Macro- and microhabitat relationships among lizards of sandridge desert in central Australia

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ABSTRACT

Macro- and microhabitat relationships were analysed within a lizard community from the Simpson Desert, Queensland, Australia. Three macrohabitat categories (dune crest, side and swale) and six microhabitat variables (soil hardness and five ground cover estimates) were investigated. Most captures of lizards (46%) and 25 of 36 species were found on dune crests, with four species being restricted almost exclusively to crests. Proportions of captures were less on dune sides and swales (28 and 26% respectively) than on crests, but 25 and 28 species respectively occurred in these habitats. At the microhabitat level the variables most frequently associated with abundance of different species of lizard were soil hardness and cover of spinifex *Triodia basedowii*. Microhabitat associations reflect selection by individuals for local sites that provide specific shelter, foraging or thermoregulation requirements, but firm conclusions are difficult to draw due to auto-correlation between microhabitat variables and limited knowledge of the autecology of most species. We conclude that differences in habitat provide an important axis for species separation among desert lizards, and that local species diversity is enhanced by dune topography.

INTRODUCTION

Lizards are conspicuously successful inhabitants of arid areas in many parts of the world, and occupy such extreme environments as flat rock desert and hyper-arid dune fields (Cloudsley-Thompson 1991). At the level of individual species, much attention has been focused on physiological and morphological adaptations that permit exploitation of arid environments (Louw and Holm 1972; Bradshaw 1986; Bauer and Russell 1991). In contrast, studies at the community level have usually sought to identify factors that permit coexistence of ecologically similar species, and have been concerned primarily with describing patterns of resource use and overlap (Pianka 1986). Soil structure has been identified as an important factor facilitating coexistence in many arid areas (Barbault and Maury 1981; Shenbrot 1988; Shenbrot *et al.* 1991). Other factors that have been identified include local climate (Whitford and Creusere 1977; Scheibe 1987), competition (Dunham 1980), perch heights (Moermund 1986), habitat structure (Pianka and Pianka 1976; Winemiller and Pianka 1990), and presence of rodent burrows, which provide shelter (Shenbrot 1988).

In Australia, communities of desert lizards are highly diverse, with up to 42 species being recorded at a site (Pianka 1969, 1986). Numbers of species and species composition often vary within a local area in relation to vegetation type or to the successional stage of vegetation regenerating after fire. For example, in spinifex grasslands, species richness of lizards is low after fire but increases with increasing size and age of grass hummocks (Fyfe 1980; Cogger 1984). Dense cover of spinifex and other microhabitats, such as leaf litter or shrubs, protects lizards from predators and extreme temperatures and provides increased opportunities for foraging (Pianka 1986). In sandridge deserts, increased topographical diversity appears to promote local species richness of lizards, with taller dunes having a suite of species that is small but distinct from that of the inter-dune swales (Read 1992; Reid *et al.* 1993). Such macrohabitat differences have been little investigated, but may contribute importantly to patterns of lizard diversity on a local scale.

In the present paper, we investigate the habitat relationships of an assemblage of lizards occupying sandridge desert in western Queensland. We define macrohabitat as position on dune (crest, side or swale), and microhabitat as soil and vegetation type at local sampling points (trap stations). We ask whether lizards differ in their use of either category of habitat, using capture data collected over the course of a study spanning 3.5 years.

STUDY AREA

Research was centred approximately 20 km north of the Ethabuka Station homestead in the Simpson Desert, southwestern Queensland (23°46′S, 138°28′E). The site is characterized by long red sand dunes up to 8 m high and 0.6–1 km apart that run roughly from south to north in line with the prevailing southerly winds. Spinifex *Triodia basedowii* dominates the ground level vegetation in the swales and on the sides of dunes. Low trees, such as mulga *Acacia aneura* and gidgee *A. cambagei*, are restricted to the dune swales.

Perennial shrubs (*Crotalaria* sp., *Enchylaena tomentosa, Sclerolaena diacantha*) occur from the dune sides to the crests. Records from the nearest weather stations (172 km north and 245 km south) suggest that annual rainfall averages between 165 mm and 264 mm (Bureau of Meteorology 1988). During summer, daily temperature maxima usually exceed 40°C and winter minima frequently fall below 5°C.

