

Ecology and Behaviour of Burton's Legless Lizard (*Lialis burtonis*, Pygopodidae) in Tropical Australia

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Abstract The elongate, functionally limbless flap-footed lizards (family Pygopodidae) are found throughout Australia, ranging into southern New Guinea. Despite their diversity and abundance in most Australian ecosystems, pygopodids have attracted little scientific study. An intensive ecological study of one pygopodid, Burton's legless lizard (*Lialis burtonis* Gray 1835), was conducted in Australia's tropical Northern Territory. *L. burtonis* eats nothing but other lizards, primarily skinks, and appears to feed relatively infrequently (only 20.8% of stomachs contained prey). Ovulation and mating occur chiefly in the late dry-season (beginning around September), and most egg-laying takes place in the early to middle wet-season (November–January). Females can lay multiple clutches per year, some of which may be fertilised with stored sperm. Free-ranging *L. burtonis* are sedentary ambush foragers, with radio-tracked lizards moving on average < 5 m/day. Most foraging is done diurnally, but lizards may be active at any time of day or night. Radiotracked lizards were usually found in leaf-litter microhabitats, a preference that was also evident in habitat-choice experiments using field enclosures. Lizards typically buried themselves in 6–8 cm of litter; at this depth, they detect potential prey items while staying hidden from predators and prey and avoiding lethally high temperatures.

Keywords Squamata, habitat use, wet-dry tropics, thermoregulation, movement, activity patterns

1. Introduction

Many lizard lineages exhibit bodily elongation and concomitant limb reduction. This morphotype has evolved independently in numerous taxa, including amphisbaenians, anguids, cordylids, dibamids, diploglossids, gerrhosaurids, skinks, and teiids (Greer, 1991). Of the phylogenetic lineages that have undergone major adaptive radiations subsequent to limb loss, by far the most speciose and diverse are the snakes, which number more than 2700 species (Greene, 1997). The success of snakes has stimulated extensive speculation on the ecological correlates of bodily elongation and limb reduction (e.g., Gans, 1975; Greene, 1983; Shine, 1986; Wiens and Slingluff, 2001). To test such ideas, ideally we

need to examine the biology of other diverse radiations of limbless (or functionally limbless) squamates. An Australopapuan lizard family, the Pygopodidae, offers a unique opportunity in this respect.

Pygopodids, or flap-footed lizards, are descendants of geckos (Donnellan *et al.*, 1999) found throughout mainland Australia, with two species ranging into southern New Guinea (Cogger, 2000). The family exhibits significant diversity both taxonomically and ecologically. The roughly 40 species (Jennings *et al.*, 2003; Kluge, 1976; Shea, 1993) can be divided into four ecological “types”: generalised insectivores (e.g., *Delma* spp.), specialist spider-feeders (*Pygopus lepidopodus*), ant-eating burrowers (*Aprasia* spp.), and analogues of macrostomatan snakes (*Lialis burtonis* and *L. jicari*) (Patchell and Shine, 1986a). Despite their diversity and abundance in most Australian ecosystems, however, the ecology and natural history of pygopodids are not well known. Diet and reproductive characteristics have been investigated in some species (Patchell and Shine, 1986a;

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Webb and Shine, 1994) and distribution and conservation status explored in a handful of others (e.g., Jones, 1992; Osborne *et al.*, 1991), but the behaviour of animals in the field has received little attention.

We carried out an extensive ecological study of one species, Burton's legless lizard (*Lialis burtonis*), in the tropical Top End of Australia's Northern Territory. *L. burtonis* is Australia's most widespread reptile; it ranges across most of the continent and is found in virtually every habitat type (Cogger, 2000). As noted above, *L. burtonis* is ecologically convergent with macrostomatan snakes. Like snakes, *L. burtonis* feeds at infrequent intervals on relatively large prey (other lizards), which are swallowed whole (Huey *et al.*, 2001; Patchell and Shine, 1986a, b). Laboratory studies (Murray *et al.*, 1991; Patchell and Shine, 1986b) suggest that the species is an ambush forager, but its behaviour in the wild has not been studied in any detail.

To gain insight into the habits of *L. burtonis* in the Top End, we examined museum specimens, radiotracked lizards, and performed experiments in naturalistic field enclosures. Among the specific questions we addressed were the following:

- 1) What do Top End *L. burtonis* eat, and how often?
- 2) Is there a seasonal pattern to reproduction?
- 3) How far and frequently do lizards move (i.e., are they indeed ambush foragers)?
- 4) At what times of day are they active?
- 5) What temperatures do lizards experience in the field?
- 6) In which microhabitats are they found?

In addition, we quantified the occurrence of sexual dimorphism and ontogenetic variation in a range of morphological traits. This study sheds further light on the ecology of *Lialis burtonis*, providing a context for the information yielded by previous laboratory studies. It is also one of the first detailed field investigations of any pygopodid lizard.

2. Material and Methods

2.1 Examination of museum specimens We examined 96 preserved *L. burtonis* at the Museum and Art Gallery of the Northern Territory (MAGNT) in Darwin. We restricted analysis to specimens from the Top End, defined as any location in the Northern Territory north of the Katherine area (specifically, north of 14°50' south latitude). This region is characterised by warm temperatures year-round and highly seasonal rainfall (with dry "winters" and wet "summers"); its common

terrestrial habitats are open forest, woodland, and seasonally inundated floodplains (Cogger, 2000). We recorded a number of morphometric variables from each lizard specimen, including snout-vent length (SVL), head length (from the quadrate to the tip of the snout), head width (at the head's widest point), and tail length. As *L. burtonis* is extremely colour-polymorphic across its range (Cogger, 2000), colour and pattern variation were also noted.

Patchell and Shine (1986a) reported dietary and reproductive information for *L. burtonis* across the entire range of the species; they did not investigate geographic patterns or analyse individual populations, and most of their animals were collected in southern Australia. To gather data on diet and reproduction in Top End animals, specimens were opened carefully with a single ventral incision. Any stomach contents were removed and identified. In adult females, the number of eggs or enlarged follicles was recorded, and the largest of these was measured to the nearest 0.1 mm with digital calipers. In adult males, the larger of the two testes was measured, again to the nearest 0.1 mm.

2.2 Telemetry Thirteen adult *L. burtonis* were hand-captured in open woodland near Fogg Dam Conservation Reserve, 60 km east of Darwin. Seven were males (mean \pm SE = SVL 17.9 \pm 0.7 cm; mean mass 17.2 \pm 2.6 g) and six were females (SVL 20.1 \pm 1.2 cm; mass 27.0 \pm 5.4 g). Temperature-sensitive radiotransmitters (mass 1.1 g; Holohil Systems Ltd., Canada) were affixed to the lizards' backs, about halfway between the snout and the vent, using Selley's Quikite superglue. Many field studies of snakes (e.g., Beupre, 1995; Fitzgerald *et al.*, 2002; Shine *et al.*, 2003b) implant telemeters into the body cavity, but the small size and slender build of *L. burtonis* precluded this procedure. The mass of transmitters never exceeded 10% that of lizards. As *L. burtonis* are capable of feeding on skinks at least 41% of their own mass (Wall and Shine, 2007), transmitters of this size should not present much of a burden to lizards in the wild.

