of the Great Sandy Desert across the Port Hedland Area to the Exmouth Gulf Area sand (see Figs. 1, 2, 4, and 6). Alternatively, of course, some of these species could have arisen on Exmouth sands and later spread eastwards into the Great Sandy Desert.

##### Shrub-Acacia Species

Although lizard species dependent upon shrub habitats seem to be definitely concentrated in the Pilbara Region and the Mulga Scrub Country of Western Australia (Fig. 8), a number occur towards the east. Two major routes by which shrub-*Acacia* species have dispersed are suggested by Figure 8. A southern corridor through the myall belt bordering the edge of the Nullarbor Plain (as well as through the shrub habitat of the Plain itself) connects the Western Mulga Scrub Country with that in the east. *Amphibolurus reticulatus* and *Sphenomorphus richardsoni* appear to have followed this route. At least eight species of shrub-*Acacia* lizards (*Amphibolurus reticulatus*, *Amphibolurus scutellatus*, *Ctenotus leonhardii*, *Diplodactylus pulcher*, *Diplodactylus squarrosus*, *Egernia depressa*, *Sphenomorphus richardsoni*, and *Nephrurus vertebralis*) appear to have crossed the continent to varying degrees along a more northern corridor which connects the Pilbara Region to the Warburton Ranges of the Central Ranges by way of the Lake Carnegie region and the southern part of the Gibson Desert.

<sup>3</sup> *Amphibolurus fordii* is also known from sandy soils (isolated patches?) in inland Victoria and New South Wales (Cogger, 1969).

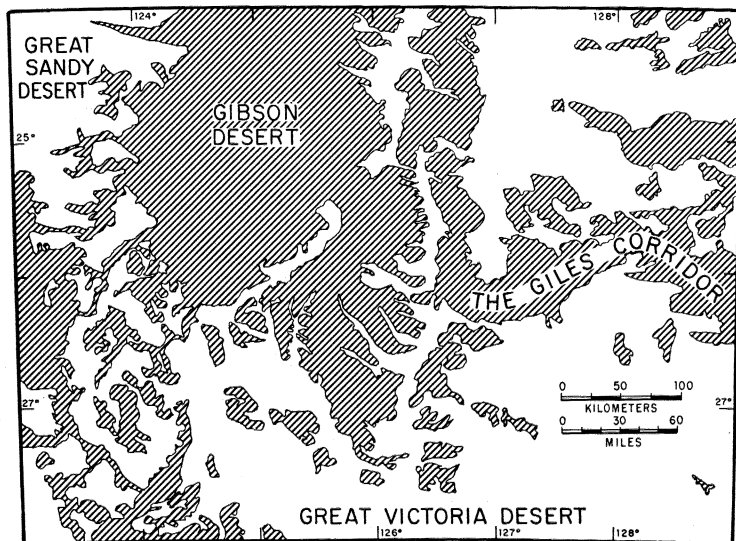


Fig. 10. A detailed map of the area marked with a rectangle in Fig. 2, based on a Western Australia Lands Department pastoral map. The map shows the extent of sandridge-sandplain habitats (open) and shrub-*Acacia* habitats (cross-hatched). The part labelled "The Giles Corridor" represents only its bottleneck portion (Warburton Ranges); the full extent of this major east-west shrub corridor is illustrated in Fig. 2 and described in the text. Note that, at the present time, shrub habitats barely separate the sandy habitats of the Great Sandy Desert from those of the Great Victoria Desert. In addition, a narrow, but open, sand corridor between the Warburton Ranges and the Gibson Desert may be seen which connects the Great Victoria Desert with the sandy habitats of the Central Ranges (upper right-hand corner of the figure).

The westernmost arm of this northern corridor is quite broad, including numerous dry lakebeds such as Rason Lake, Lake Yeo, and Lake Throssel in the western sector of the Great Victoria Desert, as well as the easternmost arm of the Pilbara Region (the Lake Carnegie area, called the Carnegie Salient by Beard, 1969) and mulga habitats in the southern part of the Gibson Desert (Fig. 10). This northern shrub-*Acacia* corridor narrows considerably at the Warburton Ranges in central Australia, and broadens out again in the southeastern part of the Central Ranges. In view of the extensive early explorations of the English explorer Ernest Giles in this "bottleneck" region (Giles, 1889), and because this shrub-*Acacia* stretch appears to be a major route by which lizards have moved east-west, I propose that it be named "The Giles Corridor."

