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Author(s): Sebastian Iglesias, Chris Tracy, Gavin Bedford, and Keith Christian

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Habitat Differences in Body Size and Shape of the Australian Agamid Lizard, *Lophognathus temporalis*

SEBASTIAN IGLESIAS,¹ CHRIS TRACY, GAVIN BEDFORD, AND KEITH CHRISTIAN

Research Institute for Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia

ABSTRACT.—Body size and morphology are important traits that can strongly influence the life history of an organism. One important factor affecting these traits is habitat. Urbanization has resulted in the significant modification of many habitats, and thus, it may be a factor affecting the body size and morphology of species living in the urban environment. In this study, we compared body size and morphology in urban and bush populations of the lizard *Lophognathus temporalis* in and around Darwin, Australia. We made monthly measurements of invertebrate abundance and soil moisture during one year to compare seasonal variation in resource availability between habitats. We also collected all matter excreted by *L. temporalis* during their first four days in captivity as an index of food consumption in the field. We found that male *L. temporalis* were larger than females and that urban *L. temporalis* were larger than bush *L. temporalis*. Males had longer front limbs, hind limbs, and tails than did females; and in urban populations, they also had larger heads. Urban *L. temporalis* had longer front and hind limbs than did bush *L. temporalis*, although head size and tail length were similar for both groups. Resource availability was seasonally more stable in urban habitats than in bush habitats, and urban *L. temporalis* consumed more than bush *L. temporalis* all year round. We conclude that differences in resource abundance between habitats may be an important factor contributing to the morphological differences between urban and bush-dwelling *L. temporalis*.

Habitat is a strong factor influencing the morphology of an organism (Losos et al., 1997; Malhotra and Thorpe, 1997; Sumner et al., 1999; Tracy, 1999; Boback, 2006). In animals with short life spans, changes in morphology can occur over a relatively short period of time (<200 years; Phillips et al., 2006; Carroll et al., 2007; Ghaleb et al., 2007; Witte et al., 2008). *Anolis* lizards, for example, exhibit significant changes in morphology within 10–14 years of first colonizing an island (Losos et al., 1997). Urbanization has led to the dramatic alteration of habitat worldwide. For species that live within the urban environment, this may in turn lead to noticeable changes in the morphology of that species (Prosser et al., 2006). Lizards are common inhabitants of many urban environments (Christian et al., 1999b; Koenig et al., 2001, 2002; Prosser et al., 2006), and some species are able to adapt quickly to changes in habitat (Losos et al., 1997; Sumner et al., 1999). Thus, lizards are ideal study animals for investigating the effects that living in a novel environment may have on morphology over time.

Lophognathus temporalis is a medium-sized agamid lizard (SVL 100 mm; Cogger, 2000) that can be readily found in the urban environment of Darwin, Australia (Blamires and Christian, 1999; Christian et al., 1999b). *Lophognathus temporalis* can also be found in natural bush habitats like seasonally inundated paperbark swamps (*Melaleuca* sp.) and open savannah woodland across Northern Australia (Cogger, 2000). Darwin is located in the wet-dry tropics of Northern Australia and experiences seasonal patterns of annual rainfall, with most of the rain occurring during the wet season (December through March) and little or no rain occurring during the dry season (June through August) (Ridpath, 1985). In natural bush habitats in and around Darwin (including paperbark swamps), water becomes scarce and even absent during the dry season causing many tropical reptiles to reduce their activity during this season (Christian et al., 1996, 1999a; Kennett, 1999). We hypothesized that artificial watering systems may afford urban dwelling *L. temporalis* a seasonally more stable habitat, in terms of food and water availability, than natural bush habitats. Further, we predicted that this difference between urban and bush habitats

may result in differences in size between urban-dwelling *L. temporalis* compared to their natural bush-dwelling counterparts.

To test our predictions, we collected body-size measurements for *L. temporalis*, from urban populations and natural bush populations, over two years in and around Darwin. As part of our study, we also tested for differences in resource availability between urban and bush habitats by sampling invertebrate abundance and monitoring soil moisture content at several sites. We also collected all the feces excreted by *L. temporalis* during their first four days in captivity as an index of feeding levels in urban and bush populations of this lizard.