All *L. burtonis* were released at their point of capture and tracked until their transmitters became detached, or until the study concluded. Telemetry was performed from 17–29 August 2003, at fairly regular intervals for each lizard. On average, lizards were followed for 7.2 \pm 1.0 days and located 24.5 \pm 3.1 times (about 3.4 times per day). A total of 318 tracking observations were made, with 201 occurring during daylight hours and 117 taking place at night. Care was taken not to disturb lizards when following them. These tracking durations were too short

to determine home range size, but much behavioural information was gathered. Specifically, data of the following types were collected:

Activity and movement data: Distances lizards travelled between tracking locations were recorded, as were other details of their behaviour such as activity (e.g., moving or motionless) and whether or not lizards were visible.

Thermal data: Temperatures recorded by the external transmitters were highly correlated with lizards' internal body temperatures (Wall M., unpublished data, 2003). We recorded lizard external body temperatures with every tracking observation and calculated hourly means for each lizard. Average hourly external-body temperatures over a composite 24-hour period were then derived from these means. Combining data from different days was justified, as the weather was similar over the course of the entire study (sunny with highs of 30–32°C and lows of 20–22°C). Environmental temperatures were also recorded with ThermoChron iButtons (Dallas Semiconductor, USA) at several locations: at ground level in the open and in deep shade, and in leaf litter at depths of 2, 4, and 6 cm.

Habitat data: Multiple microhabitat variables were scored at each tracking location. In a circle with a radius of 1 m from the lizard's location, we measured: 1) % canopy cover (vegetation cover over 2 m in height), as estimated by comparison with templates in McDonald *et al.* (1998); 2) % shrub cover (vegetation cover between 0.1 and 2.0 m); 3) % vegetative ground cover; 4) % leaf-litter ground cover; 5) % soil ground cover; 6) % rock ground cover; 7) distance to nearest tree at least 10 cm diameter at breast height; and 8) distance to nearest log at least 10 cm in width. We also recorded litter depth at multiple locations: 1) where the lizard was found; and 2) at 10, 20, 30, 40, and 50 cm away from this point in each of the four cardinal directions (to determine if *L. burtonis* selected the deepest patch of leaf litter in its immediate area).

In addition, we recorded these same variables at random points throughout the environment, one random point for each actual lizard location. Random points were selected by moving 5 m in a random direction from an actual telemetry location. This method was employed because we were interested in microhabitat selection at a small spatial scale (why lizards settled in one particular spot, and not a site a few meters away). Selecting random points within the broader study area (i.e., from a map) would not have provided this level of resolution.

For most of the above variables, means were computed for each of the 13 lizards; random and actual sites were then compared using ANOVA. Leaf-litter depths at the various distances from lizard locations, however, were

analysed differently. At each of the five distances away (10, 20, 30, 40, and 50 cm), a single mean was calculated from the four depth measurements. For example, the four depths from 10 cm away (north, south, east, and west) were averaged to yield a single number, and so forth. These means, and the depth at the actual tracking location, were compared to each other using ANOVA. The same procedure was followed for random points.

2.3 Field enclosure experiments

2.3.1 Study animals and maintenance Twenty adult *L. burtonis* (five males, 15 non-gravid females; mean SVL 18.6 cm; mean mass 19.9 g) were captured in the Top End, about 60 km southeast of Darwin, in March of 2003. Lizards were brought to the University of Sydney, where they were maintained individually in plastic cages (22 × 22 × 7.5 cm) on a 12:12 light:dark cycle and fed live skinks approximately bi-weekly. Room temperature was kept at 20°C, but heated strips running under one end of each cage allowed lizards to thermoregulate behaviourally during the diurnal part of their daily cycle. They also had access to shelter and water ad libitum.

2.3.2 Microhabitat choice experiment Field data indicated that *L. burtonis* was often associated with leaf litter microhabitats (see Results). To determine if this represented an actual preference or was merely a secondary consequence of the prevalence of this habitat type in the Top End, we performed an experiment in outdoor field enclosures at Macquarie University in Sydney. Sixteen enclosures, each measuring 2 m long × 2 m wide × 1.2 m high, were subdivided into quadrants of equal size. Each quadrant was lined with sand to a depth of 5 cm and assigned to one of four habitat types: 1) sand, which contained sand substrate and nothing else; 2) locally-collected leaf litter, to a mean depth of 8.2 cm; 3) sticks, in a jumbled pile about 30 cm high; or 4) tiles, in which nine tiles, each measuring 20 × 20 × 0.7 cm, were propped 5 cm off the ground and arranged in three rows. The location of quadrants within the enclosures was counterbalanced, so that equal numbers of each habitat type occupied each orientation; for example, four of each habitat type occupied the northwest corner of an enclosure, four the southeast corner, and so on. To determine if habitat types provided divergent thermal opportunities to lizards, four ThermoChron iButtons (Dallas Semiconductor, Sunnyvale, CA) were placed in each enclosure, one in the middle of each quadrant. According to the habitat type, iButtons were placed either at the bottom of the leaf-litter pile, at the base of the stack of sticks, beneath a tile, or on the surface of the sand. A water dish was placed in the centre of each enclosure.

On the morning of 4 January 2004, one *L. burtonis* was placed in the centre of each enclosure, at the point where the quadrants met. Five males and 11 females were used. Lizards were left for 24 h, after which time the habitat type in which they had settled was recorded.

2.3.3 Thermoregulation in leaf litter We also wished to investigate the thermal consequences of the strong association between *L. burtonis* and leaf litter. Specifically, we wanted to know what thermal opportunities litter provided, how carefully lizards regulated their body temperatures within this microhabitat, and how tightly thermoregulation and lizard movement were linked. We blocked off the northeast corner of 15 of the enclosures used in the habitat-choice experiment, thereby creating 15 arenas of $1 \times 1 \times 1.2$ m. These were filled with leaf litter to a depth of 14 cm. Eight Thermochron iButtons were installed in the centre of every arena, one each at depths of 0, 2, 4, 6, 8, 10, 12, and 14 cm below the litter's surface. In the early afternoon of 5 February 2004, one non-gravid adult female *L. burtonis* was placed in the centre of each arena. Each lizard bore a thermochron on its back, halfway between its snout and its vent, which had been affixed with Elastoplast elastic adhesive. Thermochrons were modified in the manner of Robert and Thompson (2003), reducing their dimensions to 14 mm in diameter \times 6 mm thick, and their mass to 1.5 g. Each thermochron's exposed thermistor was in direct contact with the lizard's dorsal surface; temperatures obtained using this method are highly correlated with the lizards' internal body temperatures (Shine *et al.*, 2003a).