At least two shrub-*Acacia* species have apparent isolates along The Giles Corridor: *Amphibolurus scutulatus* and *Egernia depressa* (Fig. 5). In view of the fact that these two species are widespread in shrubby habitats west of The Giles Corridor, it is likely that they have only relatively recently

invaded the shrub habitats of the Central Ranges. By contrast, it is probable that the better established shrub-*Acacia* species, such as *Ctenotus leonhardii* (Fig. 5) and *Sphenomorphus richardsoni*, crossed this corridor during some earlier time and have since expanded their ranges to include much of the shrub habitat in the Central Ranges (and, in the case of *S. richardsoni*, further east into the Eastern Mulga Scrub Country). The distribution of *Egernia stokesi* is poorly known (Fig. 5), but is probably contiguous from Western Mulga Scrub Country to Eastern Mulga Scrub Country through the shrub and myall zone north of the Nullarbor Plain (it is, of course, possible that there are western and eastern isolates in this species).

#### *Sandplain-Triodia Species*

Sandplain-specialized lizard species (Fig. 9) are distributed more continuously than the preceding two groups (compare Fig. 9 with Figs. 7 and 8), and present day isolates are much more difficult to document. *Triodia* occurs on almost all sandy soils, and the distribution of *Triodia*-specialized species cor-

responds fairly closely to that of the area occupied by both sandridge and sandplain deserts (compare Figs. 2 and 9). One could consider the sandridge species (Figs. 4 and 7) a subset of the sandplain-*Triodia* species group with an even greater degree of habitat restriction. Distribution patterns shown in Figs. 7 and 9 largely complement those summarized in Fig. 8, another indication that, as indicated earlier, sandplain-*Triodia* and shrub-*Acacia* habitats are often mutually exclusive. Barriers to the movements of sandplain species are not as evident or nearly as pronounced as those blocking the movements of sandridge and shrub-*Acacia* species. However, the zone of shrub habitat (The Giles Corridor) cutting across the center partially separates northern sandplain habitats from southern ones, and could well have been a barrier to the dispersal of some sandplain-dwelling lizards during the geologic past.

#### *A Model of Lizard Speciation in the Australian Desert*

In the Australian desert region, relatively few obvious geographic barriers, such as mountains, lakes and/or rivers exist (one such is Pleistocene Lake Dieri, invoked by Kluge (1967) as a geographic barrier promoting speciation in *Diplodactylus*). Neither have glaciers occurred in the region. Unsuitable habitats must often have constituted the major barriers to lizard dispersal. A large percentage of species of desert lizards show some degree of habitat specificity. Mayr (1963) noted that even very narrow belts of unsuitable habitat can be effective barriers to dispersal. This is particularly true for relatively sedentary terrestrial vertebrates such as lizards. According to Keast (1961), there are no mulga isolates in the Australian avifauna; but birds can fly across zones of unsuitable habitat. Lizards, on the other hand, might well find the same zone a nearly complete barrier.

Mayr (1963; p. 571) argued that habitat specificity reduces the likelihood of geographic isolation:

"Habitat selection is a conservative factor in speciation since it reduces the probability that new isolates will be established beyond the present species border. The normal habitat of the species usually does not occur beyond the species border. If a species has the ability to change its habitat preference, it

not only can expand its range but can also change genetically under the pressure of the new environment in the newly established geographical isolate. This creates conditions that are unusually favorable for rapid speciation."

Mayr's statement seems somewhat incomplete as he does not indicate precisely *how* isolation is achieved. Presumably an isolate must be formed *before* changed selection pressures can produce the genetic alterations necessary for speciation. Individuals in such an isolate can be selected to modify their habitat preferences, but only *after* gene flow has been diminished. Thus I envision a habitat breaking up into patches as a necessary precursor to selection for different habitat requirements. Such patches of isolated habitat are common in parts of the Australian deserts (Fig. 10) and would appear to constitute a very potent mechanism for the generation of new species (Pianka, 1969a).

