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The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia?

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Abstract.   Although most species of large reptiles in the Sydney region are now restricted to remnant bushland, the blue-tongued lizard (*Tiliqua scincoides*) remains abundant. How has this large, slow-moving reptile managed to persist in the suburbs? We implanted radio-transmitters into 17 adult blue-tongued lizards and tracked them for six months (October 1998 to March 1999). Radio-tracked animals utilised 5–17 suburban backyards, but each lizard spent most of its time in a few 'core' areas near 2–7 shelter sites. Males had larger home ranges than females (mean of 12 700 *v.* 5100 m^2) and moved further between shelter sites. Gravid females (mean home range 1000 m^2) were more sedentary. Lizards used corridors of dense vegetation to move between retreat sites, and actively avoided crossing roads. In sunny weather, lizards typically basked close to their overnight shelter for 1–4 h each morning until they obtained body temperatures of approximately 32°C. They maintained high body temperatures while moving about in the afternoon.

In combination, the following ecological factors may facilitate persistence of blue-tongued lizards at our suburban study sites. (i) The most important subgroup of the population in terms of conservation are gravid females, which are highly sedentary and, thus, less likely to encounter the dangers of suburbia. (ii) The more 'expendable' males move about much more, but mostly in times and places that involve minimal risk from humans and their domestic pets. (iii) Lizards show strong site fidelity, spending up to 70% of their time in 'safe' locations; importantly, they avoid roads. (iv) Blue-tongued lizards readily utilise 'artificial' shelter sites and the commensal prey species (e.g. snails) found in most gardens. (v) These lizards can grow rapidly, mature early, and produce large litters. Because blue-tongued lizards have a long life span (over 30 years in captivity), populations of adults may persist for many years in the absence of recruitment.

Introduction

Urbanisation is one of the most drastic changes that can be imposed on an environment, fragmenting the land into a mosaic of patches of differing size and shape that are surrounded by cleared areas, roads, buildings and other modified habitats (Dickman 1987). These kinds of ecological shifts associated with urban development are widespread in coastal eastern Australia. From the beginning of European settlement in Australia, a high proportion of the population has been concentrated in towns along the eastern coast. The characteristic sprawl of homes and gardens and the popularisation of the 'quarter acre' suburban block have shaped the development of cities and coastal areas. This development has led to massive alterations of the natural environment and a rapid decline of native fauna (Recher *et al.* 1993; Dickman 1994; Keast 1995). These processes are obvious in Sydney, the largest city in Australia.

The disappearance of native vertebrates from urban/suburban areas in Sydney is poorly documented, although historical records (e.g. Krefft 1869; Australian Museum registers) indicate that large reptiles were once common throughout the region. These species include the lace monitor (*Varanus varius*), the bearded dragon (*Pogona barbata*), the water dragon (*Physignathus lesueurii*), the leaf-tail gecko (*Phyllurus platurus*), the diamond python (*Morelia spilota*), the broad-headed snake (*Hoplocephalus bungaroides*), the red-bellied black snake (*Pseudechis porphyriacus*) and the eastern brown snake (*Pseudonaja textilis*). Most of these species are now restricted to remnant bushland (Slip and Shine 1988; Webb and Shine 1998) or areas adjacent to remnant bushland (Griffiths 1987). The blue-tongued lizard (*Tiliqua scincoides*) offers a striking exception to this general pattern. Not only is this species common in highly disturbed areas, but it appears to be more

abundant in such areas than in adjacent, more pristine habitats (authors' observations).

Although ecologists have traditionally paid little attention to 'urban' species, much can be learnt from taxa that exploit the newly created urban habitats (Davis 1976). The metropolitan areas and their fringes consist of a mosaic of components ranging from almost totally artificial environments to 'natural' or 'semi-natural' components (McDonnell and Pickett 1990). In many cases, elements of the urban environment can provide important habitats for wildlife (Dickman and Doncaster 1987) and, in particular, many habitat possibilities are provided in a suburban garden (Beebee 1979). By identifying reasons for the 'success' of some taxa (i.e. their persistence in the face of extreme anthropogenic habitat modification), we may better devise ways to allow a wider range of taxa to similarly survive in such areas (Shine and Fitzgerald 1996). Thus, we conducted a radio-telemetric study of blue-tongued lizards in suburban Sydney to clarify how these animals have managed to persist in the modified habitats of suburbia.

Methods

Study species

Tiliqua scincoides is the only member of its genus found in the Sydney metropolitan region, where it is relatively common in suburban gardens (Griffiths 1987; Cogger 2000). The eastern blue-tongued lizard is a large (adult snout–vent length ~ 400 mm; mass to 700 g: Table 1), heavy-bodied, dorsoventrally flattened, terrestrial lizard with small limbs. Blue-tongued lizards are viviparous, with large litter sizes (up to 18 per litter: Shea 1992), relatively early maturation (approximately 2 years: Shea 1981) and a long potential life span (>30 years: P.Harlow, personal communication). Sexual size dimorphism was minor in our sample of radio-tracked lizards (mean SVL = 306 mm for males, 313 mm for females).

Study sites

We conducted a radio-telemetric study of blue-tongued lizards at two sites in the Hornsby Shire, 23 km north-west of central Sydney. This area is a mosaic of suburban housing, parkland and bushland remnants and is typical of blue-tongued lizard habitats throughout Sydney. The two sites are similar in terms of human population demographics, road size, traffic intensity, house and block size. The two areas share a similar history of development and are located within 5 km of each other (thus experiencing a similar climate). However, Site 2 is located on the outskirts of suburbia where the houses back directly onto native bushland.

Radio-telemetry

Surgery and tracking

Seventeen adult blue-tongued lizards (10 at Site 1; 7 at Site 2) were captured by hand, and each was surgically implanted with a temperature-sensitive radio-transmitter (Model #PD-2T, Holohil Ltd). The antenna whip of the transmitter was enclosed in a Silastic catheter tube and the complete transmitter package was sealed with a waterproof coating. The final unit weighed approximately 3.5 g, less than 1% of the animal's body mass. Lizards were anaesthetised at 24–26°C with a mixture of Fluothane (5%), oxygen (0.6 L min^{-1}) and nitrous oxide (1 L min^{-1}) administered via a CIG midget anaesthetic machine.

Surgical-plane anaesthesia (assessed from the loss of muscle reflex) occurred after 20–30 min.

A short oblique, lateral incision was made on the ventral surface, 5 cm from the anal scale and offset from the midbody line. The muscle fibres and peritoneum were teased apart to allow access to the body cavity. The transmitter was inserted into the body cavity with the antenna curled into a C-shape in the lower abdominal region. Muscle closure was accomplished using coated VICRYL® sutures, and scales were sealed with Selleys® Supa glue. The incision site was coated with Cicatrin® antibiotic powder and covered with Op-site® plastic-skin spray dressing. Lizards were kept in captivity for one week after surgery prior to release.

Lizards were radio-tracked for six months (October 1998 to March 1999). As independence between successive observations is an implicit assumption in most statistical analyses of animal movement (Swihart and Slade 1985) we chose to locate lizards every second non-raining day throughout that period; initial observations showed that lizards remained inactive and sedentary on wet, cold days. This tracking interval allowed us to quantify animal movements whilst giving enough time for lizards to move. All lizards were located on the same day (where possible) and within 2–4 h of each other. Each tracking day was broken into five periods: 0800–1000, 1000–1200, 1200–1400, 1400–1600 and 1600–1800 hours (by 1800 hours lizards were sheltered in retreat sites). We varied the time at which tracking was started each day, the sequence of tracking at the two sites and the sequence of individual lizard locations within sites. Lizards were generally well separated so the tracking of one animal did not influence the behaviour of other individuals.