Thermochrons recorded lizard external-body temperatures every 10 minutes over the next three days and two nights. Hourly means were calculated for each *L. burtonis* over this period, and combined to yield an overall hourly average. *Lialis burtonis* external-body temperatures were then visually compared to temperature profiles at each of the eight litter depths to determine how lizards were moving through the litter. These data were drawn from an experiment designed primarily to investigate the thermal consequences of feeding (Wall, 2006); therefore, eight of the *L. burtonis* had recently fed, whereas seven had empty stomachs. However, pooling data for all 15 *L. burtonis* is justified, as feeding had no effect on lizard body temperatures in the enclosures (Wall, 2006).

3. Results

3.1 Examination of museum specimens

3.1.1 Sex ratios and sexual dimorphism

Twenty-four of 96 *L. burtonis* specimens were juveniles, many of which could not be sexed definitively. Of the 72 adults, 49 were females and 23 males, a significant departure from a 1:1 sex ratio (1 *df*, $\chi^2 = 4.85$, $P = 0.028$). Females were significantly longer than males (21.3 vs. 17.5 cm SVL; unpaired *t*-test: 70 *df*, $t = 6.61$, $P < 0.0001$). The sexes did not differ in relative head length (ANCOVA with SVL as the covariate: $F_{1,69} = 1.49$, $P = 0.23$) or width ($F_{1,69} = 0.05$, $P = 0.82$). Equivalent percentages of males and females had regenerated tails (78.3 vs. 75.5%, respectively; 1 *df*, $\chi^2 = 0.066$, $P = 0.80$), but the intact (non-regenerated) tails of males were longer than those of females (ANCOVA with SVL as the covariate: $F_{1,14} = 11.32$, $P = 0.0046$). Sexual dichromatism was also found: 28 of 49 females exhibited facial striping (either white stripes against a dark face or vice versa), compared to only four of 23 males (1 *df*, $\chi^2 = 10.02$, $P = 0.0016$). All of these results are summarised in Table 1.

3.1.2 Ontogenetic variation The body form of *L. burtonis* shifts as lizards increase in size. Relative to SVL, smaller lizards have longer and wider heads and shorter tails than do larger animals (Figure 1).

3.1.3 Diet Twenty of 96 (20.8%) *L. burtonis* had food in their stomachs. Seventeen of 72 adults and three of 24 juveniles contained prey; this was not a significant difference (1 *df*, $\chi^2 = 1.35$, $P = 0.25$). Among adults, males had food in their stomachs more often than did females (nine of 23 vs. eight of 49; 1 *df*, $\chi^2 = 4.51$, $P = 0.034$). Overall, 18 lizards contained a single prey item, one contained two, and one lizard contained four. Twenty-four prey items were thus recorded, for an average of 1.2 per *L. burtonis* that had fed. All food items were lizards (21 skinks, two geckos, and one agamid; Table 2). Most prey were diurnal, although some were nocturnal and/

Table 1 Morphometric characteristics of adult male and female *Lialis burtonis* from the Top End of Australia's Northern Territory. Data given are means, except for total numbers of males and females. SVL: Snout-vent length; Relative HL: Head length/SVL; Relative HW: Head width/SVL; Relative TL: Length of complete (non-regenerated) tail/SVL; % regen. tail: Percentage of lizards with regenerated tails; % facial stripes: Percentage of lizards with white stripes against a dark face or vice versa. See text for details of statistical analyses.

	Male	Female	<i>P</i> -value
n	23	49	0.028
SVL (cm)	17.5	21.3	<0.0001
Relative HL	0.115	0.113	0.23
Relative HW	0.04	0.038	0.82
Relative TL	1.3	1.16	0.0046
% regen. tail	78.3	75.5	0.8
% facial stripes	17.4	57.1	0.0016

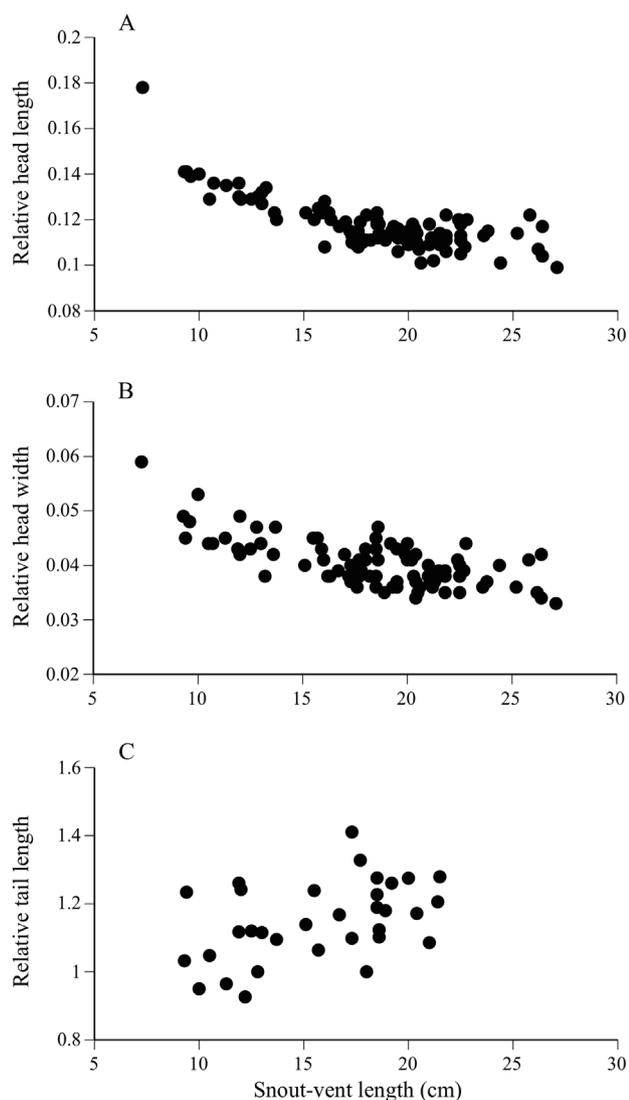


Figure 1 Relationship between snout-vent length (SVL) and: (A) relative head length (HL/SVL); (B) relative head width (HW/SVL); and (C) relative tail length (TL/SVL) in museum specimens of *Lialis burtonis*. HL was measured from the quadrate to the tip of the snout, and HW at the head's widest point. In (C), only animals with complete (non-regenerated) tails were used. All three relationships were found to be significant, using simple regression: (A) $R^2 = 0.60$, $n = 95$, $P < 0.0001$; (B) $R^2 = 0.46$, $n = 95$, $P < 0.0001$; (C) $R^2 = 0.20$, $n = 33$, $P = 0.0088$.

or crepuscular (Table 2). Males and females took similar proportions of diurnal prey (females: seven diurnal prey items, three nocturnal/crepuscular, and two of unknown activity time; males: four, two, and three, respectively). *L. burtonis* contained prey in all months of the year except February and May.