METHODS

Animals were live-captured using pitfall traps of PVC pipe (16 cm diameter, 60 cm deep) buried flush to the ground. Each trap was equipped with a 5 m long aluminium flywire drift fence to enhance trapping efficiency (Friend *et al.* 1989). Traps were arranged into square grids of 1 ha, each comprising six lines of six traps, with 20 m spacing between trap stations. One edge of each grid was positioned along a dune crest while the opposite boundary was 100 m away in the swale. Twelve grids were established. These were spaced between 0.6 and 2 km apart and ran in a north-south direction. The two extreme grids were separated by approximately 14 km. Traps were opened for 3–4 consecutive days on 15 occasions between March 1990 and June 1993. Trapping periods were during: March 1990; August 1990; September 1990; April 1991; May 1991; August 1991; October 1991; November 1991; April 1992; June 1992; August 1992; October 1992; November 1992; March 1993; June 1993.

Checks were made early in the mornings and sometimes in the late afternoons. Captured animals were identified and marked uniquely by toe-clipping. As part of a more extensive study the lizards were weighed, the lengths of the snout-vent, tail and jaw were measured and the number of tail breaks noted.

To analyse patterns of macrohabitat use, each grid was divided into three sections with the two uppermost rows of traps representing the dune crest, the adjoining two rows representing the side of the dune and the lowest two rows, the dune bottom, or swale. Inspection of the raw data suggested that there was little temporal difference in macrohabitat use, either between field trips or seasons. Hence, macrohabitat was assessed by tallying the total captures of all individuals within each macrohabitat category over all 12 grids.

Microhabitat variables were measured on five of the 12 trapping grids. These included soil hardness and percent cover estimates of live spinifex, dead spinifex, annual plants, total ground cover, and live shrubs. Each of the ground cover variables was estimated visually as the percentage of the total ground area of a circle of radius 2.5 m centred on each pit trap. Soil hardness was assessed by pushing a rod into the soil surface with constant force, and noting the depth of penetration. Hardness was scored from 1 (very hard) to 5 (very soft). The soil hardness value for each trapping station was recorded as the average of six measurements taken within 2.5 m of the pitfall trap.

Microhabitat use by lizards was assessed by tallying captures of individuals of each species at each trap over the entire period of the study. Product-moment correlations were calculated between capture frequencies and microhabitat variables for pitfall traps within each category of macrohabitat.

RESULTS

Captures

A total of 1 421 individuals of 36 lizard species was captured during the study (Table 1). A further four species, observed at the site, were not caught in the pitfall traps. There were 906 individuals of 31 species trapped on the five grids used for microhabitat analysis. Abundances were variable with *Lerista labialis* (319 captures) being the most common and five species (*Ctenotus schomburgkii, Tiliqua multifasciata, Varanus gilleni, Diplodactylus elderi* and *Delma tincta*) being represented by only one capture (Table 1). *Diplodactylus conspicillatus, D. stenodactylus* and *Lialis burtonis* were each observed only once and none was trapped.

Macrohabitat

Forty-six per cent of all lizard captures occurred on the dune crests. The mid-dune region accounted for 28 per cent and the dune bottom had 26 per cent. The numbers of species caught in each dune region were 25, 25 and 28 for the crests, sides and dune bottom respectively.

The lizard fauna contained both macrohabitat specific species and generalists. Figure 1 shows the percentage of captures of each species, for which $n > 10$, in each macrohabitat category. *Eremiascincus fasciolatus, Diporiphora winneckei, Ctenotus brooksi* and *Lerista aericeps* are primarily dune crest dwellers. They have a high proportion of captures along the dune crests with only small numbers along the sides. No individuals of these species were caught in the swales. In

Table 1. Lizard species and total numbers of captures recorded during the study. Species observed but not trapped are marked with an asterisk (*).

Species	Total captures
SCINCIDAE	
Ctenotus ariadnae	102
Ctenotus brooksi	31
Ctenotus dux	70
Ctenotus lateralis	33
Ctenotus leae	66
Ctenotus pantherinus	187
Ctenotus regius	2
Ctenotus schomburgkii	1
Egernia inornata	19
Eremiascincus fasciolatus	16
Lerista aericeps	13
Lerista labialis	319
Menetia greyii	27
Menetia maini	9
Morethia ruficauda	3
Tiliqua multifasciata	1
AGAMIDEA	
Ctenophorus isolepis	233
Ctenophorus nuchalis	83
Diporiphora winneckei	13
*Lophognathus gilberti**	0
Moloch horridus	3
Pogona vitticeps	17
VARANIDAE	
Varanus brevicauda	44
Varanus eremius	35
Varanus gilleni	1
Varanus gouldii	44
Varanus tristis	2
GEKKONIDAE	
Crenadactylus ocellatus	2
Diplodactylus ciliarus	2
*Diplodactylus conspicillatus**	0
Diplodactylus elderi	1
*Diplodactylus stenodactylus**	0
Gehyra variegata	4
Heteronotia binoei	2
Lucaseum damaeum	3
Nephrurus levis	18
Rhyncoedura ornata	9
PYGOPODIDAE	
Delma tincta	1
*Lialis burtonis**	0
Pygopus nigriceps	6
Total	1 421

