Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards

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Abstract   Body temperatures of active lizards and their correspondence with microhabitat occupation were studied for nine species of agamid lizards in the central Australian arid zone. Thermoregulatory behaviour was also documented using several measures, such as the use of shade and perch height. The effects of thermal environment on lizard habitat occupation were hypothesized to be significant, because desert regions experience daily and seasonal extremes of temperature that are well in excess of a lizard's preferred temperature range. All species, except *Ctenophorus isolepis* and *Diporiphora winneckei*, were found to have body temperatures that corresponded closely to ground and surface temperatures. Thermoregulatory behaviour was also found to be important throughout a lizard's daily activity; all study species, other than *Ctenophorus isolepis*, were found to increase their perch height in the middle of the day. *Ctenophorus isolepis* was shown to be a strictly terrestrial species that uses the shade of spinifex in its thermoregulatory behaviour. Species exhibited a non-random selection of microhabitats and a preference for a particular set of thermal and structural factors. In this study, it was shown that structural factors were particularly important in microhabitat occupation. Thermal factors accounted for a smaller proportion of variance in microhabitat occupation, but still played a considerable role in the microhabitat use in central Australian agamids.

Key words: activity patterns, Agamidae, arid-zone lizards, ecology, microhabitat occupation, thermoregulatory behaviour.

INTRODUCTION

Lizard ecologists have placed much importance on the study of microhabitat occupation, usually by investigating resource partitioning and interspecific competition (Toft 1985). Despite the importance of temperature in lizard ecology, comparatively few studies have considered the influence of thermoregulation on habitat use in desert regions (Huey & Pianka 1977; Avery 1978; Adolph 1990). Physiological and biochemical processes are strongly influenced by body temperature (Huey *et al*. 1991). Reproduction, rates of growth, feeding and mobility are whole-body functions dramatically affected by temperature (Huey 1982). Consequently, temperature is the most important physical factor in the ecology of lizards (Heatwole 1976) and a large proportion of a lizard's day is spent responding to the thermal environment.

In desert regions, with daily and seasonal extremes of weather, thermal biology may restrict the use of microhabitats by lizards. Thermal microhabitat constraints arise because the body temperature of an ectotherm is a complex function of its biophysical environment (Gates 1980). Thus, thermoregulating

lizards are constrained to occupy specific thermal microclimates when they are active: to feed, defend territories, acquire mates and avoid predators. These constraints are especially important for desert lizards that occupy an environment of extreme temperatures, so that failure to select an appropriate thermal microclimate for even a few minutes can result in dangerously high body temperatures or even death.

Consequently, the availability of thermally appropriate microhabitats is potentially a major limiting factor affecting lizards in desert regions. Thermal constraints vary in time and space because the physical environment is temporally and spatially variable with respect to a variety of factors, such as the thermal inertia of substrates, air temperature and vegetation structure (Hertz *et al*. 1993). These climatic factors interact with the surface heat transfer properties of a lizard to produce a distribution of available temperatures in time and space within which a lizard can survive (Stevenson 1985). Thus, a lizard will occupy a restricted range of microhabitats within its overall habitat.

There have been very few detailed studies examining the habitat occupation of agamid lizards, especially those in desert regions and our study provides a quantification of structural and thermal microhabitat occupation in a number of these species. Agamids occupy a wide variety of habitats in Australia, such as

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tropical rainforests (*Hypsilurus boydii*), cool temperate woodlands (*Tympanocryptis diemensis*), stony deserts (*Tympanocryptis lineata*), desert dunes (*Ctenophorus isolepis*) and dry salt lakes (*Ctenophorus maculosus*). However, they reach their highest diversity in the semi-arid and arid regions of Australia. The alpha diversity of lizards in arid Australia is high relative to deserts on other continents (Pianka 1986). This has been attributed to the diversity of microhabitats and the diversity of food resources (Pianka 1986), which vary dramatically with habitat type (Morton & James 1988). For this reason, and the fact that temperature plays an important role in desert environments, we tested the hypothesis that active body temperature is correlated with microhabitat occupation in nine species of desert agamids. We examined this by recording active field body temperatures and quantifying the thermal and structural microhabitat occupation of the study species.

METHODS

Study species

Agamids are diurnal heliotherms that are primarily sit-and-wait predators (Huey & Pianka 1981). They comprise approximately 20% of the lizard fauna in desert regions of Australia (Pianka 1986). We studied nine agamid species at four sites in central Australia (Fig. 1). Eleven agamid species were caught in the present study but the only species included in the analysis were those for which we caught greater than 15 individuals. The two species not included were *Ctenophorus clayi* (one individual was caught at field site 3) and *Pogona mitchelli* (two individuals were caught at field site 1). The nine agamid species included in the present study are made up of five genera: *Ctenophorus*, *Diporiphora*, *Lophognathus*, *Pogona* and *Tympanocryptis*. All species, except *C. pictus*, were caught at more that one field site (Table 1). The *Tympanocryptis lineata* caught in the present study all belonged to the subspecies *centralis*.