Each time a lizard was located we recorded the following data: time; location (plotted on a cadastral 1:4000 map); a description of the macrohabitat and microhabitat in which the animal was found; behaviour, activity and response to disturbance; shaded air and substrate temperature; weather conditions; proportion of the lizard's body in sun *versus* shade; and the pulse interval of the transmitter signal (for later conversion to lizard body temperature, using previously determined calibration curves).

Home range, core areas and movements

Locational data from the radio-telemetry were used to calculate home-range areas for individual lizards. We used the minimum convex polygon method (MCP) (Jennrich and Turner 1969) to estimate home-range sizes and the adaptive kernel method (AK) (Worton 1989) to estimate utilisation distributions and identify 'core areas' of activity (Kie *et al.* 1994).

We used straight-line distances between two points as an estimate of distance travelled. Plausibly, the routes travelled by lizards may be highly non-random (e.g. they may remain within 'corridors' of dense vegetation or avoid roads). To evaluate such possibilities we compared actual movement patterns to randomly generated patterns. To calculate these 'random walk' trajectories we used a computer program (Osterwalder and Klingenboeck 1999) that uses the actual sequence of distances moved each day by each telemetered lizard but allocates the direction of movement randomly. That is, at the conclusion of each day's travel the direction of the next move is randomly determined (i.e. from a choice of 360°). From this model, the number of road crossings for 20 'random' walks was calculated for each individual telemetered lizard and compared with the actual number of observed road crossings. Roads were used for this test because they provide an obvious potential barrier to movement and their locations can be specified precisely.

Site fidelity

To further evaluate patterns of space use we calculated four values for each lizard: (i) the number of independent visits to a shelter site (i.e. cases where an animal returned to a shelter site after having been seen

at a different shelter site); (ii) the duration of stay at each of these 'repeated' shelter sites; (iii) the time between returns to a repeated shelter site; and (iv) the percent of total time spent at these repeated sites, compared with the total duration of tracking for that lizard.

Habitat use

Each time a lizard was located it was classified into one of three macrohabitats: 'garden' (artificial to semi-natural vegetated areas directly under the influence of human activity, including residential gardens, grassy ovals and weed thickets); 'forest' (any areas of native bush); and the 'built environment' (roads, houses, pathways, sheds and other non-vegetated 'artificial' habitats). Within these macrohabitat classifications, we identified three types of microhabitats: hard cover (i.e. piles of metal and timber, car tyres, rock crevices, pipes and drains), open areas and vegetative cover.

To see whether the lizards selectively used particular habitat types we laid a grid (15 m × 15 m squares) over each lizard's home range and recorded the macrohabitat at each of the sites where gridlines intersected. This procedure allowed us to calculate an 'expected' value for the proportion of time an individual spent in each macrohabitat (based on the availability of habitat components within the home range) to compare with observed usage as determined by telemetry locations.

Temperature regulation

Transmitters were calibrated prior to implantation and lizard body temperatures in the field were determined from the pulse interval of the transmitter. While we recorded both ambient air and substrate temperatures, we used ambient air temperature values to compare with lizard body temperature. Although substrate temperatures influence lizard body temperatures, their greater spatial heterogeneity (due to variation in substrate types within the study areas) made them less suitable for overall (among-lizard) comparisons. We used physical models (hollow copper tubing 15 cm long and 3 cm diameter) attached to thermal data loggers (HOBO^{TM} data loggers) to measure the maximum and minimum operative (environmental) temperatures available to our study animals (e.g. Peterson *et al.* 1993).

Activity and behaviour

A lizard was classified as 'active' if it was sighted or if its body temperature was 5°C higher than the ambient temperature. Each time a lizard was located and 'active', we classified its behaviour into one of the following five categories: basking (stationary in sun), moving, foraging, stationary (not in sun) and not seen (i.e. active but sheltering).

Mean selected temperatures in the laboratory

Mean selected temperatures (MST) were measured in the laboratory at the conclusion of the telemetric study (March 1999). Thirteen of the lizards used in the telemetry study were housed separately in cages (measuring 100 × 50 cm) within which a thermal gradient from 22 to 38°C was maintained. The body temperature of each lizard was recorded every 30 min from 0800 hours to 2200 hours. Animals had access to water but were fasted for five days prior to the trial (so that metabolic heat production would not affect the results) and were not provided with shelter (so as not to influence their choice of position in the cage). Data loggers (HOBO^{TM}) recorded the maximum and minimum temperature in each cage. To estimate each animal's MST we used the mean of all readings taken after the initial heating/basking period.

Feeding habits

We analysed the scats of freshly caught blue-tongued lizards from suburban Sydney and examined the stomach contents of preserved specimens in the collection of the Australian Museum. All of the invertebrate material was classified to Order and plant material and seeds were identified where possible.

Data analysis

We collected relatively equal numbers of males and females at each of the study sites and the reproductive status of females was determined during surgery. Because pregnancy substantially modifies movement patterns and thermoregulation in many reptile species (Shine 1980; Beuchat 1986), we have separated data for gravid *versus* non-reproductive females. Unfortunately, this subdivision did not fall neatly across the two study sites. Thus, for most tests we have analysed data for each site separately using one-factor analysis of variance (ANOVA) to compare data between the three 'sex' categories (males, gravid females and non-reproductive females). As there was only one non-gravid female at Site 2, her values were omitted from these site-specific analyses but are included in some tables for comparison. Paired *t*-tests were used to compare the actual telemetry observations with results from a model of random usage.

Relevant assumptions of parametric statistical tests (normality and homogeneity of variances) were checked prior to analysis. If values did not fit a normal distribution they were transformed to remove this problem. Data were tested for significance at the $P = 0.05$ level. We have treated successive telemetry locations as independent values, but did not combine data from different individuals.

Results

Radio-telemetry

Home range, core areas and movements

The 17 radio-tracked lizards were monitored for an average of 102 days each (range 50–135 days; see Table 1). Each lizard exhibited a discrete home range, as can be seen by plotting the distance from original release against time since release (Slip and Shine 1988). The 'plateau' (i.e. the point after which successive locations did not reveal any further travel distance) generally occurred after approximately 50 days (Fig. 1). The home-range size (MCP) was calculated for each telemetered animal using 26–64 observations (Table 1; Figs 2, 3). A one-factor ANOVA on ln-transformed data showed significant differences in home-range size between the sexes. At both sites, males had a significantly larger mean home-range size (95% and 100% MCP) than did females in either group (gravid or non-reproductive; Table 2). There were no significant differences in mean home-range size (95% and 100% MCP) between the two sites for either males ($F_{1,7} = 2.49$, $P = 0.16$) or gravid females ($F_{1,2} = 0.50$, $P = 0.55$).