3.1.4 Reproduction Reproductive females contained either one ($n = 4$) or two ($n = 16$) eggs or enlarged follicles. Ovulation and egg-laying appear to occur mainly from the late dry-season to the mid wet-season (September–January; Figure 2). In males, testes are

largest from August–November (Figure 2), suggesting that most matings may take place during or shortly after this period.

3.2 Telemetry

3.2.1 Activity and movement data Lizards moved an average of 4.9 m/d. Larger *L. burtonis* did not move significantly farther than smaller animals (regression of distance per day vs. SVL: $R^2 = 0.022$, $n = 13$, $P = 0.63$). Female *L. burtonis* moved 2.7 m/d on average and males 6.8 m/d; this was not a significant difference (ANOVA: $F_{1,11} = 2.69$, $P = 0.13$).

Lizards were usually motionless and hidden from view when located. In a total of 318 tracking observations, lizards were visible only 54 times (17%) and were found moving on only nine occasions (2.8%). Ten of 13 *L. burtonis* were immobile for periods of at least 22 h, six passed at least 40 consecutive h without moving, and two remained motionless for 102 and 116 h, respectively.

Lialis burtonis were active at all hours, and lizards moved both day and night. However, movements made after dark tended to be longer. Nocturnal movements averaged 1.9 m/h, compared to 0.3 m/h during the day; this was nearly a significant difference (paired *t*-test; 9 *df*, $t = 2.15$, $P = 0.060$). Of 61 moves made during the day, only 9 (14.8%) covered more than 2 m, compared to 9 of 19 (47.4%) nocturnal movements (1 *df*, $\chi^2 = 7.97$, $P = 0.003$). Further, all nine occasions during which lizards were observed moving (see above) occurred after dark.

3.2.2 Thermal data During the hottest part of the day (11:00 h–15:00 h), *L. burtonis* maintained a relatively

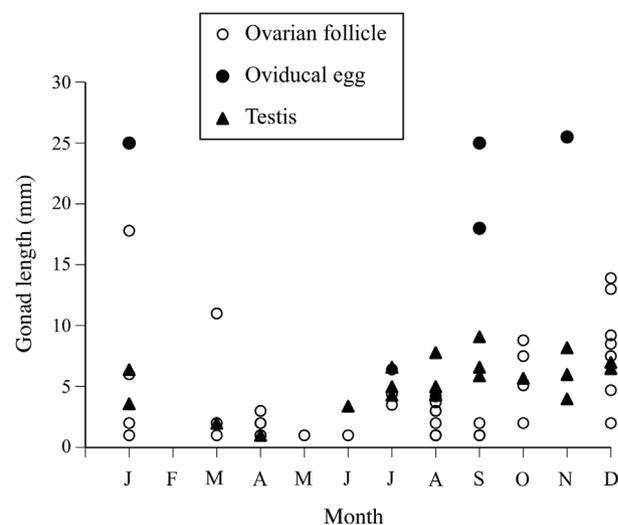


Figure 2 Seasonal distribution of gonad size in adult *Lialis burtonis* from the tropical Northern Territory, Australia. The largest follicle or egg was measured in females, and the larger of the two testes in males. Measurements given are lengths (mm).

constant external-body temperature, between 34.9°C and 35.8°C (Figure 3). In the open during this time, temperatures at ground level and 2–4 cm deep in the leaf litter rose to well above lethal levels (> 50°C: see Figure 4 A). At 6 cm deep in the litter, temperatures were much lower (< 40°C: see Figure 4 B).

3.2.3 Habitat data For most of the habitat variables measured, there was no significant difference between lizard locations and random sites (Table 3). The exception was leaf-litter depth: lizards were found in deeper litter than expected by chance (5.9 vs. 2.7 cm; ANOVA: $F_{1,24} = 22.01$, $P = 0.0001$; Table 3). Further, litter depth decreased as the distance from lizard locations increased (ANOVA: $F_{5,72} = 4.97$, $P = 0.0006$; Figure 5 A), indicating that *L. burtonis* were selecting the deepest patch of litter within a 50-cm radius. No such pattern was evident for random

Table 2 Prey items found in the stomachs of *Lialis burtonis* from the tropical Northern Territory (n = 20 with food). C: Crepuscular; D: Diurnal; N: Nocturnal; U: Unknown; *: Personal observations made in 2003.

Prey species	n	Activity time (Authority)
Family Agamidae		
Unknown	1	D (Cogger, 2000)
Family Gekkonidae		
<i>Heteronotia binoei</i>	2	N (Cogger, 2000)
Family Scincidae		
<i>Carlia</i> spp.	5	D (Cogger, 2000)
<i>Carlia gracilis</i>	1	D (Cogger, 2000)
<i>Ctenotus</i> spp.	4	D (Cogger, 2000)
<i>Ctenotus spaldingi</i>	1	D (Cogger, 2000)
<i>Glaphyromorphus</i> spp.	2	C/N (Cogger, 2000; Wall M., pers. obs.)*
<i>G. isolepis</i>	2	C/N (Cogger, 2000; Wall M., pers. obs.)*
<i>Lerista carpentariae</i>	1	N (Cogger, 2000)
Unknown	5	U
Total	24	12 D, 4 C/N, 3 N, 5 U

Table 3 Quantification of habitat variables at locations where 13 radiotracked *Lialis burtonis* were found (actual) and at random sites (random). Percentages refer to the composition of a circle with a radius of 1 m around the central location (either an actual or random site). Canopy: Vegetation cover ≥ 2 m in height; Shrub: Vegetation cover < 2 m in height but above the ground; GV: Ground vegetation; Dist. to tree: Nearest tree with a diameter ≥ 10 cm at breast height; Dist. to log: Nearest log ≥ 10 cm wide. All statistical tests performed were ANOVAs.

Variable	Actual	Random	P-value
% canopy cover	38.6	32.5	0.25
% shrub cover	18.3	15	0.55
% litter cover	71.7	59.7	0.19
% GV cover	13.2	14.1	0.8
% soil cover	13.1	23	0.1
% rock cover	2	2.9	0.63
Litter depth (cm)	5.9	2.7	0.0001
Dist. to tree (cm)	288.2	328.4	0.68
Dist. to log (cm)	576.9	555	0.9

sites (ANOVA: $F_{5,72} = 0.034$, $P = 0.999$; Figure 5 B).