MATERIALS AND METHODS

Field Sites.—Between December 2005 and February 2007, 305 lizards were captured by hand and by noose using a modified fishing pole, from urban sites and bush sites in and around Darwin, Australia. Sites were considered “bush” if they received no artificial irrigation and were at least 2 km, but typically much further, from the nearest source of artificial irrigation. Sites were considered “urban” if they were situated within Darwin city and received periodic artificial irrigation.

Bush sites included Mickett creek (S12°24'39", E130°56'37"), Howard Springs (S12°27'39", E131°04'26"), Howard River (S12°27'21", E131°03'11") and Gunn Point (S12°26'53", E131°08'23"). Bush sites were characterized by seasonally inundated *Melaleuca* sp. swamps and open savannah woodlands and were dominated by tall grass (*Sorghum* sp.) and Pandanus (*Pandanus spiralis*). Water in the swamps was present only during the wet season (December through March) and during the wet-dry transition (April through May).

Urban sites included the Darwin Royal Botanic Gardens (S12°26'45", E130°50'17"), Fannie Bay Gaol gardens (S12°25'30", E130°50'17"), Charles Darwin University (S12°24'39", E130°56'37"), and a council park in the suburb Coconut Grove (S12°23'44", E130°51'16"). Urban sites were characterized by landscaped gardens with large open areas of lawn (*Digitaria didactyla*, *Paspalum notatum*), numerous palms (*Archontophoenix*

¹Corresponding Author. E-mail: mrsiglesias24@hotmail.com
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alexandrae, *Carpentaria acuminata*), and some trees (*Calophyllum inophyllum*, *Plumeria rubra*).

Study Animals.—Lizards were brought back to the lab within 12 h of capture, and body mass was measured to the nearest 0.01 g with an electronic balance. Snout–vent length (SVL), forelimb length (FLL), hind-limb length (HLL), and tail length (TL) were measured to the nearest 1.0 mm using a ruler. Head width (HW) and head length (HL) were measured to the nearest 0.01 mm using digital calipers. Only sexually mature adults were included in this study. Female lizards with a SVL ≥ 70 mm were considered adults, based on the smallest gravid female we captured. Male lizards that had a SVL ≥ 80 mm were considered adults, based on a previous study (Christian et al., 1999b).

The lizards were held in cloth bags and kept inside constant temperature cabinets at 30°C for four days. All feces produced by the lizards, from the time of capture through their first four days in captivity, were collected and dried at 60°C to constant weight. The dry mass of the feces was measured to the nearest 0.01 g with an electronic balance, to be used as an index of the amount of food consumed by each lizard in the field (Avery, 1971). The use of this index is limited because some prey items may be more completely digested than others; thus, the amount of feces produced underestimates the actual amount of prey consumed. Nonetheless, given that the diet of lizards in urban sites and bush sites is similar (S. Iglesias, pers. obs.) and that our interest lies not in determining actual feeding levels but rather in comparing feeding levels between these groups, we believe the use of this index is justified. The mean mass of feces excreted by animals was calculated for each of the following tropical seasons: dry season (June through August), dry–wet transition (September through November), wet season (December through March), and the wet–dry transition (April through May).

At the conclusion of experiments, lizards were returned to within 5 m of their point of capture and released. Lizards were marked with a number on their ventral surface using a felt-tipped pen before release, to reduce our rates of recapture. The marker lasted for at least one month during the wet season and up to three months during the dry season.

Resource Abundance.—From June 2005 to May 2006, we also measured invertebrate abundance and soil moisture each month at two city sites and two bush sites. *Lophognathus temporalis* is primarily an insectivorous lizard (Cogger, 2000); thus we used invertebrate abundance as an index of food availability for lizards in each habitat. Invertebrate abundance in trees and on the ground was sampled using a converted leaf vacuum that was fitted with a thin nylon mesh bag to collect all the material sucked up by the vacuum during sampling. Each tree sample consisted of 50, 3–5-sec suction bursts, each made within a 2-m wide and 40-m long belt transect of trees and shrubs at each site. Each ground sample consisted of 50, 3–5-sec suction bursts of an arc approximately 1 m in diameter swung 0.1 m above the ground along a 40-m transect at each site. Samples were brought back to the laboratory and frozen no more than 4 h after sampling. The samples were later removed from the freezer, and the invertebrates collected were counted and classified to the level of order. Tree samples and ground samples were combined into a single monthly sample for each site. Invertebrates deemed too small to be considered a prey item for *L. temporalis* (<0.001 g) were not included.