We calculated a series of percentage contours (10–90%) for the adaptive kernel to identify centres of activity within each home range. Blue-tongued lizards at both sites had definite core areas, as illustrated when the percentage values for the adaptive kernel analysis are plotted against the estimated utilisation distribution (Fig. 4). In each case, approximately 70% of all observed locations fell within a small proportion (approximately 20%) of the total home range. Analyses of the utilisation distribution showed a similar pattern to those described above for overall size of the home range. At both sites, males had significantly larger

Table 1. Minimum Convex Polygon estimates of home-range size (m^2) for radio-tracked blue-tongued lizards

The first column shows an animal's individual identification number, based on its transmitter frequency. Female (g) = gravid female.
SVL = snout–vent length. MCP = Minimum Convex Polygon, calculated from either all telemetry locations (100%) or excluding
exterior margins of the home range used on only 5% of locations (95% MCP)

Animal #	Site	Sex	Mass (g)	SVL (mm)	Tracking days	No. of observations	MCP 100% (m^2)	MCP 95% (m^2)
551	1	Female	542.2	330	127	58	4253	2580
669	1	Female	607.5	320	112	47	1557	1557
808	1	Female	401.5	295	105	50	4155	2296
508	2	Female	612.5	320	135	64	16780	14070
769	1	Female (g)	725.4	330	73	32	741	741
852	1	Female (g)	321.3	275	87	42	904	327
629	2	Female (g)	501.3	305	118	55	3222	2921
830	2	Female (g)	637.8	335	58	26	1023	134
490	1	Male	407.3	300	123	58	9069	7293
572	1	Male	400.1	300	129	56	17120	13690
710	1	Male	432.2	297	107	52	23670	10690
730	1	Male	441.8	310	50	26	8320	7072
789	1	Male	364.3	280	115	51	7219	7197
461	2	Male	446.7	310	65	28	11130	8759
530	2	Male	416.1	310	131	61	26970	17930
646	2	Male	409.9	325	133	61	34910	32130
968	2	Male	514.3	320	60	27	10400	9483

total activity areas than did females of either group (gravid or non-reproductive; see Table 2). However, the activity areas calculated at the lower AK levels (i.e. the core areas within each home range) showed less divergence between the sexes (Table 2).

There was no significant difference in body sizes of lizards between the sites, for either snout–vent length or body mass (all $P > 0.30$). Looking at the sexes separately, there were no significant differences in body size (snout–vent length) between the two sites for males ($F_{1,7} = 20.84$, $P = 0.19$) or females ($F_{1,6} = 0.406$, $P = 0.55$). There was no correlation between body size and home-range size within either sex (males $r^2 = 0.024$, d.f. = 1,8, $P = 0.91$; females: $r^2 = 0.203$, d.f. = 1,3, $P = 0.55$; gravid females: $r^2 = 0.0008$, d.f. = 1,3, $P = 0.91$).

The sexes differed significantly in the mean distances that they travelled between successive shelter sites (Site 1: $F_{2,7} = 5.53$, $P = 0.036$; Site 2: $F_{1,4} = 70.74$, $P = 0.001$). At each study site, males travelled further between retreat sites than did females of either group. This mean displacement distance did not differ significantly between the sites for gravid female lizards ($F_{1,2} = 0.134$, $P = 0.75$) but did so for males ($F_{1,6} = 15.49$, $P = 0.007$). Males at Site 2 travelled further between successive shelters than did males at Site 1. The displacement distance averaged 29.6 m for males at Site 1 (s.d. = 7.15), 41.3 m for males at Site 2 (s.d. = 0.59), 17.5 m for non-gravid females (both sites: s.d. = 6.84) and 11.7 m for gravid females (both sites: s.d. = 1.73). The distance travelled between successive shelter sites remained relatively constant for all groups throughout the duration of the study (Fig. 5).

The mean distance travelled per day (i.e. total distance travelled throughout the tracking period divided by the number of tracking days) was significantly greater for males than for either group of females (Site 1: $F_{2,14} = 22.84$, $P < 0.0001$, Fg < F < M; Site 2: $F_{1,4} = 45.45$, $P = 0.003$, Fg < M). Overall mean values for daily distance travelled were 13.2 m for males (s.d. = 3.35), 8.0 m for non-gravid females (s.d. = 2.71) and 4.5 m for gravid females (s.d. = 0.74). The 'random walk' model provided strong evidence that blue-tongued lizards do not move randomly through their habitat: their movement patterns reveal clear avoidance of roads. A paired *t*-test showed that the observed number of road crossings per lizard differed significantly from the number of crossings expected if the lizard did not actively avoid roads (13 of 16 lizards never crossed a road during the study: $t = 8.99$, d.f. = 16, $P < 0.0001$).

Site fidelity

Lizards at both sites exhibited strong site fidelity. Individual lizards returned to the same shelter site (in some cases up to eight times) and each lizard had 2–7 'repeated' shelters. The number of repeated shelters did not differ significantly between the groups at either site (Site 1: $F_{2,7} = 0.61$, $P = 0.57$; Site 2: $F_{1,4} = 0.23$, $P = 0.66$). The average length of stay at a repeated shelter (mean = 5.12 days, s.d. = 2.39), the time until the lizard next visited a repeated shelter (mean = 15.3 days, s.d. = 4.56) and the percentage of total time spent at repeated shelters (range 53–94%) also did not significantly differ between the groups at either site ($P > 0.05$ in all tests). There were no significant sex or reproductive-state differences in the total number of sites visited by each
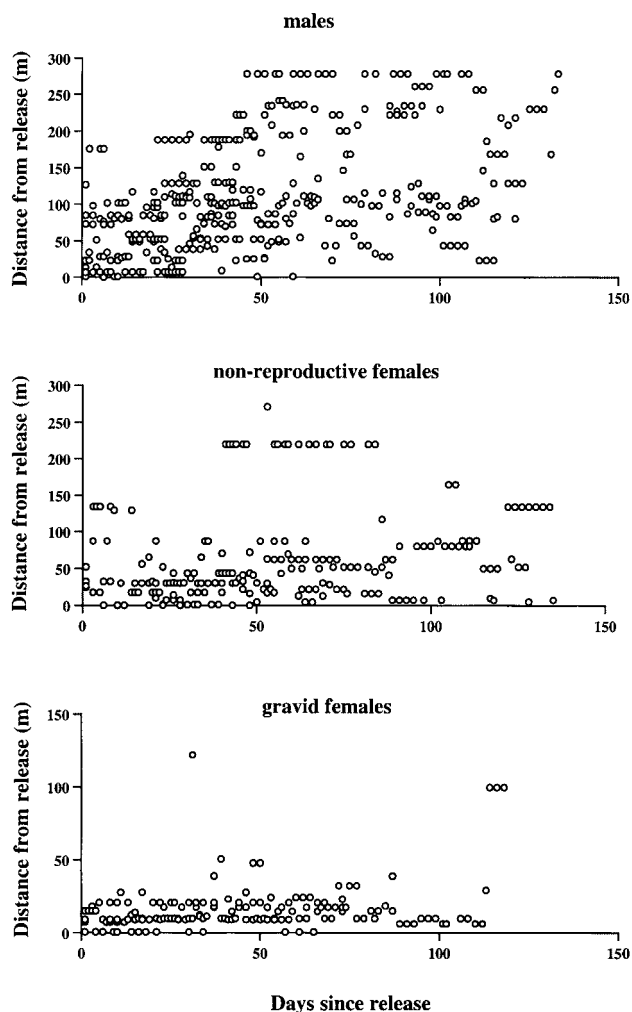
Fig. 1.   The distances that radio-tracked lizards moved from their original release site, as a function of the duration of time since their release.
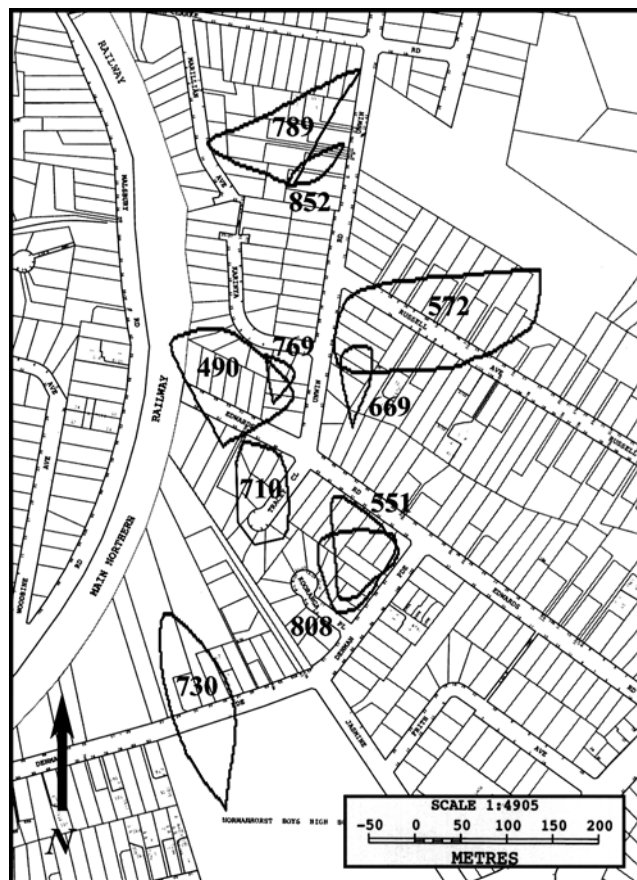