3.3 Field enclosure experiments

3.3.1 Microhabitat choice experiments Fifteen of 16 *L. burtonis* were found in leaf litter, a number significantly greater than that expected by chance (3 df, $\chi^2 = 54.00$, $P < 0.0001$). In the middle of the day, temperatures in the sand quadrant were much higher than temperatures in the other three habitat types (Figure 6). There was no significant difference, however, among temperatures measured in the litter, stick, and tile quadrants (repeated-measures ANOVA with sand temperatures excluded and data log-transformed: $F_{2,21} = 2.09$, $P = 0.15$; Figure 6). Mean temperatures during the hottest part of the day were well below 40°C in all three habitat types.

3.3.2 Thermoregulation in leaf litter Comparison of *L. burtonis* external-body temperatures and temperatures at various litter depths suggests that lizards remained about 6–8 cm deep over the duration of their time in the enclosures (Figure 7).

4. Discussion

4.1 Morphological characteristics and sexual dimorphism In the Top End, adult female *L. burtonis* grow larger than males (Table 1). This is not surprising; the same trend is evident in many gekkonid and pygopodid species, including *L. burtonis* in other parts of its range (Fitch, 1981; Patchell and Shine, 1986a). Further, females have relatively longer trunks than do males (i.e., the tails of males comprise a greater percentage of their total length; Table 1). Both of these characteristics, which are common in snakes (King, 1989; Shine, 1993), are likely manifestations of fecundity selection for greater abdominal volume in females. Accommodating the reproductive organs is likely not a factor in the evolution of longer tails in male pygopodids, unlike the case in snakes. Even in female pygopodids, tails are longer than SVL, providing abundant room for hemipenes and their associated musculature (Table 1). Although larger females cannot increase their number of eggs per clutch (all pygopodids have a fixed maximum clutch size of two; Pianka and Vitt, 2003), they can likely produce larger offspring, which may stand a better chance of surviving to maturity (Brown and Shine, 2004; Ferguson *et al.*, 1982; Ferguson and Fox, 1984; Fox, 1975). Further, larger lizards may possess more substantial fat stores, giving them a better chance of laying multiple clutches per year (which *L. burtonis* is capable of doing; see below).

More mysterious is the observed sexual dimorphism in facial pattern (Table 1). The facial striping in Top

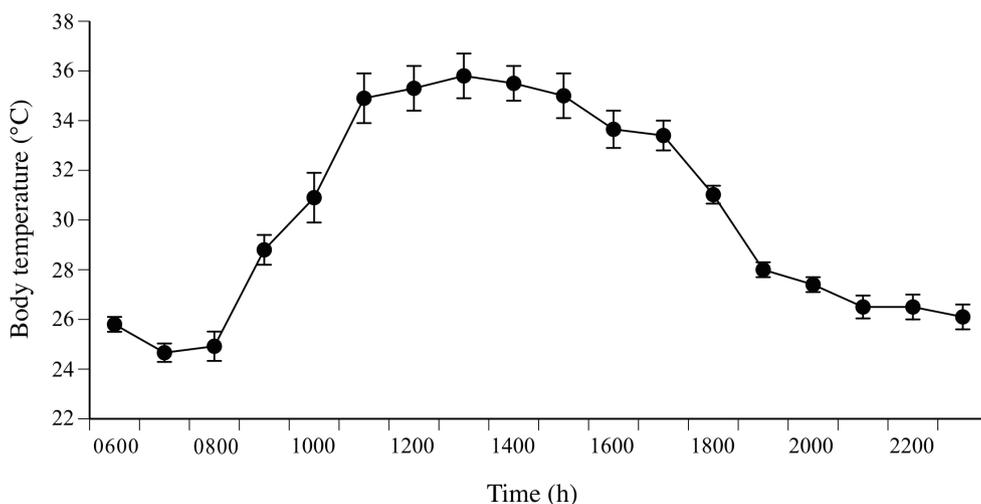


Figure 3 Hourly body temperatures of 13 radiotracked *Lialis burtonis*. Temperatures were averaged over the course of the field study. Points represent means \pm one standard error.