contrast, we found no swale specific species. The species with the highest percentage of captures in the swales (*Menetia greyii, Egernia inornata* and *Ctenotus pantherinus*) were also caught on the dune crests at least 18 per cent of the time (Fig. 1). We identified a number of macrohabitat generalists including all three goanna species included in this analysis (*Varanus brevicauda*, *V. eremius* and *V. gouldii*). Captures for these species were spread uniformly across all macrohabitats as were those of *Nephrurus levis, Ctenotus ariadnae* and *Ctenophorus isolepis*.

Microhabitat

Comparison of mean values of each of the measured habitat variables with dune position shows a number of trends consistent with those expected for an active sand ridge system (Fig. 2) (Shephard 1992). Along the dune crest, where the sand is mobile (and therefore relatively unconsolidated), there is little ground cover. The cover that is present comprises a higher proportion of annual plants and live shrubs than the sides and swales, where the predominant ground cover is spinifex.

Microhabitat variables were auto-correlated with dune position, so the data were separated into the three macrohabitat categories and analysed separately. Statistically significant correlations between lizard species and measured microhabitat characteristics are presented in Table 2. Soil hardness and spinifex cover are the microhabitat variables correlated most frequently with presence of particular lizard species. In the upper region of the sandridges, *Ctenotus dux* was captured more often in traps surrounded by high spinifex cover. *Ctenotus leae* and *Lerista labialis* were associated with traps with less spinifex cover. On the dune crests, the macrohabitat generalist, *Ctenotus ariadnae* (Fig. 1), was more frequently caught in traps in relatively hard soil. Conversely, captures of two species (*Ctenotus leae* and *Lerista labialis*), which were predominantly caught along the dune tops, were correlated positively with soil softness. In the mid-region of the sand dunes species richness was positively correlated with spinifex cover ($r = 0.28$, $p = 0.03$). In the swales, *Ctenotus pantherinus* abundance increased positively with increasing live shrub coverage and a similar relationship was seen between *C. dux* and coverage of annual plants (Table 2). *Ctenophorus isolepis* was caught more frequently on hard soil (Table 2).

DISCUSSION

Topographical diversity within sandridge desert appears to provide an important axis for habitat separation by lizards. Although all species were captured on the sides of dunes, four species occurred almost exclusively on dune crests and were not captured more than 60 m down the dune side. Conversely, for seven species, less than 30 per cent of captures occurred on dune crests. Reid *et al.* (1993) concluded that a distinctive group of reptiles could be associated with taller dunes near Uluru, although they did not clearly identify the species comprising this group.

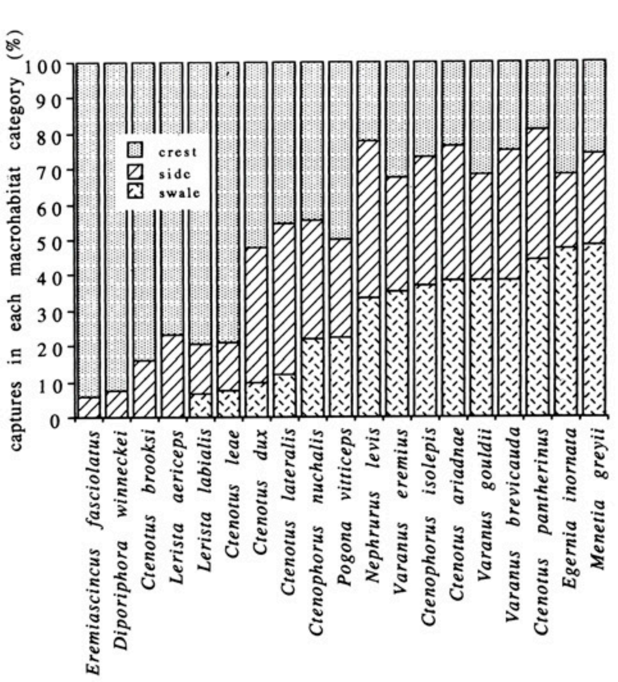

Fig. 1. Proportional macrohabitat usage by common lizards (n > 10 captures) during the 40-month study.