Fig. 2.   Home ranges of blue-tongued lizards at Site 1, Normanhurst (100% Minimum Convex Polygon). Numbers are individual identifiers: male lizards: #789, 572, 490, 710, 730; non-gravid female lizards: #551, 808, 669; gravid female lizards: #852, 769.

animal (Site 1: $F_{2,7} = 2.448$, $P = 0.16$; Site 2: $F_{1,4} = 3.667$, $P = 0.13$). Lizards used 3–17 shelter sites (mean = 11, s.d. = 4.30) over the 60–150-day tracking period. However, the total number of sites visited was significantly correlated with the duration of the tracking period ($r^2 = 0.42$, d.f. = 1,16, $P = 0.005$).

Habitat use

At Site 1 there were no significant differences between males, non-gravid females and gravid females with respect to the proportion of time spent in the garden *versus* the built environment ($F_{2,7} = 1.77$, $P = 0.24$). Similarly, at Site 2 male and gravid lizards did not differ significantly in the proportion of time they spent in the built environment ($F_{1,4} = 0.89$, $P = 0.26$), garden ($F_{1,4} = 4.20$, $P = 0.11$) or forest ($F_{1,4} = 2.57$, $P = 0.18$). We have averaged the proportion of macrohabitat use for all groups at each site for graphical representation (Fig. 6).

There were no significant differences between the groups (at either site) in the proportion of time spent in each microhabitat ($P > 0.05$ in all cases). However, lizards spent more time under hard cover at Site 1 than at Site 2 ($F_{1,15} = 4.74$, $P = 0.045$). As there were no distinct patterns of microhabitat use between the groups, the proportional use was combined at each site for graphical representation (Fig. 7). From this graph it is evident that lizards spent over 75% of their time under hard cover (including crevices, pipes, and drains) or thick vegetation.

The radio-tracked lizards did not use habitat randomly: the proportion of time spent in each macrohabitat was significantly different from the null expectation based on habitat availability. At Site 1, the overall proportions of records of lizards in each macrohabitat did not differ from those expected under the model of random use ($t = 2.15$, d.f. = 9, $P = 0.06$). However, when split by sex, the proportion of time that males were located in gardens was significantly greater than expected by chance, with a corresponding decrease in the proportion of records of this sex from the built environment ($t = 3.73$, d.f. = 4, $P = 0.02$).
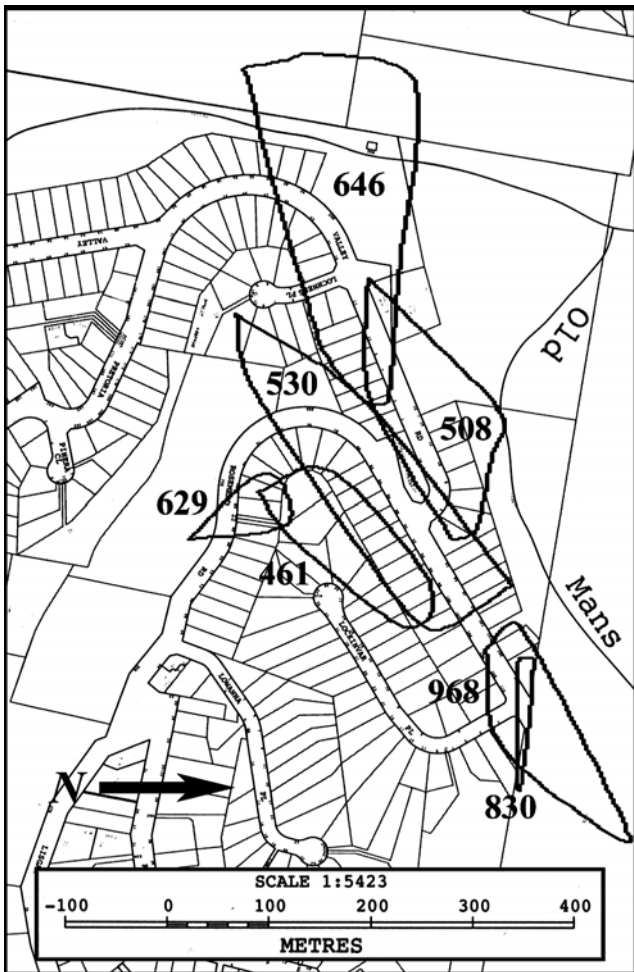
Fig. 3. Home ranges of blue-tongued lizards at Site 2, Hornsby (100% Minimum Convex Polygon). Numbers are individual identifiers: male lizards: #646, 530, 461, 968; non-gravid female lizards: #508; gravid female lizards: #629, 830.

At Site 2, lizards were recorded in the garden significantly more than expected under the null hypothesis of random usage ($t = 4.08$, d.f. = 5, $P = 0.009$) while the number of lizards in the built environment was significantly less than expected ($t = 6.83$, d.f. = 5, $P = 0.001$). There was no significant difference between the expected and observed values in relation to the proportion of time spent in the forest ($t = 0.46$, d.f. = 5, $P = 0.67$). The results from each site reflect a general tendency for lizards to spend most of their time in garden habitats rather than in the built environment or the forest.

Temperatures of free-ranging lizards

Air temperatures at our study sites ranged from 10 to 35°C over the course of the radio-telemetric study, and the mean daily temperature was 24.8°C. Temperatures were more variable inside copper models that were exposed to solar radiation. The 'hot' model attained temperatures above 40°C on a regular basis, while the model placed in the shade displayed a thermal regime similar to ambient shaded temperature.