Soil moisture was measured each month in three randomly chosen areas within two urban sites and two bush sites using a

Theta Probe soil moisture sensor (Measurement Engineering Australia, Inc.).

Statistical Analysis.—All size data were log transformed prior to statistical analysis. Log mass, log SVL, and body condition index results of all *L. temporalis* captured were analyzed using a two-factor ANOVA to test for sex and habitat differences. The body condition index was calculated using: Body condition = mass/snout–vent length³ $\times 10^6$ (Romero and Wikelski, 2001). Linear measurements (log HW, log HL, log FLL, log HLL, log TL) of all *L. temporalis* captured were compared using a two-factor ANCOVA with sex and habitat as factors and log SVL as a covariate, to determine differences in body shape.

We tested for differences in maximum size between habitats using log mass and log SVL of the largest 20% of the lizards captured at each site in a nested ANOVA with site and habitat as factors. By using the largest 20% instead of the means of all the lizards captured, problems associated with sampling bias and small sample sizes are minimized, resulting in a more accurate estimate of maximum size (see Stamps and Andrews, 1992; Tracy, 1999).

The mean amount of feces excreted by all lizards captured was log transformed and analyzed using a three-factor ANCOVA with sex, habitat, and season as factors and log lizard mass as the covariate to compare the amount of feces excreted by bush and urban *L. temporalis* when mass effects were accounted for.

Invertebrate abundance was compared using two-factor ANOVA to test for habitat and seasonal differences. Monthly soil moisture in each habitat was compared using repeated-measures ANOVA.

The homogeneity of slopes assumption was tested prior to analysis wherever ANCOVA was used. All tests were performed using the SuperANOVA statistical package (Abacus Concepts, Inc.).

All reported means are arithmetic means \pm standard error, unless otherwise stated. Differences in means were considered statistically significant when $P < 0.05$.

RESULTS

Maximum Body Size.—Both habitat and site were significant factors affecting maximum body mass and SVL in male *L. temporalis* (Table 1). However, despite significant variation among sites, there was no overlap in the maximum body masses attained by male *L. temporalis* from urban sites (60.0–75.5 g) compared to those from bush sites (30.0–49.6 g) and no overlap in the maximum SVL attained by male *L. temporalis* from urban sites (121.0–128.6 mm) compared to those from bush sites (101.3–116.3 mm; Table 2).

Both habitat and site were significant factors of maximum body mass in female *L. temporalis* (Table 1). However, although habitat was a significant factor of maximum SVL in female *L. temporalis*, site was not (Table 1). As was the case with males, despite significant variation among sites, there was no overlap in the maximum body masses attained by female *L. temporalis* from urban sites (23.8–32.6 g) compared to those from bush sites (19.6–19.7 g) (Table 2). Maximum SVL was greater in female *L. temporalis* from urban sites (94.5–103.9 mm) than in female *L. temporalis* from bush sites (84.5–87.5 mm) (Table 2).

In the comparisons that follow, we pooled our results into two groups, urban and bush *L. temporalis*. We used all the body-size data we collected for all the lizards we captured to examine the effects that habitat type has on mean body size and morphology

TABLE 1. Results of nested ANOVAs (site nested within habitat) for the largest 20% of *Lophognathus temporalis* in urban and bush sites. Habitat is a significant factor affecting maximum body size across all groups.