Field work

Structural and thermal microhabitat characteristics were recorded at four field sites (Fig. 1). Field sites were chosen to provide a wide range of habitat types, including flat spinifex desert (sites 2, 3 and 4), sand ridges (sites 3 and 4), rocky spinifex desert (site 1), desert ranges (sites 1 and 3), gibber plains (site 4), acacia woodlands (sites 1, 2, 3 and 4) and riverine eucalypts (sites 1, 2 and 3). The data were recorded by driving or walking throughout each field site from approximately 07.00 until 19.00 hours. This method ensured coverage of the entire range of structural and thermal microhabitats available. This was done over a 6-week period from October to December 1999, with approximately 10 days spent at each location. Data were only collected on sunny, warm days when lizards could be fully active.

Active lizards were caught with the use of a noose or by hand. Body temperature was recorded by using a
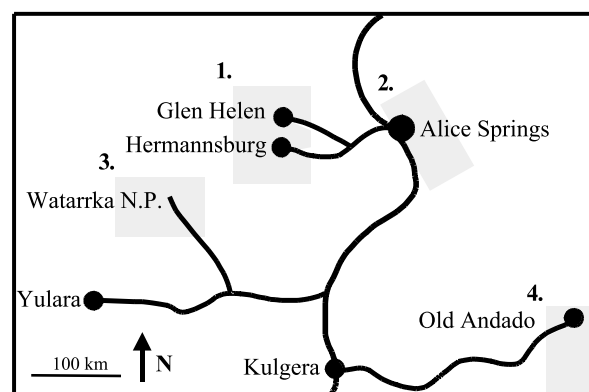

Fig. 1. Map of the four field sites. All field work was conducted in National Parks or on leasehold land. Field site 1 included Larapinta and Namatjira Drives, West MacDonnell Ranges National Park and Finke Gorge National Park; field site 2 included the Old South Road, Roe Creek and Stuart Highway (north of Alice Springs); field site 3 included Watarrka National Park; field site 4 included the four-wheel-drive track between Mount Dare Station and Andado Station.

Table 1. Presence of agamid species at each field site and general description of habitats in which the species occurs

Species	Field site no.	Habitat category	General habitat description
Ctenophorus caudicinctus	1, 3	Saxicolous	Desert ranges; rocky outcrops
Ctenophorus isolepis	2, 4	Ground-dwelling	Sandy spinifex desert
Ctenophorus nuchalis	1, 2, 3, 4	Ground-dwelling	All open habitats with non-rocky substrate
Ctenophorus pictus	4	Ground-dwelling	Sandy substrates with open shrub cover
Diporiphora winneckei	3, 4	Semi-arboreal	Sandy spinifex desert
Lophognathus gilberti	1, 2	Semi-arboreal	Mulga woodlands
Lophognathus longirostris	1, 2, 3	Semi-arboreal	Mulga and riverine woodlands
Pogona vitticeps	1, 2, 4	Semi-arboreal	Open habitats with heterogeneous vegetation
Tympanocryptis lineata	1, 4	Saxicolous	Rocky spinifex desert

thermistor and lizards were sexed before being released. Ten structural and three thermal characteristics of the microhabitat for each lizard caught were recorded. The structural variables were: 1, visual estimate of percent canopy cover in a 3-m² radius surrounding lizard; 2, visual estimate of percentage shrub cover in a 3-m² radius surrounding lizard; 3, visual estimate of percentage ground and grass cover in a 3-m² radius surrounding lizard; 4, perch surface: rock, litter, ground, log, branch or tree trunk; 5, distance to the nearest vegetation in cm; 6, distance to the nearest shelter in cm; 7, shelter type (burrow, rock, vegetation, litter); 8, visual estimate of percentage rock cover (< 50 cm in diameter); 9, visual estimate of percentage rock cover (> 50 cm in diameter); 10, height lizard is perched off ground in cm. The thermal characteristics recorded were: 1, shaded temperature of surface on which lizard is perched; 2, shaded air temperature taken 15 cm above surface; 3, whether lizard is in the shade, dappled sunlight or full sun.

To determine whether lizards were selecting microhabitats non-randomly, 45 random perch-sites were recorded at field sites 1 and 4. A 400-m transect, which traversed the range of microhabitats at these field sites, was used to record a random perch-site every 10 m. The random perch-site was determined by throwing a small trowel, which was within the size and weight range of agamids, in a random direction and then recording the microhabitat variables, as we would an actual lizard, at the point where the trowel landed. The random data points were only recorded at times of the day when lizards were active, allowing a relevant estimate of thermal conditions.

Statistical analysis

The mean value of each variable for each species was used in statistical analyses. All percentage variables were arcsine-transformed prior to analysis. A principal components analysis (PCA) was used to reduce the 10 structural and three thermal variables to a smaller number of components that describes the underlying dimensions in the data. The principal components were extracted from a correlation matrix of the raw data. The number of principal components (henceforth PCs) utilized in the analysis was determined by using the scree test of eigenvalues plotted against factors, maximizing the adequacy of extraction. Principal components axes were named by the correlations of the original variables to the PC: correlations with absolute values of greater than 0.5 were considered important (Tabachnick & Fidell 1989).