Fig. 8 displays a typical temperature profile for a lizard's body temperature measured continually throughout the day (based on mean values from 10 animals) and simultaneously measured environmental temperatures. Unsurprisingly, the graph shows that the copper model in an open area (i.e. exposed to direct solar radiation) rapidly exceeded ambient air temperature. Lizard body temperatures fell to ambient levels overnight, but rose during the morning. The lizards attained temperatures of 30–35°C by midday, and maintained these levels until late in the evening. Indeed, lizard temperatures remained high even after sunset, presumably reflecting their high thermal inertia (compared with the copper models) and, perhaps, the selection of warm nocturnal retreats and heat-conserving postures (e.g. Peterson *et al.* 1993).

Table 2. Differences in home-range size and activity areas of the different 'sex' classes of radio-tracked blue-tongued lizards

Results from one-factor ANOVA comparing home ranges (based on Minimum Convex Polygons, MCP) and activity areas (based on Adaptive Kernels, AK) within each site are shown. M = male, F = non-gravid female, Fg = gravid female. Asterisks indicate a significant result ($P < 0.05$); significant *post hoc* interactions are shown. For Site 1, all d.f. = 2,7; for Site 2, all d.f. = 1,4

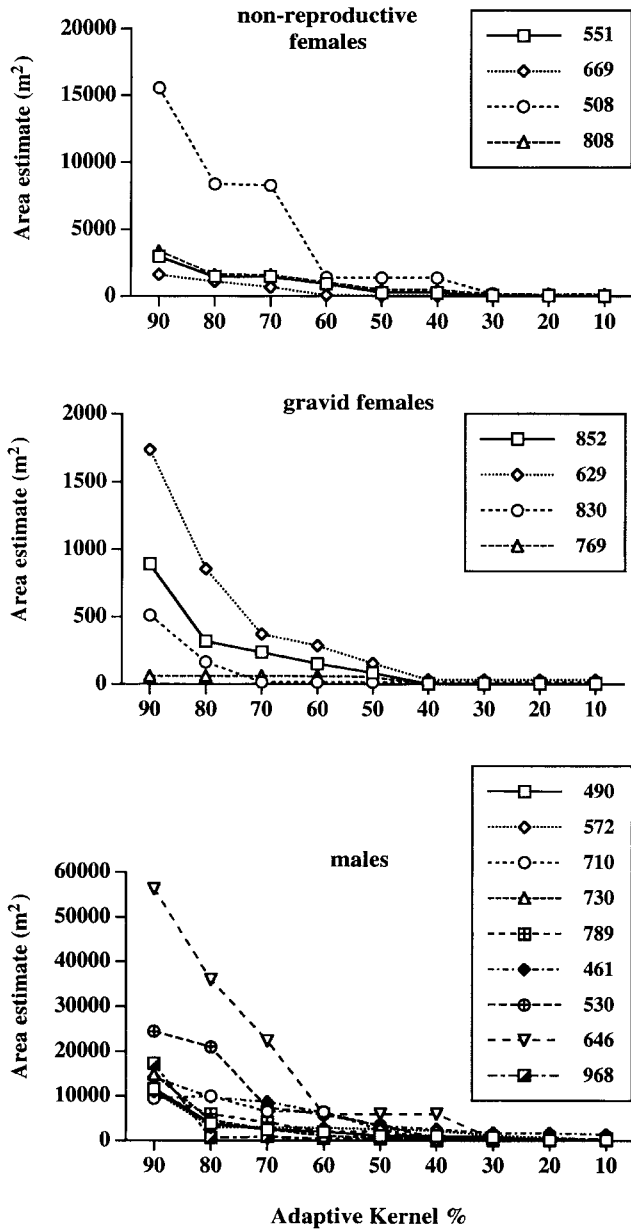| Estimate	Site 1 F	P	Post hoc	Site 2 F	P	Post hoc
MCP 100%	21.94	0.001*	Fg < F < M	15.79	0.017*	Fg < M
MCP 95%	53.55	<0.0001*	Fg < F < M	9.11	0.04	Fg < M
AK 90%	18.97	0.0015*	Fg < F < M	30.08	0.005*	Fg < M
AK 80%	28.13	0.0005*	Fg < F < M	4.62	0.098	No int.
AK 70%	27.97	0.005*	Fg < F < M	9.35	0.038*	Fg < M
AK 60%	9.18	0.01*	Fg/F < M	8.28	0.045*	Fg < M
AK 50%	10.41	0.008*	Fg/F < M	11.84	0.027*	Fg < M
AK 40%	9.96	0.009*	Fg < M/F	19.51	0.012*	Fg < M
AK 30%	9.18	0.0110*	Fg < M/F	8.79	0.041*	Fg < M

Fig. 4. The estimated activity areas for individual lizards using different adaptive kernel percentages. Numbers in legend indicate individual lizards used for radio-tracking.
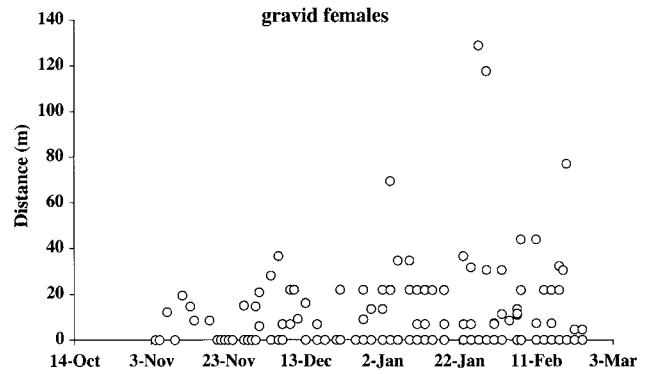

Fig. 5. Monthly distribution of displacement distances (distance between shelter sites) for males, non-reproductive females, and gravid female lizards throughout the telemetry study.
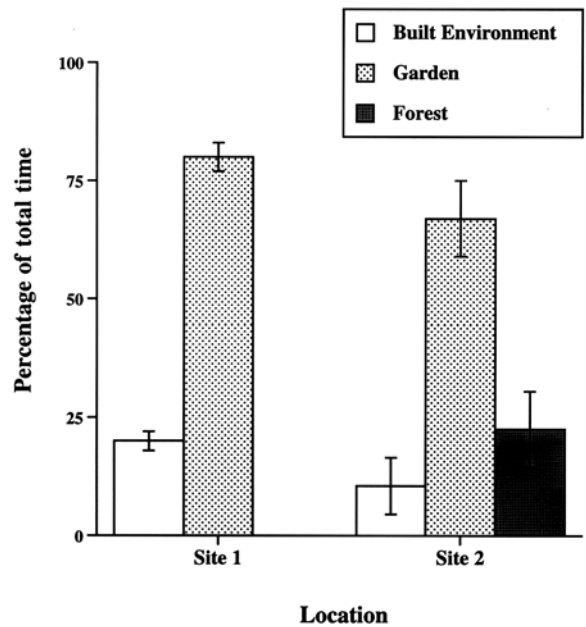

Fig. 6. The average percentage of time a radio-tracked lizard was recorded in each of the macrohabitats: built environment (BE), garden or forest (± standard error).

The maximum body temperature exhibited by a lizard in the field was 38.7°C (11 February 1999, 1725 hours, air temperature 25°C). The minimum (inactive) body temperature recorded was 9.6°C (23 November 1998, 1120 hours, air temperature 21°C), while the minimum recorded body temperature of an active lizard was 14.4°C (28 November 1998, 1000 hours, air temperature 21°C). The average body temperature of active lizards in the field was 31.9°C (s.d. = 2.47, n = 17), and did not differ between the sexes or between gravid and non-gravid female lizards ($F_{2,14}$ = 1.34, P = 0.29).