Dependent variable	Sex	Source	df	F	P
Mass	Males	Habitat	1	17.19	0.010
		Site(Habitat)	5	20.46	<0.001
	Females	Habitat	1	10.17	0.033
		Site(Habitat)	4	6.05	0.003
Error			38		
SVL	Males	Habitat	1	7.05	0.045
		Site(Habitat)	5	16.63	<0.001
	Females	Habitat	1	14.34	0.019
		Site(Habitat)	4	2.76	0.058
Error			19		

in these lizards. Although we acknowledge the limitations of this approach (i.e., variability attributable to site is assumed to be minimal), small sample sizes from some of our study sites precluded other types of analysis. However, given that there was a significant effect of habitat on maximum mass and SVL in *L. temporalis*, even when site effects were taken into account (Table 1), and also that there was no overlap in maximum body mass or maximum SVL between urban and bush populations of *L. temporalis* (Table 2), we believe these comparisons to be reasonable and valid.

Mean Body Size, Body Condition, and Morphology.—Mean body mass and mean SVL were significantly greater in urban *L. temporalis* than in bush *L. temporalis* (Table 3). Urban males were on average 1.7 times heavier and 1.1 times longer than bush males, whereas urban females were on average 1.4 times heavier and 1.1 times longer than bush females (Table 4). Sex is also a strong factor affecting size in these lizards. Male *L. temporalis* had significantly greater mass and SVL than did female *L. temporalis* (Table 3). In urban habitats, males were 2.3 times heavier and 1.3 times longer than females, whereas in bush habitats, males were 1.9 times heavier and 1.2 times longer (Table 4).

The body condition index of urban *L. temporalis* was significantly higher than that of bush *L. temporalis* (Table 3). The interaction between habitat and sex was significant. Although urban males had a better body condition index than did urban females ($P < 0.001$), bush males and bush females had similar body condition indexes ($P = 0.108$).

TABLE 2. Maximum body masses and SVL of adult *Lophognathus temporalis* in four urban sites and three bush sites. Values are the means of the largest 20% of lizards captured at each site \pm SE. Despite some variation attributable to site, there was little overlap in maximum body mass and SVL between lizards from urban sites and those from bush sites. Superscript letters represent significant differences between the means for each trait between sites (i.e., down each column).

	Males			Females		
	N	Mass (g)	SVL (mm)	N	Mass (g)	SVL (mm)
Urban sites						
Darwin Botanic Gardens	8	64.79 \pm 1.78 ^a	121.8 \pm 1.6 ^a	5	28.92 \pm 0.99 ^a	101.0 \pm 1.6 ^a
Fannie Bay Gaol	13	75.50 \pm 1.37 ^b	128.6 \pm 1.0 ^b	8	32.64 \pm 0.90 ^b	103.9 \pm 0.9 ^a
Charles Darwin University	6	63.34 \pm 3.53 ^a	121.0 \pm 2.3 ^a	2	26.78 \pm 0.79 ^{a,c}	94.5 \pm 0.5 ^a
Coconut Grove	3	60.03 \pm 2.23 ^a	121.7 \pm 3.8 ^c	2	23.83 \pm 0.03 ^c	96.0 \pm 1.0 ^a
Bush sites						
Mickett Creek	4	49.63 \pm 1.32 ^c	116.3 \pm 1.1 ^c	0		
Gunn Point	8	35.48 \pm 1.32 ^d	105.9 \pm 1.0 ^d	2	19.69 \pm 0.83 ^d	87.5 \pm 2.6 ^b
Howard Springs	3	29.97 \pm 0.61 ^e	101.3 \pm 0.9 ^d	2	19.59 \pm 2.78 ^d	84.5 \pm 3.5 ^b

TABLE 3. Results of two-factor ANOVA (habitat and sex as factors) for each of three analyses: mass, SVL, and body condition index of *Lophognathus temporalis* in urban and bush habitat.

Dependent variable		df	F	P
Mass	Habitat	1	61.81	<0.001
	Sex	1	0.02	<0.001
	Habitat \times sex	1	3.84	0.051
	Error	301		
SVL	Habitat	1	57.28	<0.001
	Sex	1	0.021	<0.001
	Habitat \times sex	1	1.75	0.187
	Error	301		
Body condition index	Habitat	1	22.91	<0.001
	Sex	1	30.17	<0.001
	Habitat \times sex	1	7.36	0.007
	Error	301		

Head size (HL and HW) was similar between urban and bush *L. temporalis* (Table 5). Male *L. temporalis* had longer heads than did female *L. temporalis*, and in urban habitats, males also had wider heads than did females ($P = 0.021$), although in bush habitats HW was similar between the sexes ($P = 0.154$).