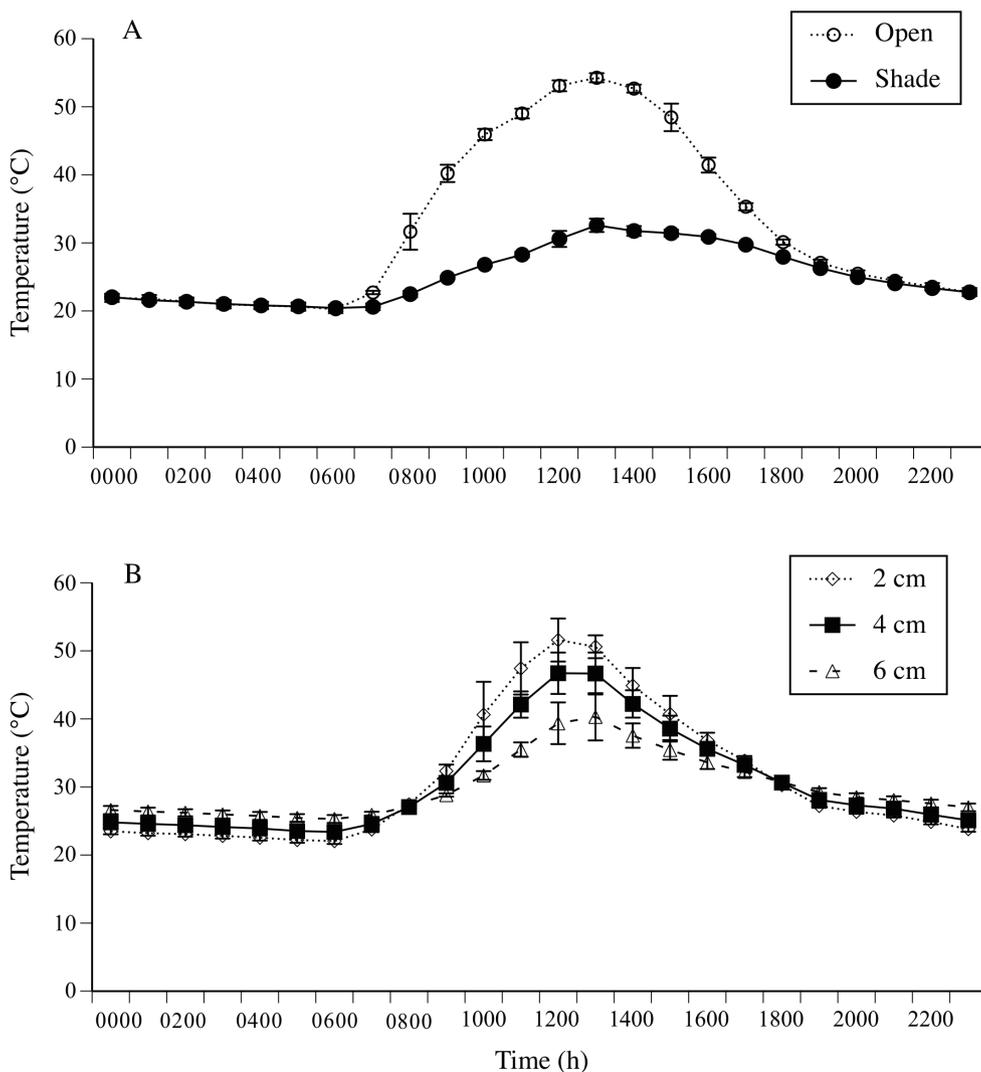


Figure 4 Mean temperatures (A) at ground level (in deep shade and in the open) and (B) at 2, 4, and 6 cm deep in leaf litter in habitats where *Lialis burtonis* were radiotracked. Temperatures were averaged over the course of the field study. Points represent means \pm one standard error.

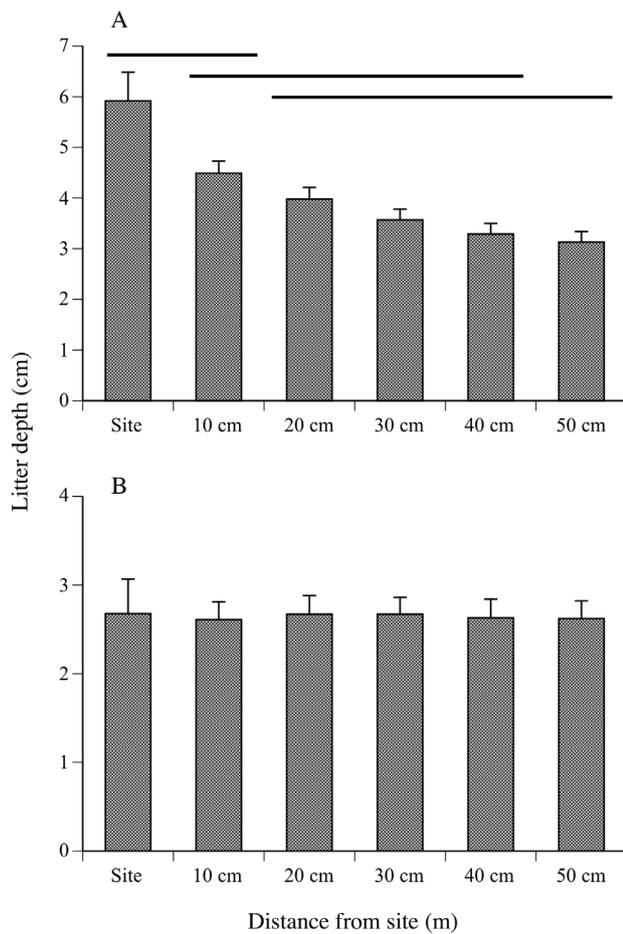


Figure 5 Depth (cm) of leaf litter at several distances from (A) actual *Lialis burtonis* radiotracking locations and (B) random sites nearby. Columns represent means \pm one standard error; lines connect columns that are not significantly different from each other. See text for details of statistical analyses.

End *L. burtonis* results in a dark line running through or just above the eye, a phenomenon common in ambush-foraging snakes such as boas, vine snakes, and vipers. Such eyelines may serve to mask the eye (Lillywhite and Henderson, 1993) and/or assist in tracking fast-moving prey (Ficken *et al.*, 1971); in venomous snakes, these dark stripes also may shield the venom glands from destructive ultraviolet radiation (Pough *et al.*, 1978). Why female *L. burtonis* should exhibit eyelines significantly more often than males is not immediately apparent; the sexes take the same prey (skinks) and seem to behave similarly in the field. Perhaps a longer-term field study involving more animals would detect some relevant behavioural differences.

As in other parts of Australia (Patchell and Shine, 1986a), female *L. burtonis* from the Top End are disproportionately represented in museum collections

(Table 1). This is somewhat puzzling, as males and females of most other pygopodid species are more equally represented (Patchell and Shine, 1986a). It is unknown if sex ratios of *L. burtonis* are female-skewed in the wild, or if collection bias is responsible for this pattern. Females were not more mobile than males during this study and thus do not seem more likely to be encountered by collectors. However, we tracked lizards for only a short time during August; the situation may be different at other times of year, especially during the reproductive season. It is possible that gravid females embark upon long-distance migrations to find suitable oviposition sites, as some oviparous snakes are known to do (Bonnet *et al.*, 1999). Suggestively, more than half of adult *L. burtonis* specimens for which the capture date is known (34 of 67; 23 females and 11 males) were caught during the peak period of follicle development and egg-laying (September–January). Radiotracking *L. burtonis* at this time of year would thus be of interest.

The ontogenetic variation in body proportions displayed by *L. burtonis* makes sense in light of its foraging biology. Like snakes, *L. burtonis* is a gape-limited predator; a larger head thus translates into an ability to swallow a wider range of prey. Such a constraint is likely more significant to relatively smaller lizards, as their predatory options are already more limited. Therefore, selection to increase head size should be stronger in hatchlings and juveniles than it is in adults (Forsman, 1996; King *et al.*, 1999). The same is true of relative trunk length: a longer trunk increases the size of the gut, facilitating the accommodation of larger prey items. Small *L. burtonis* need to be able to take relatively large prey, for even hatchlings feed entirely on other lizards.

4.2 Diet Top End *L. burtonis* prey exclusively on lizards, especially skinks (Table 2). Most prey species are surface-active; only one *L. burtonis* had eaten a fossorial lizard (*Lerista carmentariae*; Table 2). These data are consistent with information for the species across its entire range (Patchell and Shine, 1986a). Feeding occurs year-round, and must take place chiefly during daylight hours: *L. burtonis* hunts by ambush (see below) and most prey items are diurnal (Table 2). However, *L. burtonis* is flexible, taking crepuscular or nocturnal lizards such as geckos when the opportunity presents itself (Table 2). As *L. burtonis* is a visually-oriented predator, cueing its strikes on prey movement (Wall, 2006), its opportunistic post-sunset hunting may be limited to dusk or moonlit nights. Alternatively, the species may have inherited from its gecko forebears visual acuity in low light levels.