Not surprisingly, the body temperatures of lizards were influenced by environmental temperatures. Linear regression of lizard body temperature against ambient temperature showed a significant positive relationship for the overall data (when sexes were combined, r^2 = 0.28, d.f. = 1,702, $P < 0.0001$). Analysis of thermal data gathered on clear sunny days (when the lizards presumably were able to attain high temperatures if they so desired) showed significant positive correlations between body temperature and ambient temperatures for all three reproductive categories (males: r^2 = 0.24, d.f. = 1,239, $P < 0.0001$; females: r^2 = 0.10, d.f. = 1,129, P = 0.0001; gravid females: r^2 = 0.056, d.f. = 1,84, P = 0.03). However, the slopes of these regression lines differed significantly among the three
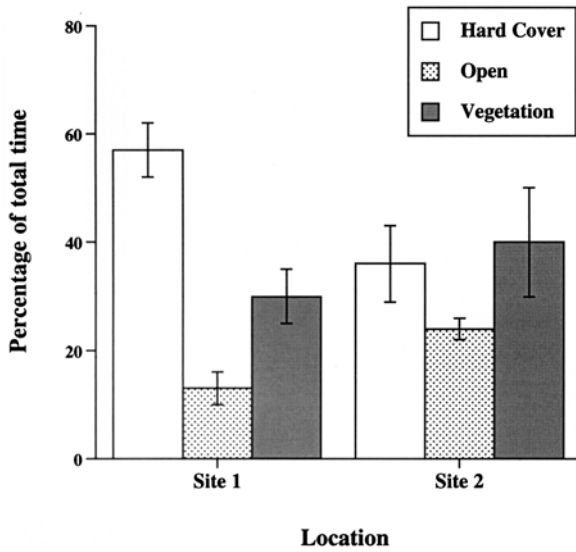
Fig. 7. The average percentage of time that radio-tracked lizards spent in each of the microhabitats: hard cover, open or vegetation (± standard error).
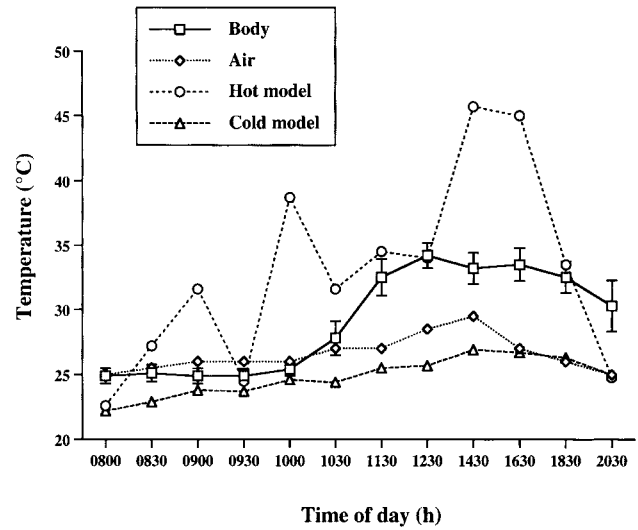

Fig. 8. A typical field temperature profile, as shown by data recorded on 17 February 1999. Body temperature was averaged from 10 individual lizards (± standard error).

groups (heterogeneity of slopes test, with air temperature as the covariate and body temperature as the dependent variable: $F_{2,563} = 6.24$, $P = 0.002$).

This thermal divergence between the sexes is also evident from analyses of data taken at different times of the day. Regressions between lizard body temperature and air temperature showed a significant, positive relationship for males for every two-hour period between 0800 hours and 1600 hours (Table 3). However, there was no significant correlation at any period between the body temperature of gravid female lizards and air temperature (Table 3). Non-reproductive females showed a significant correlation for the first period only (0800–1000 hours; Table 3). These results concur with the overall analyses, and indicate that body temperatures of gravid female lizards were less closely tied (albeit still correlated) to ambient temperatures than was the case for males and non-reproductive females.

Activity

Environmental temperatures were correlated with lizard activity in the field. For testing, we divided air temperatures into four categories (14–18°C, 18–22°C, 22–26°C, and 26–30°C). Chi-square analysis showed that activity levels (relative numbers of records of active *v.* inactive lizards) differed among these thermally defined categories for each of our reproductive categories of lizards (males: $\chi^2 = 62.17$, d.f. = 4, $P < 0.0001$; non-gravid females: $\chi^2 = 24.39$, d.f. = 4, $P < 0.0001$; gravid females: $\chi^2 = 12.71$, d.f. = 4, $P = 0.01$). Because sample sizes were large, we then compared activity levels among these reproductive categories within each of the four ambient air temperature categories. These analyses showed significant differences in levels of activity between the three groups even under the same weather conditions. However, the effects varied among temperature categories. Under very cool conditions (14–18°C), there was no significant difference in activity between these groups ($\chi^2 = 4.69$, d.f. = 2, $P = 0.096$), because almost all lizards were inactive. For the next two categories (18–22°C and 22–26°C) there were significant differences between the reproductive groups ($\chi^2 = 7.28$, d.f. = 2, $P = 0.026$; $\chi^2 = 6.44$, d.f. = 2, $P = 0.04$ respectively). These significant results reflect a tendency for longer periods of activity and more careful thermoregulation in gravid females than in males.

Table 3.   Results from linear regressions of air temperature *versus* lizard body temperature, conducted separately for each two-hour period for the 'sex' classes

Asterisks indicate a significant result ($P < 0.05$)

Time (h)	Males			Non-gravid females			Gravid female		
	r^2	d.f.	P	r^2	d.f.	P	r^2	d.f.	P
0800–1000	0.42	1,37	<0.0001*	0.25	1,27	0.0068*	0.15	1,12	0.19
1000–1200	0.12	1,76	0.0016*	0.05	1,42	0.13	0.13	1,23	0.08
1200–1400	0.15	1,38	0.013*	0.04	1,21	0.35	0.05	1,17	0.36
1400–1600	0.15	1,30	0.033*	0.06	1,19	0.32	0.17	1,11	0.18
1600–1800	0.11	1,27	0.09	0.22	1,12	0.10	0.01	1,14	0.72

Table 4. Differences between the 'sex' classes in the proportion of lizards active in each time period during the day, provided by a one-factor ANOVA

Asterisks indicate a significant result ($P < 0.05$). Significant *post hoc* interactions are also shown. All d.f. = 2,14

Time (h)	F	P	Post hoc
0800–1000	19.353	<0.0001*	Fg >F >M
1000–1200	6.051	0.013*	Fg/F >M
1200–1400	1.977	0.18	
1400–1600	1.053	0.37	
1600–1800	0.351	0.71	

Table 5. Frequency of occurrence of items in stomach contents and scats of blue-tongued lizards

Values refer to the number of stomachs or scats containing a particular item

Food type	Scats ($n = 22$)	Stomach contents ($n = 14$)
Gastropoda (snail)	10	7
Coleoptera	1	4
Blattodea	1	1
Hemiptera	3	1
Dermaptera	2	1
Chiloptera	1	3
Hymenoptera	3	1
Crustacea	–	1
Araneida	–	1
Plant material	11	5
Seeds	4	2
Lizard scales	2	2
Fungi	–	2
Other	2[A]	3[B]

[A]Newspaper, hair.
[B]Chicken bone, dog food.