Regression analyses were used to assess whether there was a significant relationship between the active field body temperatures of species and the microhabitats they occupy. The PC axes were used in this analysis as an estimation of microhabitat.

Random microhabitat data from sites 1 and 4 were analysed separately with PCA (using the methods already described). Study species that were recorded at each site were included in the analyses. However, univariate and multivariate tests of normality indicated that there were not enough individuals of some species at these field sites to allow a random sample of the population (Tabachnick & Fidell 1989). Consequently, these species were excluded from the random habitat analysis: *Pogona vitticeps* (field site 1) and *Ctenophorus nuchalis* (field site 4). However, all the study species were included in the analysis of either field site 1 or 2. An analysis of variance and least significant difference post hoc test of the PC factors at field sites 1 and 2 were used to test whether the microhabitat occupation of the study species differed from random.

RESULTS

Field body temperatures

The mean field body temperatures (Table 2) of the study species ranged from 32.9°C (*P. vitticeps*) to 37.7°C (*Diporiphora winneckei*). An ANOVA identified significant differences among the species ($F_{8,234} = 9.76$,

Table 2. Active field body temperatures and proportion of lizards observed in the shade

Species	n	Body temp (°C)	Lizards in shade (%)
Ctenophorus caudicinctus	28	34.2 (0.41)	0.0
Ctenophorus isolepis	25	37.2 (0.36)	56.82
Ctenophorus nuchalis	69	35.8 (0.43)	2.77
Ctenophorus pictus	28	34.4 (0.41)	0.0
Diporiphora winneckei	24	37.7 (0.25)	0.0
Lophognathus gilberti	27	33.7 (0.55)	67.31
Lophognathus longirostris	34	33.9 (0.49)	21.36
Pogona vitticeps	18	32.9 (0.88)	0.0
Tympanocryptis lineata	28	35.1 (0.36)	0.0

Values provided for temperatures are species means and standard errors of the mean in brackets.

P < 0.001). A Fisher's LSD post hoc test indicated that the saxicolous species *Ctenophorus caudicinctus* had a significantly lower body temperature than *C. isolepis* (*P* < 0.001), *C. nuchalis* (*P* = 0.006) and *D. winneckei* (*P* < 0.001). The ground-dwelling species *C. isolepis* had a significantly higher body temperature than all other species (*P* < 0.001), except *D. winneckei*. The mean body temperature of the semi-arboreal species *P. vitticeps* was significantly lower than all species (*P* < 0.001), except for the saxicolous species *C. caudicinctus* and the arboreal species *Lophognathus gilberti* and *Lophognathus longirostris*.

Body temperature did not vary over the course of the day in any species (Fig. 2). The ground-dwelling species *C. isolepis* and the semi-arboreal species *D. winneckei* show little fluctuation in body temperature despite very high surface temperatures where they were caught during the middle of the day, and their body temperatures were not significantly related to air or surface temperatures (Table 3). However, the body temperatures of the semi-arboreal species *L. gilberti*,

L. longirostris and *P. vitticeps* correspond significantly to surface and air temperatures throughout the day (Table 3).