Top End *L. burtonis* are infrequent feeders; only 20.8%

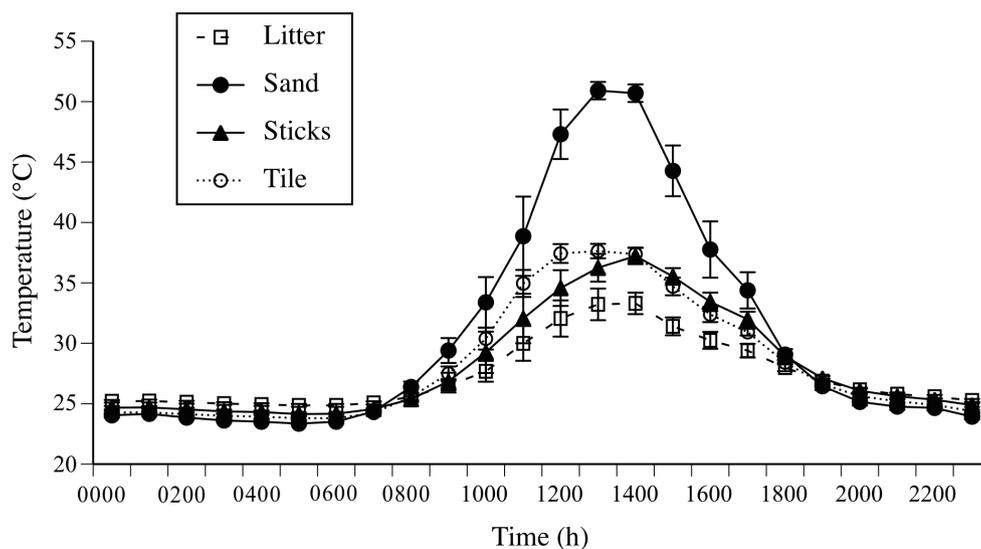


Figure 6 Mean temperatures recorded in each of the four habitat types available to 16 *Lialis burtonis* in the habitat-choice experiment. Temperatures were measured at the bottom of the litter, under the pile of sticks, beneath a tile, and in the open on the sand's surface. Points represent means \pm one standard error. See text for details of statistical analyses.

of lizards had food in their stomachs (Table 2). Most other lizard species feed far more frequently (Huey *et al.*, 2001). This difference highlights the fact that *L. burtonis* is not a “typical” lizard; ecologically it is highly convergent with ambush-foraging snakes, taking relatively large prey items at infrequent intervals. Indeed, its feeding frequency is similar to that of such ambush-hunting snakes as boas and pit-vipers (Holycross *et al.*, 2002; Martins *et al.*, 2002; Rodriguez-Robles *et al.*, 1999). Patchell and Shine (1986a) found food items in a significantly higher percentage of *L. burtonis* across the range of the species (59%); this disparity could be indicative of geographic variation in feeding frequency, but it is more likely the result of methodological differences. We only recorded stomach contents, whereas it appears that Patchell and Shine (1986a) examined food items in the entire gut.

In some snake species, gravid females cease or seriously curtail feeding, mediated via either physiological appetite suppression or a reduced ability to capture prey (Daltry *et al.*, 1998; Gregory *et al.*, 1999). However, this does not seem to be the case in *L. burtonis*; four of 20 reproductively active adult females (i.e., females with oviducal eggs or enlarged follicles) contained food, a similar proportion to that for adult females in general (eight of 49). Thus, some other phenomenon is likely responsible for the difference in feeding frequency between males and females (39.1% vs. 16.3% with food, respectively). Differences in mobility may play a role. If females do indeed move more than males during the reproductive season (see above speculations), they likely have fewer feeding

opportunities at this time, for extensive movement is incompatible with ambush foraging (Daltry *et al.*, 1998).

4.3 Reproduction As in other parts of its range (Patchell and Shine, 1986a), reproduction of *L. burtonis* in the Top End appears to be seasonal: ovulation occurs primarily in the late dry-season (beginning around September), and most females lay eggs in the early to middle wet-season (November–January). This pattern is common in many other Top End reptile species (James and Shine, 1985; Shine and Lambeck, 1989). However, *L. burtonis* reproduction is not limited to these periods; females are capable of laying more than one clutch per year, and heavily gravid lizards can be found in February and March (Wall M., personal observation, 2003). Clutches may be laid in quick succession. Two captive females caught in mid-August both laid their first clutch in early November; one then laid a second clutch in late December, and the other laid again in mid-January (Wall M., unpublished data, 2004). Such subsequent clutches may be fertilised by stored sperm (or, alternatively, may result from parthenogenesis); neither female had had any contact with males since her capture.

4.4 Behaviour in the field As laboratory studies suggest (Patchell and Shine, 1986b; Murray *et al.*, 1991), *L. burtonis* in the Top End are sedentary ambush foragers. Lizards moved 4.9 m/d on average, but usually much less; this number was inflated by seven long-distance moves (> 15 m) made by four lizards. Lizards remained in one spot for long periods of time (over 100 h in the case of two

animals), presumably waiting for prey to happen by.

It is unlikely that the burden presented by radiotransmitters artificially reduced *L. burtonis* mobility or greatly affected lizard behaviour in any other way. All lizards were capable of long-distance movement: the smallest individual tracked during the study (11.1 g) made one move of 40 m, and, as stated above, three other lizards travelled farther than 15 m in one movement. Lizards did not lose condition in the time they were radiotracked, and

one was recaptured with a prey item in its stomach (Wall M., unpublished data, 2003). Further, another, longer-term (~28-day) study of a *L. burtonis* population near Sydney corroborates the patterns observed in Top End animals. Sydney-area animals moved even less (1.4 m/d) and also continued to feed despite the presence of telemeters (Wall M., unpublished data, 2005).