There was no significant difference in activity between the reproductive groups at air temperatures greater than 26°C ($\chi^2 = 1.48$, d.f. = 2, $P = 0.48$) because most animals were active under these conditions regardless of their sex or reproductive status.

An ANOVA on the proportion of lizards active in each time period found significant differences between the sexes (Table 4). *Post hoc* analyses showed that at the first two periods (0800–1000 and 1000–1200 hours) the proportion of active lizards was lower for males than for either group of females.

Behaviour

A two-factor ANOVA showed significant effects of sex and time of day on the frequency of records of the three main behaviours (basking, not seen and stationary). There was a significant effect of time of day on the proportion of lizards basking at Site 1 ($F_{4,35} = 4.87$, $P = 0.003$) and at Site 2 ($F_{4,20} = 3.34$, $P = 0.03$). In both cases, the earlier timeslots (0800–1200 hours) had a higher proportion of lizards basking. At

Site 2 there was also an effect of sex on behaviour ($F_{2,20} = 0.024$, $P = 0.024$), with gravid females basking more often than males. However, there was no significant interaction between time and sex ($F_{8,20} = 1.53$, $P = 0.21$).

For the proportion of lizards stationary, there was a significant sex effect at Site 1: gravid female lizards were recorded as 'stationary (not in sun)' less often than were the other reproductive group ($F_{2,4} = 3.67$, $P = 0.036$). There were no interactions between sex and time slot with respect to the proportion of lizards stationary at Site 2. At both sites there was a significant effect of time of day on the proportion of lizards 'not seen' when they were located telemetrically (Site 1: $F_{4,35} = 4.03$, $P = 0.008$; Site 2: $F_{4,20} = 4.52$, $P = 0.009$). Data from both sites showed the same trend, whereby an increased proportion of lizards were 'not seen' later in the day.

Mean selected temperatures in the laboratory

The daytime temperature available across the thermal gradient in each cage ranged from 22°C to 40°C, dropping to an even 18°C at night. The mean selected body temperature (MST) for all lizards averaged 33.2°C (s.d. = 1.67, $n = 13$). There was no significant difference between males and females in mean selected body temperatures ($F_{1,11} = 0.32$, $P = 0.59$). However, there were significant differences in heating rates between males and females. Males heated more slowly than females under the same temperature conditions. Males and females exhibited similar body temperatures at 0900 hours, when the lights were turned on. As the range of substrate temperatures in each cage increased, the difference between male and female body temperatures approached significance, and by 1100 hours the two sexes displayed significantly different body temperatures ($F_{1,11} = 6.09$, $P = 0.031$). After this time the two sexes exhibited increasingly similar body temperatures. These thermal levels remained constant (around the MST) until the lights were turned off at 1800 hours.

Feeding habits

Identifiable components from the scats of telemetered animals are listed in Table 5. The dry mass of these scats ranged from 0.58 g to 8.32 g (mean = 2.11 g, s.d. = 1.61, $n = 22$). The composition of scats may not be representative of the diet because of differential digestibility. Nonetheless, some components were common in the samples (e.g. snail shells, insect parts). In most cases, fibrous plant material made up the bulk of the scat.

Data on the stomach contents of dissected lizards (from the Australian Museum collection and from road-kills on site) are also presented in Table 5. The volume of the contents ranged from 1 to 27 mL (mean = 7.18 mL, s.d. = 7.12, $n = 14$). However, this volume was heavily influenced by the amount of digestion that had taken place and does not represent the holding capacity of the stomach. Again, there are a few consistencies throughout these

samples (e.g. snails, various insects and plant material) as well as a few more unusual items (e.g. a feathered chicken wing, freshwater crab, newspaper, hair and dog food). One of our monitored lizards was found dead at a local high school and it contained chicken bones and watermelon seeds in its digestive tract. Clearly, suburban *T. scincoides* are omnivorous and take a wide variety of food items.

Discussion

Our study indicates that blue-tongued lizards move about within discrete 'home ranges'; all of the telemetered animals remained relatively close to their initial capture locations (Fig. 1). A longer period of study (i.e. over several years) might well reveal occasional use of other areas and/or shifts to other areas. However, long-term studies on a closely related species, the shingleback (*Tiliqua rugosa*), show that these lizards stay in restricted home ranges for substantial periods (Satrawaha and Bull 1981; Bull 1987). The size of the home range used by an adult blue-tongued lizard depends upon its sex and reproductive status. The mean home range of males (taken as 95% MCP) was more than twice that of non-gravid females, and up to 30 times larger than that of gravid females (Table 2). While many studies have found differences in home-range size between the sexes (Rose 1982) the home-range size of gravid female blue-tongued lizards is remarkably small for such a large animal. It is reasonable to expect that gravid females will behave differently to non-reproductive animals (male or female) as the physical burden of the developing offspring may slow maternal movements, and embryonic thermal requirements may increase the time devoted to basking (Shine 1980; Beuchat 1986). However, the degree of difference is surprising considering that studies on other closely related large skinks have reported no differences in home-range size between gravid females and non-reproductive animals (Fergusson and Algar 1986) or between males and females (Dubas and Bull 1992; Osterwalder and Klingenboeck 1999).

While the body temperatures and activity patterns of blue-tongued lizards in the field are closely related to environmental temperatures, the thermal profiles of lizards were also affected by their sex and reproductive state. The thermal biology of gravid female blue-tongued lizards was different in many respects from that of male and non-reproductive female lizards. Gravid females were more active at lower temperatures, were active earlier in the day, and their body temperatures were less highly correlated with (and thus, less constrained by) ambient temperatures than was the case for other groups. This result reflects a pattern that has been well documented in many viviparous reptiles (see Shine 1980; Mathies and Andrews 1997). Developmental rates of reptilian embryos depend on temperature (Schwarzkopf and Shine 1991) and embryos develop most rapidly within a narrow temperature range (Beuchat 1986). Temperatures above or below this 'selected'

level may be detrimental to the embryo (Shine and Bull 1979; Mathies and Andrews 1997). Presumably for this reason, gravid females tend to spend longer at 'optimum' temperatures by basking at all available opportunities. The high frequency of basking by gravid female lizards will influence other aspects of their ecology, such as home-range size. For example, the movements of gravid females may be restricted by their attempts to maintain relatively constant body temperatures.

Blue-tongued lizards actively utilise the human-modified habitats of suburbia, rather than remnant patches of less disturbed areas. At the macrohabitat scale, our radio-tracked lizards used the garden habitat to a greater extent than the other categories. This use was not a simple reflection of availability but an apparent active selection of garden habitats. While the low use of the built environment is not surprising (e.g. such areas contain fewer food resources than the garden), it is surprising that lizards at Site 2, who had the choice of being in gardens *versus* the more natural forest habitats, chose the garden. Very few studies have quantified such extensive use of gardens by large native animals or, indeed, the apparent choice of such habitats over more natural ones. In most cases, animals that venture into the urban environment live in patches of remnant forest and only move into the towns to forage (e.g. foxes and badgers: Harris 1981, 1984).

Our data provide some insights into how and why blue-tongued lizards are able to persist in suburbia. It seems there is no single aspect of the lizards' ecology that can explain their continued existence, but rather a combination of factors enable them to live in these 'artificial' habitats.