The patterns of perch height throughout the day differed between the species (Fig. 3), where four distinct behaviours could be distinguished. *Ctenophorus isolepis* remained on the ground throughout the day and was never observed perching off the ground. Four species (*Ctenophorus caudicinctus*, *C. nuchalis*, *C. pictus* and *Tympanocryptis lineata*) began the day on the ground and moved higher in the middle of the day, before returning to the ground at the end of the day. The semi-arboreal and arboreal species, *L. gilberti*, *L. longirostris* and *D. winneckei*, started close to the ground in the morning and moved significantly higher than the other species in the middle of the day ($F_{1,112}$ = 30.36, *P* < 0.001). The semi-arboreal species *P. vitticeps* was recorded off the ground throughout the day. Only the three semi-arboreal species, *L. gilberti*, *L. longirostris* and *P. vitticeps*, showed a significant relationship between height off the ground and air
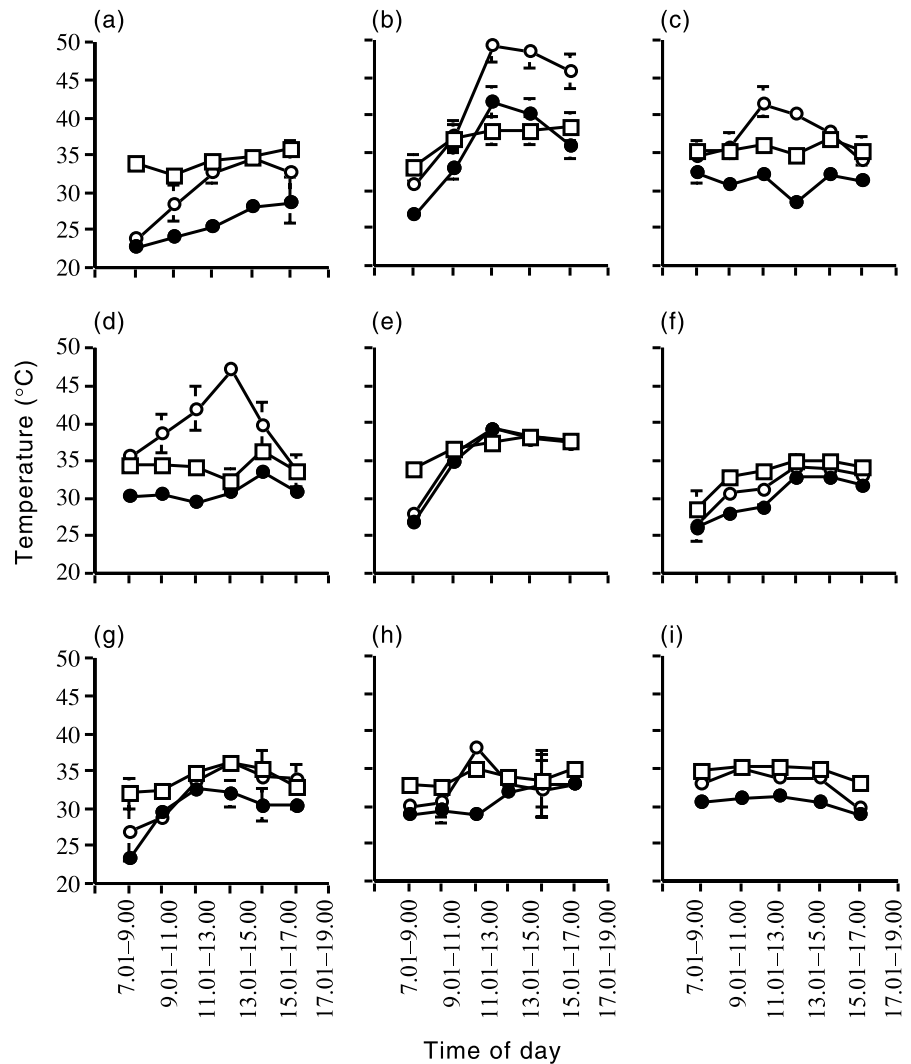

Fig. 2. Body temperature, air temperature and surface temperature throughout the day for each species. Standard errors are provided for temperature data but are small enough in most cases that they do not appear on the compressed graphs. (a) *Ctenophorus caudicinctus* (*n* = 28); (b) *Ctenophorus isolepis* (*n* = 25); (c) *Ctenophorus nuchalis* (*n* = 69); (d) *Ctenophorus pictus* (*n* = 28); (e) *Diporiphora winneckei* (*n* = 24); (f) *Lophognathus gilberti* (*n* = 27); (g) *Lophognathus longirostris* (*n* = 34); (h) *Pogona vitticeps* (*n* = 18); (i) *Tympanocryptis lineata* (*n* = 28). (□), Body temperature; (●), air temperature; (○), surface temperature.

temperature (Table 3), where the lizards moved higher off the ground as air temperature increased.

Microhabitat occupation and body temperature

The values for structural microhabitat variables recorded for each species are shown in Table 4. The PCA that incorporated three factors accounted for 79.51% of the variance of the raw data (Table 5). The first PC was positively correlated with the perch height, perch surface, shelter type and the percentage of shrub cover, and negatively with perch surface, shelter type, distance to nearest vegetation and the percentage of rock cover. Thus, the PC1 axis described a structural gradient in which high PC scores denoted association with vegetation, especially shrub cover and negative PC scores denoted a rocky microhabitat with little or no vegetation within a 3-m radius of the lizard (Fig. 4). The second PC axis was positively correlated with shelter type, air temperature and surface temperature, and negatively correlated with perch surface, distance to nearest shelter, shelter type, percentage of ground cover and percentage of tree cover. This represents a scale of

thermal and structural characteristics, in which low PC2 scores denoted cool microhabitats with high levels of tree cover and high scores denoted hot microhabitats with limited or no vegetation at ground level and no tree cover (Fig. 4).

Figure 4 shows that the semi-arboreal and arboreal species *P. vitticeps*, *L. gilberti* and *L. longirostris* occupy cool microhabitats with some tree cover and litter. However, the arboreal species *D. winneckei* occupies habitats more similar to those of the ground-dwelling species *C. isolepis*, which are hot sandy spinifex deserts. The two saxicolous species *C. caudicinctus* and *T. lineata* occupy similar microhabitats, which have rocky substrate, little vegetation and a moderate microclimate. The two ground-dwelling species *C. nuchalis* and *C. pictus* occupy sandy deserts with a moderate level of vegetation and moderate microclimate.