Diurnal and nocturnal movements seem to have different functions. Daytime moves are relatively short

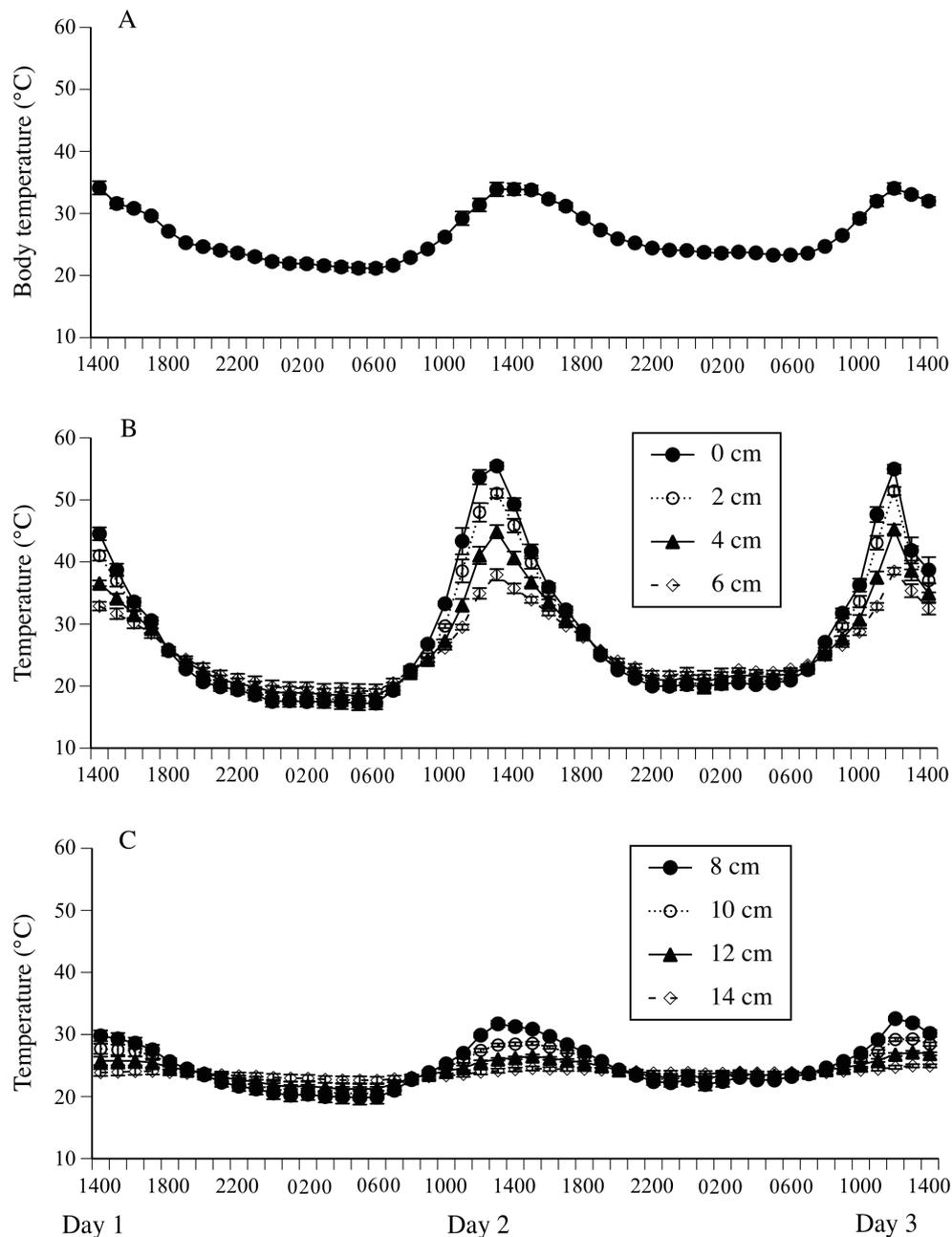


Figure 7 Body temperatures of 15 *Lialis burtonis* in field enclosures filled with leaf litter to a depth of 14 cm (A), leaf litter temperatures at every 2 cm of depth from 0 to 6 cm (B), and leaf litter temperatures at every 2 cm of depth from 8 to 14 cm (C). Points represent means \pm one standard error.

and likely involve minor thermoregulatory or postural adjustments; lengthier night-time moves, in contrast, probably serve to seek out new foraging sites. Restricting long-distance moves to night-time in the Top End might reflect several issues. First, surface temperatures in exposed areas rise rapidly to lethal levels during the day (Figure 4). Second, predation pressure is intense, as the high tail-loss rates among Top End *L. burtonis* (> 75%; Table 1) attest. Most of the major predators are likely diurnal, especially raptors. Dense populations of whistling kites (*Haliastur sphenurus*), black kites (*Milvus migrans*), and blue-winged kookaburras (*Dacelo leachii*) occur at the study site (Wall M., personal observation, 2003), and all prey to some extent on lizards and snakes (Barker and Vestjens, 1989). Many *L. burtonis* bear bill-shaped scars on their bodies and tails, testaments to their encounters with avian predators (Wall M., personal observation, 2003).

Leaf litter is an important microhabitat for *L. burtonis* in the Top End. Litter was more than twice as deep where radiotracked lizards settled than it was at random sites (Table 3), and lizards tended to be found in the deepest patch of litter in their immediate area (Figure 5 A). Further, litter provided cover to radiotracked *L. burtonis* on more than 93% of telemetry observations. These patterns are not simply indirect consequences of the fact that litter is the most common cover type at our study site (Table 1). Rather, they likely indicate an actual preference for leaf litter on the part of *L. burtonis*, for lizards choose litter even when given several thermally comparable alternatives.

Leaf litter probably serves *L. burtonis* in a number of ways. The chief thermoregulatory challenge of *L. burtonis* in the Top End, and for many other tropical reptiles (Shine and Madsen, 1996), is to avoid overheating. Litter is a good insulator, protecting lizards from potentially lethal heat. At our study site, surface temperatures consistently exceed 50°C during the day in exposed areas (Figure 4 A); however, at 6 cm deep in the litter (the average depth where lizards were found; Table 3) they rarely top 40°C (Figure 4 B). By making slight movements and postural adjustments in the litter (see above), *L. burtonis* is able to maintain external-body temperatures around 35°C (Figure 3) during the hottest time of the day.

As an ambush forager, *L. burtonis* is dependent to a large extent on crypsis (Pianka and Vitt, 2003), and leaf litter helps lizards avoid detection by both predators and prey. In a typical ambush posture, the body and tail of *L. burtonis* are completely buried (often to a depth of 6–8 cm; Figures 3, 4 B, and 7), with only the head protruding

from the litter (Wall M., personal observation, 2003). In this position, lizards can hunt while avoiding both overheating and detection; further, they are very difficult to see (at least for a human observer: Wall M., personal observation, 2003). Finally, leaf litter also provides *L. burtonis* with many foraging opportunities; at our study site, prey skinks such as *Carlia* spp. are common in this microhabitat (Wall M., personal observation, 2003).

Taken together, these data provide a detailed picture of the ecology of *L. burtonis* in the Northern Territory's tropical Top End. As the species is found over virtually all of mainland Australia, as well as parts of New Guinea (Cogger, 2000), it would be interesting to perform similar in-depth studies in different parts of its range. What, for example, are lizards doing in the deserts of central Australia, where leaf litter microhabitats are decidedly scarce? Such a widespread species must display substantial flexibility in factors such as microhabitat use and activity times (as our telemetry study of lizards in the Sydney area suggests; Wall M., unpublished data, 2005). Such complementary studies of wide-ranging taxa would yield insight into the mechanisms determining species distributions.

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