Movement patterns

At first sight, the large home-range sizes and movement distances of our radio-tracked blue-tongued lizards are surprising. Several studies have shown that animals are particularly vulnerable to predation or automobile-inflicted injuries while moving about (Bonnet *et al.* 1999). Thus, we might expect that low mobility would enhance lizard survival. In terms of conservation, however, the important issue is not simply the overall rate of mortality, but the distribution of that mortality among various components of the population. The most significant group within the population is the gravid females, and these animals are highly sedentary. The greatest movements occur in the most 'expendable' group (males). As long as enough males survive to find reproductive partners, and gravid females are able to produce enough offspring to replace the male lizard population, then this increased 'vulnerability' of males whilst moving may have relatively little impact on population viability. The large movements of male lizards may enhance their numbers of mating partners. Our telemetry observations and results from a series of scent-recognition trials (Koenig 1999) suggest that the extensive movements by males may be driven by in-

teractions with one or more female blue-tongued lizards. Perhaps these interactions serve to increase chances of reproduction in subsequent years and/or allow the male to 'know' where to find reproductive partners. Such an ability might well decrease the male's movements (and hence his vulnerability) during the mating season as he would not need to wander aimlessly in search of females.

The small home ranges of the 'valuable' gravid females may be particularly important. Although gravid females are 'valuable' in the sense that they are critical for population renewal, their modified movement patterns are not derived from this importance to the population. Instead, the small home ranges of gravid female lizards may simply reflect an emphasis on thermoregulation and perhaps a lowered rate of foraging. This behavioural shift has the effect of decreasing their movements, and therefore they become less vulnerable. All gravid females in our study were sedentary throughout gestation. They spent this time in sites with abundant food sources that were well protected from predators and that provided opportunities for undisturbed thermoregulation (e.g. deep inside a compost heap situated in direct sun). This site selection not only served to protect the mothers throughout gestation but also provided a safe haven for newborn lizards. Our telemetry observations suggest that newborn lizards may not disperse from their birth sites for at least three months after birth. If newborn lizards are provided with abundant food in their first season, they are able to grow rapidly (captive neonates can grow from 180 mm to 450 mm total length in one year: Shea 1981). Perhaps the neonates remain in these secure, food-rich environments until their body size increases and they are less vulnerable to predation (especially from domestic cats) (Koenig 1999) before dispersing to other areas.

Site fidelity

The site fidelity and use of 'repeated' sites by our blue-tongued lizards may contribute to the animal's ability to persist in suburbia. Familiarity with refuges in the home range and use of core areas may minimise exposure of the occupant to disease, predators, stress and adverse interactions with other animals (Dubas and Bull 1992). Our telemetered lizards spent over 70% of their time in relatively 'safe' locations (core areas and repeated shelter sites). Thus, they were most vulnerable on the relatively infrequent occasions when they moved between sites.

Avoidance of roads

Movements between core areas were not random, as the lizards consistently avoided roads. Often, lizards moved through the 'corridors' of thick vegetation along fence lines. In combination, these factors reduce the visibility of lizards to potential predators, and thus their vulnerability throughout the movement period.

Activity patterns

An interesting, though entirely coincidental, phenomenon was evident at our study sites: the main activity periods of humans and blue-tongued lizards showed very little overlap. In the suburbs we studied, both men and women typically left home to work during the day. These 'quiet' times corresponded with the peak periods of lizard activity, which were constrained (by thermoregulatory demands) to late morning and early afternoon. While the lack of human activity was true for only five days each week, this provides considerable time for blue-tongued lizards to move about.

Exploitation of 'artificial' habitats

The way in which individuals respond to different habitat types can determine how populations are affected by urban development (Recher *et al.* 1993). Habitat generalists may be more resilient to modifications of the natural environment and able to exploit the newly created habitats in urban areas (Webb and Shine 1997). Blue-tongued lizards are able to utilise highly 'artificial' garden habitats. In fact, they show a preference for these areas over the more natural forest habitat.

Blue-tongued lizards also make use of the abundance of 'artificial' hard-cover shelters in suburbia. Lizards were found in shelters ranging from drainage pipes to backyard sheds and concrete crevices. Most backyards in our study sites include disused and un-kept areas (e.g. overgrown wood piles) that provide an ideal habitat for blue-tongued lizards. Our lizards spent most of their time under cover, where they are less visible and presumably less vulnerable. Even when in the bush, blue-tongued lizards chose hard cover shelters (unlike shinglebacks, *T. rugosa*, which often shelter in or under clumps of vegetation: Bull 1987). While this use of hard cover may be biased by the disturbance made when we were locating the animals, the same disturbance response (retreat to hard-covered shelter) may be useful in escaping predation attempts by domestic pets (dog or cat) and birds.

Exploitation of commensal species as food

Food habits can influence the suitability of an environment for a particular animal species, with dietary specialists limited by the distribution of their 'preferred' food (Pough *et al.* 1998). Previous reports of identifiable digesta in *T. scincoides* include fruit, fungi, snails, grasshoppers, beetles, cockroaches, lepidopteran larvae, millipedes and bird and possum remains (Rose 1974; Webb 1983; Angus 1994). Blue-tongued lizards are generalist omnivores and are able to exploit the abundant food sources in suburban gardens. The introduced snail *Helix aspersa* plays an important role in the diet of suburban blue-tongued lizards. The lizard's ability to exploit commensal prey items in suburban gardens may be one of the reasons why they spend more time in garden habitats (where they have access to increased food resources) than in less highly disturbed areas.

Differential mortality of different components of the population

In order to evaluate the impact of mortality on a population we need to understand patterns associated with the fatalities. For example, what component of the population is most at risk, and at what times of the year do most fatalities occur? Information from a community wildlife rescue database and museum specimens suggests that the group of lizards most vulnerable to mortality are adult male blue-tongued lizards during the mating season in spring (Koenig 1999; Koenig *et al.* unpublished). As noted above, fatalities in this group are likely to have less impact on the viability of the population than if it were the gravid females that were most affected. However, the data also showed another, more worrying, peak of mortalities in summer, this time involving the mortality of newborn lizards. Without significant recruitment of juveniles into the system each year, the population would see a gradual decline as older lizards die. Nonetheless, this may be a very long process as captive lizards can live for more than 30 years (P. Harlow, personal communication).

Life-history traits

Although our study did not provide data on this topic, previous work suggests that *T. scincoides* displays three life-history traits that may facilitate their continued survival in suburban areas. Firstly, these lizards are highly fecund, with litter sizes of up to 18 neonates (Shea 1981, 1992). Secondly, neonates grow rapidly and mature within 2–3 years (Shea 1981). Thirdly, adults are long-lived. In combination, these traits may enable populations of *T. scincoides* to persist despite high mortality rates.

Due to the short duration of our study, it is difficult to evaluate whether the two populations of suburban blue-tongued lizards that we studied are stable, increasing, or decreasing. Because blue-tongued lizards have a long life span, populations of adults may persist for long periods even in the absence of recruitment. However, there is no reason to believe that this is the case for the populations we studied. Over half of the females were gravid and we observed all size-classes in the field. Although only one of our telemetered lizards was killed during the study, data from the Wildlife Information and Rescue Service indicates a massive rate of injury and mortality in blue-tongued lizards (over 2000 'rescues' reported in Sydney over three years: Koenig *et al.* unpublished). Paradoxically, this is an encouraging result because it suggests that the population density of these lizards may be high in suitable areas, and that such areas occur over a considerable proportion of the city and its suburbs. The use of non-territorial, overlapping home ranges in a food-rich environment, means that suburban areas can potentially support large numbers of blue-tongued lizards.

Acknowledgments

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