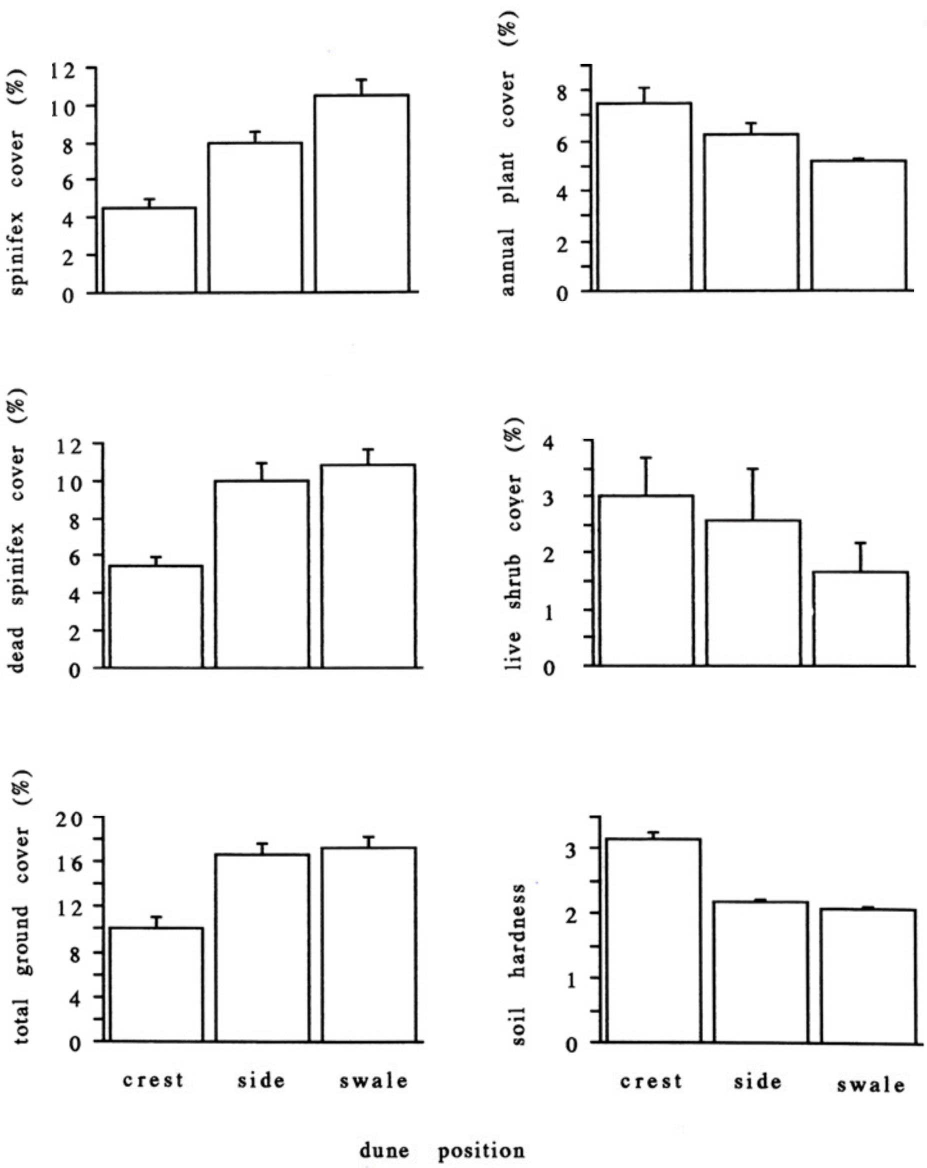

Fig. 2. Distribution of microhabitat variables in each macrohabitat category (dune position) (mean ± std. error).

Table 2. Species-microhabitat correlations. All species were tested against each microhabitat variable. Only statistically significant results are reported.