A regression analysis was used to determine if there was a correlation between active body temperatures of species and their microhabitat occupation. The PC axes were used as estimates of microhabitat occupation. There was a significant relationship between body temperature and PC2 ($r = 0.86$, $P = 0.003$), where

Table 3. Results of regression analyses

Regression	r	Slope	P
Body temperature *vs* surface temperature			
Ctenophorus caudicinctus	0.30	0.55	0.003*
Ctenophorus isolepis	0.08	0.29	0.196
Ctenophorus nuchalis	0.39	0.62	< 0.001*
Ctenophorus pictus	0.01	−0.09	0.637
Diporiphora winneckei	0.02	0.15	0.51
Lophognathus gilberti	0.61	0.78	< 0.001*
Lophognathus longirostris	0.59	0.77	< 0.001*
Pogona vitticeps	0.71	0.84	< 0.001*
Tympanocryptis lineata	0.30	0.54	0.003*
Body temperature *vs* air temperature			
Ctenophorus caudicinctus	0.28	0.53	0.004*
Ctenophorus isolepis	0.16	0.40	0.072
Ctenophorus nuchalis	0.62	0.79	< 0.001*
Ctenophorus pictus	0.20	0.45	0.018*
Diporiphora winneckei	0.03	0.18	0.401
Lophognathus gilberti	0.53	0.73	< 0.001*
Lophognathus longirostris	0.53	0.73	< 0.001*
Pogona vitticeps	0.80	0.90	< 0.001*
Tympanocryptis lineata	0.12	0.34	0.077
Perch height vs. air temperature			
Ctenophorus caudicinctus	0.01	0.03	0.810
Ctenophorus isolepis		No variation in perch height	
Ctenophorus nuchalis	0.01	0.03	0.825
Ctenophorus pictus	0.04	0.19	0.371
Diporiphora winneckei	0.30	0.55	0.004*
Lophognathus gilberti	0.38	0.22	0.024*
Lophognathus longirostris	0.32	0.23	0.042*
Pogona vitticeps	0.09	−0.30	0.312
Tympanocryptis lineata	0.11	0.33	0.082

*Significant.

Table 4. Vegetation and substrate characteristics of each species

| Species | n | Nearest vegetation (cm) | Vegetation cover (%) | | | Rock cover (%) | |
			Ground	Shrub	Tree	< 50 cm diameter	> 50 cm diameter
Ctenophorus caudicinctus	28	170.18 (10.269)	4.82 (0.864)	3.86 (0.840)	0.61 (0.538)	26.46 (2.918)	28.02 (2.590)
Ctenophorus isolepis	25	27.04 (9.595)	14.82 (1.916)	0.96 (0.626)	0.68 (0.498)	0.0 (0.0)	0.0 (0.0)
Ctenophorus nuchalis	69	248.38 (40.127)	3.87 (0.792)	1.03 (0.252)	0.154 (0.086)	3.95 (0.309)	0.0 (0.0)
Ctenophorus pictus	28	119.15 (37.479)	6.07 (1.200)	1.423 (0.633)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Diporiphora winneckei	26	0.0 (0.0)	4.00 (1.886)	32.69 (3.117)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Lophognathus gilberti	27	19.04 (8.422)	8.50 (2.766)	4.57 (1.168)	15.04 (1.396)	6.42 (4.537)	0.19 (0.192)
Lophognathus longirostris	34	23.78 (8.583)	24.67 (4.477)	6.97 (2.064)	10.79 (1.902)	5.97 (1.354)	0.21 (0.161)
Pogona vitticeps	18	145.88 (61.250)	12.35 (4.916)	10.00 (5.315)	5.88 (3.272)	2.29 (1.740)	0.0 (0.0)
Tympanocryptis lineata	28	248.75 (57.636)	4.36 (1.162)	0.43 (0.249)	0.0 (0.0)	31.32 (4.739)	1.89 (0.633)

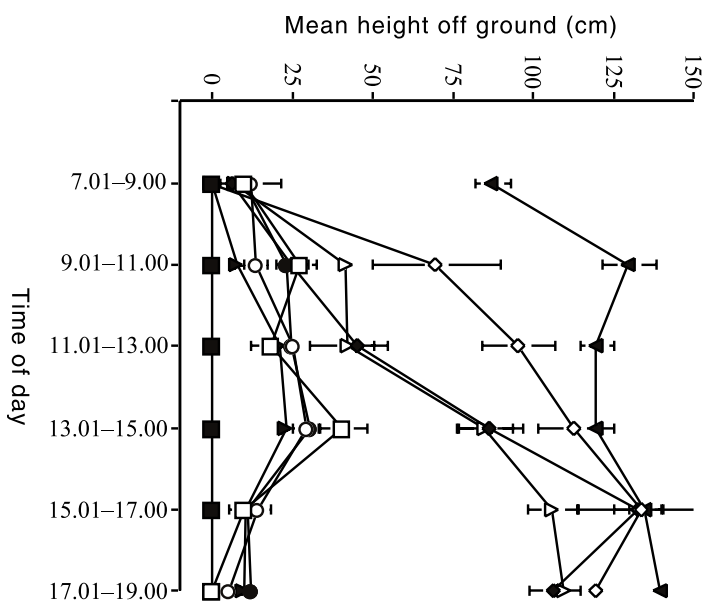Means are provided, with standard errors in brackets.