Changes in habitat requirements have doubtless accompanied speciation in some Australian desert lizards, as evidenced by the fact that, in each of at least seven genera, habitat-restricted species are known to occur in two or three of the habitat types (e.g. *Amphibolurus*, *Diporiphora*, *Varanus*, *Ctenotus*, *Sphenomorphus*, *Diplodactylus*, and *Nephurus*; see Table 2). However, some speciation appears to have taken place *within* the habitat-restricted genera as well, especially in the scincid genus *Ctenotus* (Table 3). Here I propose a mechanism by which habitat specificity could *enhance*, rather than reduce, opportunities for speciation.<sup>4</sup>

Suppose that large areas of shrub-*Acacia* habitat are surrounded and separated by sandplain-*Triodia* habitat. Further, suppose that during geologic time long-term soil and/or climatic changes occur causing shrub habitats to encroach gradually upon sandplain habitats. Eventually the situation could become reversed, with shrubby habitats isolating sandplain habitats. Indeed, Beard (1969) suggests that, at the edges of the Great Victoria Desert, sandy topsoils are being swept up onto sandridges, often exposing lateritic subsoils or loamy soils beneath. These soils are better substrata for shrubs and *Acacia* than for

<sup>4</sup> Similar models of speciation have been suggested for South American *Anolis* lizards (Williams and Vanzolini, 1966; Vanzolini and Williams, 1970) and for Amazonian birds (Haffer, 1969). In these cases the habitat types are grasslands and forests.

TABLE 2. SPECIES GROUPS WITH CLOSELY-RELATED SPECIES RESTRICTED TO DIFFERENT HABITATS. Species whose habitat requirements are questionable are listed in parentheses.

Genus	Sandridge	Shrub-Acacia	Sandplain-Triodia
<i>Amphibolurus</i>	<i>clayi</i>	<i>reticulatus</i>	<i>inermis</i>
<i>Amphibolurus</i>	<i>fordi</i>		<i>isolepis</i>
<i>Diporiphora</i>	<i>winneckeii</i>	<i>amphiboluiroides</i>	( <i>bilineata</i> )
<i>Varanus</i>		<i>caudolineatus</i>	<i>eremius</i>
<i>Ctenotus</i>	<i>colletti</i> & <i>leae</i>		<i>calurus</i>
<i>Ctenotus</i>	<i>dux</i>	( <i>atlas</i> )	<i>piankai</i> & <i>quattuordecimlineatus</i>
<i>Ctenotus</i>		<i>leonhardii</i>	<i>helenae</i> & <i>grandis</i>
<i>Ctenotus</i>	<i>brooksi</i>		<i>schomburgkii</i>
<i>Sphenomorphus</i>		<i>richardsoni</i>	( <i>fasciolatus</i> )
<i>Diplodactylus</i>		<i>strophurus</i>	<i>elderi</i>
<i>Nephhrurus</i>	<i>laevis</i>	<i>vertebralis</i>	<i>levis</i>

*Triodia*. Thus windblown shifting sands have probably altered the junctures of the two habitats. Similarly, climatic changes (especially in rainfall) occurring with the waxing and waning of the glacial and interglacial periods (Crocker and Wood, 1947; Fairbridge, 1953; Littlejohn, 1967) could easily have reversed habitat junctures several

times. Rather little is known definitely about the recent geological history, paleobotany, and post-Pleistocene climatic changes in central Australia, but it is generally accepted that an east-west "arid belt" moved north and south, respectively, with glacial advances and retreats (Keble, 1947). During glacial periods shrub habitats presumably expanded at the expense of *Triodia* (grassy) habitats, and vice versa during interglacials.

TABLE 3. CLOSELY-RELATED ECOLOGICALLY SIMILAR SPECIES RESTRICTED TO AND OCCURRING IN SYMPATRY IN THE SAME HABITAT.

Genus	Species	Authority
<i>Amphibolurus</i>	<i>scutulatus</i> <i>cristatus</i>	Pianka (1971d)
<i>Ctenotus</i>	<i>grandis</i> <i>helenae</i>	Pianka (1969c)
<i>Ctenotus</i>	<i>piankai</i> <i>quattuordecimlineatus</i>	Pianka (1969c)
<i>Ctenotus</i>	<i>colletti</i> <i>leae</i>	Pianka (1969c)
<i>Ctenotus</i>	<i>mimetes</i> <i>leonhardii</i> <i>severus</i> <i>uber</i>	Storr (1968b, 1969)
<i>Egernia</i>	<i>striata</i> <i>kintorei</i>	Storr (1968a)
<i>Egernia</i>	<i>depressa</i> <i>stokesi</i>	Glauert (1961)