Dune position	Species	Microhabitat variable	Correlation (r)	P-value
Crest	*Ctenotus ariadnae*	Soil hardness	−0.348	0.008
	Ctenotus dux	% live spinifex	+0.328	0.010
	Ctenotus leae	% dead spinifex	−0.253	0.050
		Soil hardness	+0.409	0.002
	Lerista labialis	% dead spinifex	−0.319	0.010
		Soil hardness	+0.615	<0.0001
Swale	*Ctenotus dux*	% annual plants	+0.561	<0.0001
	Ctenotus pantherinus	% live shrubs	+0.279	0.032
	Ctenotus isolepis	Soil hardness	−0.295	0.022

Two of the four species restricted to the dune crests and sides burrow below the sand surface, and hence may select the more extensive areas of loose sand on the dune crests to facilitate movement. For *Eremiascincus fasciolatus*, sub-surface locomotion is probably assisted further by smooth, glossy scales; in *Lerista aericeps*, limb reduction is associated with fossorial habit (Wilson and Knowles 1988). In contrast to the burrowing habits of these two species, *Ctenotus brooksi* is active on the ground surface and *Diporiphora winneckei* in shrubs. In other parts of the Simpson Desert these lizards are often associated with cane grass *Zygochloa paradoxa* on the dune crests (Gibson and Cole 1988). Although a similar association may occur between the lizards and cane grass in our study area, it is likely to be weak as this plant species is locally rare.

Several species of lizards showed clear associations with particular microhabitats, suggesting that microhabitat may also be an important axis for species separation. Two microhabitat variables stand out, soil hardness and cover of spinifex. On the dune crests, the abundance of *Ctenotus leae* and *Lerista labialis* tended to be correlated negatively with cover of dead spinifex and positively with soft soil (Table 2). Soil softness probably facilitates burrowing for *L. labialis,* as for *L. aericeps,* and this is particularly evident in patches away from cover. *Ctenotus leae* is active on the sand surface and is unusual for a small skink (<5 g) in including much plant material as well as invertebrates in its diet (Pianka 1969). Invertebrate abundance is higher in open sand on dune crests than under spinifex (Fisher and Dickman 1993), and it is possible that seeds, fruits or other plant material in the diet of *C. leae* are also more abundant in the open. The correlation of *Ctenotus dux* with live spinifex cover and of *C. ariadnae* with hard soil may likewise reflect preferred refuge or foraging sites, but the autecology of these species is too poorly known to warrant further speculation.

We note further that since the variables of soil hardness and percentage spinifex cover are auto-correlated ($r = 0.48$, $p < 0.0001$), it confounds their relative importance as correlates of lizard numbers.

At lower positions on the dune, fewer obvious associations emerged between lizards and microhabitats. On the dune side, species richness of lizards was correlated negatively with spinifex cover (Table 2). Correlations between *Ctenotus dux* and cover of annual plants and between *C. pantherinus* and cover of live shrubs in the swale (Table 2) may reflect selection for protective refugia, whereas the association of *Ctenophorus isolepis* with compacted soils probably reflects selection of firm substrate for rapid locomotion in pursuit of formicid prey (Pianka 1971).

Despite the several associations of lizard numbers with habitat variables, we have probably underestimated the extent of habitat selection throughout the lizard community. First, we omitted 21 species from the analyses because they were represented by few (<10) captures. Some species may have been difficult to catch due to rarity in the study area (e.g., *Crenadactylus ocellatus*), but others probably occupy specific microhabitats that were poorly sampled. For example, pitfall traps were not placed within spinifex hummocks as burying the trap within a hummock destroys the plant, and this would have under-sampled spinifex specialists such as *Diplodactylus elderi* (Pianka 1986). Arboreal species such as *Gehyra variegata, Lophognathus gilberti, Varanus gilleni* and *V. tristis* would also have been under-represented in traps. Secondly, our categorization of habitat variables may have been too coarse to detect associations for some species. For example, the geckos *Rhyncoedura ornata* and *Lucasium damaeum* shelter primarily in spider burrows, whereas the pygopodids *Delma tincta* and *Pygopus nigriceps* are often associated with termitaria or fallen timber (Wilson and

Knowles 1988; Henle 1990). Finally, large specimens of some species, such as *Tiliqua multifasciata,* sometimes move over open traps without being caught (pers. obs.), whereas large goannas, such as *Varanus gouldii* and *V. tristis* could potentially climb out of the traps once caught.

In conclusion, the results of the present study support earlier work in demonstrating clear habitat associations among desert lizards, and in showing that the topography of sandridges can promote species richness on a local scale. Future research should seek to experimentally distinguish the relative importance of habitat variables that are auto-correlated, and attempt to determine how habitats are used by individual species, such as for foraging, shelter or thermoregulation.

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