Fig. 3. Mean perch height of species throughout the day. Standard error bars are provided for all means. (▼) *Pogona vitticeps*; (◇) *Diporiphora winneckei*; (◆) *Lophognathus gilberti*; (△) *Lophognathus longirostris*; (□) *Ctenophorus caudicinctus*; ; (●) *Ctenophorus pictus*; (○) *Ctenophorus nuchalis*; (▲) *Tympanocryptis lineata*; (■) *Ctenophorus isolepis*.
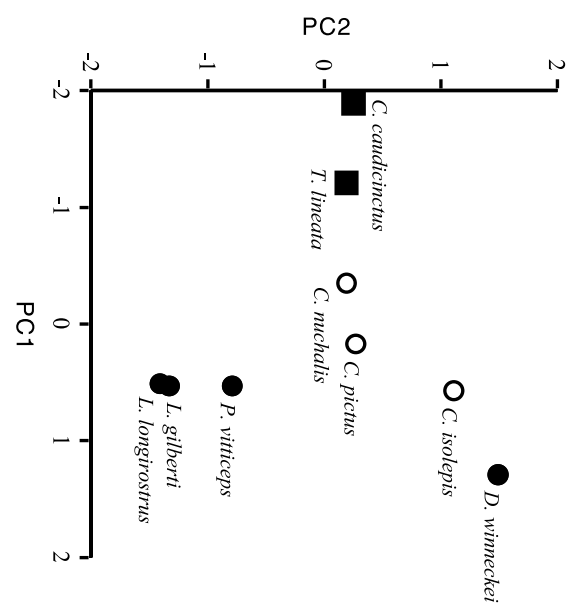

Fig. 4. Distribution of central Australian agamids in two-dimensional ecological space, based on principal components (PC) scores. PC1, vegetation cover and substrate type; PC2, shrub cover and temperature. (■), Saxicolous; (●), semi-arboreal and arboreal; (○), ground dwelling.

PC2 describes thermal and structural microhabitat characteristics.

Non-random selection of microhabitat

To test whether species were selecting microhabitats non-randomly, random microhabitat variables were recorded at field sites 1 and 4. Principal components analyses were performed separately on data from each site; random microhabitat variables and ecological data of species recorded at those sites were included in the analyses.

The PCA of microhabitat data from field site 1 (Fig. 5) incorporated two factors that accounted for 64.35% of the variance of the raw data. The PC1 axis described a structural gradient in which high PC scores denoted association with vegetation, especially tree cover, and negative PC scores denoted a rocky microhabitat with little or no vegetation within a 3-m radius of the lizard (Fig. 5). The second PC axis represented a scale of thermal and structural characteristics, in which low PC2 scores denoted cool microhabitats with high levels of tree cover, and high scores denoted hot microhabitats with limited or no vegetation at ground level and no tree cover (Fig. 5). An analysis of variance

Fig. 5. Random habitat measures at field sites (a) 1 and (b) 4, indicated by a dashed-line 95% confidence ellipse. The 95% confidence ellipses of the ecological distribution of agamid species recorded at each field site are also provided, based on principal components (PC) scores. PC1, vegetation cover and substrate type; PC2, shrub cover and temperature.
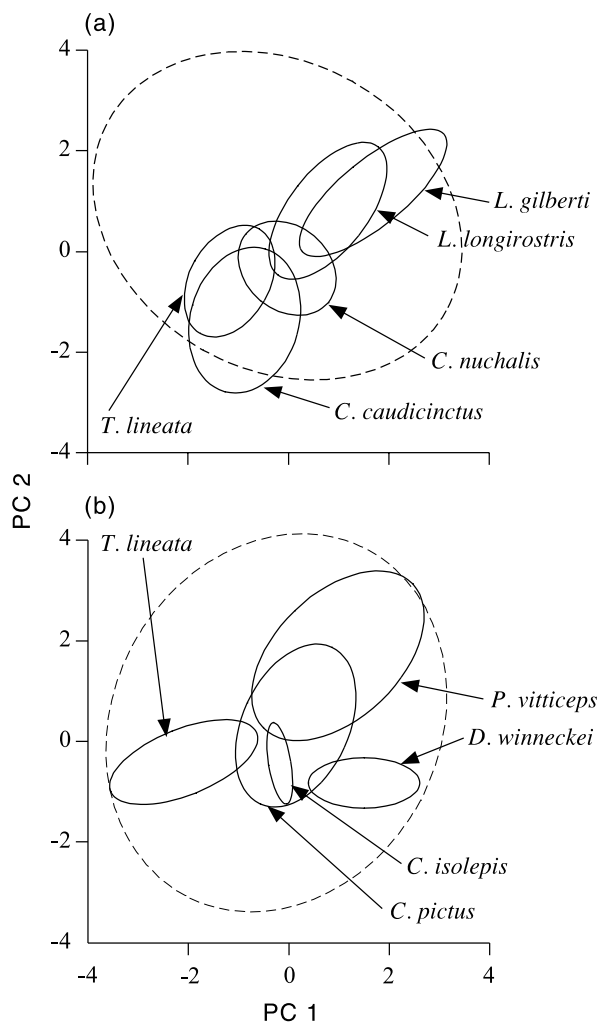
Table 5.   Principal component axis loadings