Between the Lake Carnegie district of the Pilbara Region and the Gibson Desert, there is a narrow zone where the sandplains and sandridges of the Great Sandy Desert almost come into contact with those of the Great Victoria Desert (Figs. 2 and 10). Here northern sandridge and sandplain habitats are nearly, but not quite, contiguous with southern ones. This area is also crossed east-west by the shrub habitats of The Giles Corridor. Immediately to the east of Lake Carnegie, shrub-*Acacia* habitats (the Carnegie Salient) make contact with those in the southern part of the Gibson Desert (Fig. 2), which, in turn, nearly contact the shrub-*Acacia* habitats in the Warburton Ranges of the Central Ranges (Fig. 10). It seems highly likely that climatic changes (including associated windblown sands) during the geologic past have altered habitat junctures in regions like these, perhaps alternately isolating eastern and western populations of shrub-*Acacia* specialized lizard species and then northern and southern populations of lizards specialized to sandridge and sandplain habitats. Indeed, habitats in the region shown in Fig. 10 appear to be very delicately balanced, for the shrub-*Acacia* corridor could



easily be broken with increasing aridity as *Triodia* invades existing shrub habitats.

Other potential bottlenecks between the habitat-types, similar to this one, occur in the southernmost part of the Northern Territory, and on both the eastern and the western sides of the Nullarbor Plain (Fig. 2). I conclude that the past history of these relatively restricted geographic regions may well hold many of the answers to the speciation and present-day distributions of habitat-restricted Australian desert lizards.

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- DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF TEXAS AT AUSTIN, AUSTIN, TEXAS 78712.

## Thermoregulation and Evaporative Cooling in the Chuckwalla, *Sauromalus obesus*

TED J. CASE

At an ambient temperature of 47.0 C *Sauromalus obesus* can maintain its body temperature 4.0 C lower for periods of at least three hours. Such thermoregulation under heat stress is accomplished by evaporative cooling. The magnitude of thermoregulatory response and of water loss appears to vary seasonally: animals captured in the spring are far more effective thermoregulators than animals captured in the fall.

### INTRODUCTION

THE ability of desert reptiles to regulate their body temperatures behaviorally has been well documented (Bogert, 1949, 1959; Heath, 1965; Schmidt-Nielsen, 1964; DeWitt, 1967). In addition, many recent studies have examined the physiological responses of reptiles to various temperatures (Dawson, 1967). One significant finding emerging from these studies is that pulmocutaneous water loss is much greater than previously had been supposed (Bentley and Schmidt-Nielsen, 1966), but there is an inverse relationship between the aridity of the reptile's environment and the amount of pulmocutaneous water loss (Bentley and Schmidt-Nielsen, 1966; Dawson, Shoemaker, and Licht, 1966; Warburg, 1965). Accordingly, workers have suggested that evaporative cooling is not one of the usual mechanisms to which desert lizards resort when subjected to heat stress (Warburg, 1965; Templeton, 1960).

The chuckwalla, *Sauromalus obesus* Baird, is a large herbivorous iguanid that inhabits rocky areas in desert regions of the southwestern United States and Mexico. Specimens were collected at Amboy Crater, a lava flow area in San Bernardino County, California, in the spring of 1968 (May) and

fall of 1969 (September and November). In July, air temperatures in the sun have been measured in excess of 47.0 C. Even well-sheltered rock crevices may reach 44 C (chuckwallas utilize such crevices to escape the midday sun in summer), and surface temperatures of exposed lava are often over 60 C. Because it was apparent that chuckwallas are potentially exposed, at least temporarily, to temperatures approaching lethality, this study undertakes to examine their responses to very high ambient temperatures.

### MATERIALS AND METHODS

Animals were kept in the laboratory under conditions intended to stimulate existing field conditions. Twenty-one lizards captured in the spring were kept in a large observation pen with rocky microhabitats and a thermal gradient maintained by sun lamps. The animals were provided with lettuce and occasionally water, which they drank infrequently. Many of these animals gradually lost weight in captivity. Nine animals captured in the fall were kept in similar but smaller boxes and not fed or watered; these were tested within two weeks after capture.

The experimental procedure consisted of placing a chuckwalla whose body temperature was stable at 37.0 C inside a ¼ inch