| | Principal component loadings | | |
	I	II	III
Perch height	0.559*	−0.304	0.689*
Perch surface – ground	0.423	0.169	−0.742*
Perch surface – rock	−0.934*	−0.024	0.328
Perch surface – vegetation	0.688*	−0.036	0.567*
Perch surface – litter/log	0.094	−0.743*	−0.413
Nearest shelter	0.268	−0.807*	0.032
Shelter type – burrow	−0.041	0.033	−0.706*
Shelter type – rock	−0.911*	0.001	0.385
Shelter type – vegetation	0.684*	0.501*	0.340
Shelter type – litter/log	0.309	−0.888*	−0.165
Nearest vegetation	−0.750*	0.037	−0.334
Vegetation cover – ground	0.378	−0.515*	−0.041
Vegetation cover – shrub	0.554*	0.339	0.577*
Vegetation cover – tree	0.336	−0.856*	0.212
Rock cover –< 50 cm diameter	−0.871*	−0.054	0.328
Rock cover –> 50 cm diameter	−0.748*	0.093	0.405
Surface temperature	0.288	0.791*	−0.417
Air temperature	0.477	0.646*	0.063
Total percentage variance explained	34.989	25.183	19.337

*Component loadings with absolute values of greater than 0.5 are considered important (Tabachnick & Fidell 1989).

showed that the microhabitat PC scores for the species recorded at field site 1 and the random habitat data differed on both PC1 ($F_{4,160} = 52.57$, $P < 0.001$) and PC2 ($F_{4,160} = 22.55$, $P < 0.001$). Fisher's LSD post hoc test showed that mean scores for all species differed significantly from the random habitat data ($P < 0.001$). The mean PC scores for the species recorded at field site 1 were significantly positively correlated ($r = 0.93$, $P = 0.008$), indicating that species occupied a continuum of microhabitats from cool areas with tree cover to hot, open rocky microhabitats.

The PCA of microhabitat data from field site 4 (Fig. 5) incorporated two factors that accounted for 68.74% of the variance of the raw data. The PC1 axis described a structural gradient in which high PC scores denoted association with vegetation, especially shrub cover and negative PC scores denoted a sandy microhabitat with little or no vegetation within a 3-m radius of the lizard (Fig. 5). The second PC axis represented a scale of thermal and structural characteristics, in which low PC2 scores denoted cool microhabitats with shrub cover and high scores denoted hot microhabitats with no vegetation (Fig. 5). An analysis of variance showed that the microhabitat PC scores for the species recorded at field site 4 and the random habitat data differed on both PC1 ($F_{4,154} = 10.99$, $P < 0.001$) and PC2 ($F_{4,154} = 24.38$, $P < 0.001$). Fisher's LSD post hoc test showed that mean scores for all species differed significantly from the random habitat data ($P < 0.001$). The lowest PC2 scores for the species recorded at field site 4 were -1.78, whereas 16.8% of the random habitat scores were less than -1.78, indicating that species were selecting cooler, more vegetated microhabitats than random.

DISCUSSION

Field body temperatures

Field body temperatures have previously been recorded in *L. longirostris*, *C. caudicinctus*, *C. nuchalis*, *C. isolepis*, *D. winneckei*, *P. vitticeps* and *T. lineata* (Greer 1989). Our study found that active body temperatures were slightly lower than those recorded in previous studies, possibly because our study was conducted mostly in spring, when ambient temperatures are lower and substrates are generally cooler than in summer. Preferred and active body temperatures have been found to vary seasonally in *C. isolepis* (Heatwole & Taylor 1987), and this is probably the case with other arid zone agamids. The concept of seasonally variable body temperatures in central Australian agamids is corroborated by the correlation between active body temperatures and environmental temperatures in our study.

However, body temperature in *C. nuchalis*, *C. isolepis* and *C. pictus* were lower than the surface temperature

in the middle of the day. This has previously been found in *C. nuchalis* (Heatwole 1970), which in cool conditions has a body temperature exceeding the air and surface temperature, whereas in hot conditions is cooler than surrounding conditions. Thermal shifts, such as this, are characteristic of many diurnal lizards and may indicate that lizards are selecting microhabitats for thermoregulatory purposes or are controlling body temperature through thermoregulatory behaviour (Huey & Pianka 1977). For example, *C. isolepis*, a strictly terrestrial species, can maintain body temperatures below environmental temperatures by using the shade of spinifex in its thermoregulatory behaviour, as shown in the present study and others (Losos 1987, 1988).

Hertz *et al.* (1993) suggested that using the correlation between air temperature and body temperature is inappropriate, as air temperature is only one of many important biophysical factors that may contribute to an animal's body temperature. In addition, they argue that using the air temperature at the microhabitat selected by an animal may provide a biased measure of available environmental temperatures. These are valid arguments, but by measuring a random selection of microhabitats, our study has shown that agamid species select microhabitats within the range available. Selection of a particular thermal microhabitat was very evident at field site 4, on the edge of the Simpson Desert, where species selected microhabitats that were cooler and more vegetated than the randomly recorded microhabitats.

All study species, other than *C. isolepis*, were found to increase their perch height in the middle of the day, as reported previously in *C. nuchalis* (Heatwole (1970). Our study showed that even though the terrestrial species increase their perch height during the hottest part of the day they do not perch as high as the arboreal or semi-arboreal species. Selection of basking site is important, as some microhabitats provide greater exposure to the sun than others and surfaces possess different thermal properties (Huey & Pianka 1977). The perches used in the morning often differ from those used at other times of the day, as they may be used for different purposes, such as basking in the morning, avoiding heat stress in the middle of the day and even social or territorial behaviour. During the middle of the day, the ground becomes hot, radiating heat that increases the temperature of the air above it, and by moving further away from the ground, lizards encounter cooler air temperatures.

Previous studies have found that arid-zone lizards exhibit bimodal activity patterns (Simon & Middendorf 1976; Grant & Dunham 1988). We observed some individuals of *C. pictus* and *C. nuchalis* seeking shelter in burrows during the heat of the day and other species were seen to use shade frequently during the hottest part of the day (e.g. *L. longirostris*, *L. gilberti* and

C. isolepis). However, we caught lizards throughout the day, with no significant decrease in the middle of the day. Lizards can use behavioural tactics, such as microhabitat selection, and even physiological changes to remain active throughout the day. Christian *et al.* (1996) found that some agamid species possess the ability to alter the absorbance of their skin through colour change. For example, *C. caudicinctus* can increase absorbance from 77 to 87.7%. An increase usually means higher body temperatures, which would be particularly important in microclimate conditions below optimal. This would allow lizards to increase absorbance, which would raise their body temperatures in cool conditions and then lower absorbance once warmer conditions prevail, allowing more activity time without overheating.

Microhabitat occupation and body temperature

All species exhibited a non-random selection of microhabitats and a preference for a particular set of thermal and structural factors. Our study showed that both structural and thermal factors are important in microhabitat occupation. Thermal variables did not account for the largest proportion of variance in microhabitat occupation, but still played a considerable role in the microhabitat use in the study species. The selection of specific microhabitat characteristics by members of lizard communities has been reported in many studies (Paulissen 1988). In the current study, microhabitat use is strongly related to vegetation, substrate and thermal characteristics. Other studies of lizard communities have found very similar factors to be involved in the use of microhabitats. Shenbrot *et al.* (1991) reported that the particle size of the substrate and the shelter available in the form of burrows or vegetation were the most important factors in determining the use of microhabitats by some desert-dwelling lizards. A number of studies of lizards in temperate climates have found that vegetation characteristics are of primary importance in microhabitat use (Dent & Spellerberg 1987; Paulissen 1988; Brown & Nelson 1993). Similarly, the importance of factors of lesser significance, especially the abundance of shrubs and perennial grasses, in determining the spatial distribution of desert lizards has been emphasized in a number of species (Pianka 1975, 1980; James 1991; Shenbrot *et al.* 1991).

Our study specifically quantifies the microhabitat occupation of central Australian agamids. Other studies have investigated vegetation associations (Pianka 1986) and general habitat characteristics in some species of arid-zone agamids, particularly *C. isolepis* and *C. nuchalis* (Masters 1996; Dickman *et al.* 1999). Masters (1996) found that *C. nuchalis* was caught more commonly in areas regenerating after fire, whereas *C. isolepis* was captured more frequently

in areas of mature spinifex desert. They attributed this variation to the sparse vegetation in regenerating areas, providing little shelter from heat or predation. *Ctenophorus nuchalis* is known for its extreme heat tolerance and habit of moving among shaded and open perches, whereas *C. isolepis* utilizes spinifex for shelter from heat and predators. Our study reflects these habitat preferences, as *C. nuchalis* was shown to occupy open areas with sandy substrates, whereas *C. isolepis* was strongly associated with vegetation, especially spinifex, and hot sandy substrates. However, there are no other studies available that investigate the causes of microhabitat use in the agamids of central Australia.

Our study showed that there is a significant relationship between active body temperatures and the thermal and related structural characteristics of a microhabitat. This indicates that thermoregulatory considerations play a role in the microhabitat use of agamids. Many lizards require thermal patchiness (areas of sun and shade and high and low wind speeds and air temperatures) to enable the regulation of body temperatures (Tracy & Christian 1986). This patchiness is derived from changes in the thermal environment over the day and thermal heterogeneity over space. However, body temperature was not correlated to the structural factors of microhabitats, such as vegetation cover and substrate type, which accounted for the largest proportion of variation in microhabitat occupation in the study species. Consequently, factors other than thermoregulatory requirements must play a role in microhabitat use, such as social factors, competition, morphological restrictions, dietary requirements and predation (Toft 1985).

Although our study indicates that thermoregulatory factors are not the only cause of microhabitat use in agamids in central Australia, it must be considered that this work was conducted in spring, when it is cool enough for lizards to be active throughout the day. During the hottest time of the year the role of thermoregulation may play a much more significant role in the use of microhabitats in central Australian agamids.

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