Urban *L. temporalis* had longer limbs (FLL and HLL) than did bush *L. temporalis*, and males had longer limbs than did females in both habitats (Table 5). Tail length was similar between urban and bush *L. temporalis*, but males had longer tails than did females in both habitats (Table 5).

Feces Excreted.—During their first four days of captivity, urban *L. temporalis* excreted more feces than did bush *L. temporalis*, even when differences resulting from body mass were taken into account (Table 6). Males and females from both habitats excreted similar amounts of feces; however, season had a significant effect on the amount of feces excreted by all groups (Table 6). The season \times habitat interaction was also significant indicating that the effect of season was not the same in both habitats. Lizards in each habitat excreted the most feces during the wet season. However, urban lizards excreted the least amount of feces during the dry season, whereas bush lizards excreted the least amount of feces earlier, during the wet–dry transition (Fig. 1). Further analysis showed that urban lizards excreted similar amounts of feces during the wet season and the wet–dry transition ($P = 0.164$).

Invertebrate Abundance.—Insect abundance was not significantly affected by season in urban habitats ($F_{(3,20)} = 271.694$, $P = 0.606$). However, insect abundance was significantly affected by

TABLE 4. Means \pm SE and ranges of body size measurements for *Lophognathus temporalis* from urban and bush habitats. Range is given in parentheses. Superscript letters represent significant differences between the means for each trait between each group (i.e., across each row).

	Urban males (N = 151)	Bush males (N = 60)	Urban females (N = 71)	Bush females (N = 23)
Mass (g)	47.60 \pm 1.33 ^a (12.90–84.20)	27.81 \pm 1.17 ^b (11.55–52.80)	20.44 \pm 0.82 ^c (9.6338.65)	14.88 \pm 1.11 ^d (8.33–26.70)
Body condition index	33.27 \pm 0.39 ^a (20.04–47.82)	28.92 \pm 0.42 ^b (23.94–35.64)	28.51 \pm 0.37 ^b (21.72–36.05)	27.30 \pm 0.61 ^b (22.19–33.19)
Snout–vent length (mm)	111.1 \pm 1.1 ^a (80–136)	97.5 \pm 1.1 ^b (82–114)	88.3 \pm 1.1 ^c (72–108)	80.7 \pm 1.7 ^d (70–95)
Head length (mm)	28.49 \pm 0.29 ^a (19.76–36.60)	25.09 \pm 0.43 ^a (17.47–35.56)	21.69 \pm 0.34 ^b (12.39–28.82)	19.99 \pm 0.52 ^b (16.19–26.34)
Head width (mm)	18.26 \pm 0.21 ^a (11.49–23.11)	15.46 \pm 0.25 ^{a,b} (11.32–19.88)	13.42 \pm 0.18 ^b (10.32–17.15)	12.50 \pm 0.31 ^b (9.93–15.43)
Fore limb (mm)	46.3 \pm 0.3 ^a (35–55)	41.5 \pm 0.5 ^b (33–49)	37.5 \pm 0.4 ^c (31–42)	34.5 \pm 0.6 ^d (30–40)
Hind limb (mm)	91.4 \pm 0.5 ^a (74–105)	82.4 \pm 0.8 ^b (67–95)	75.0 \pm 0.7 ^c (63–84)	69.3 \pm 1.2 ^d (60–79)
Tail length* (mm)	317.4 \pm 2.6 ^a (227–380)	287.0 \pm 3.8 ^a (223–360)	253.2 \pm 3.0 ^b (204–299)	237.8 \pm 5.4 ^b (198–277)

*Lizards with damaged or regenerated tails were excluded. The actual number of lizards used in tail measurement were as follows: N = 137 for urban males, N = 60 for bush males, N = 63 for urban females, and N = 20 for bush females.

season in bush habitats ($F_{(3,20)} = 4.766$, $P = 0.011$), with insect abundance being highest during the wet season and lowest during the dry season.

Within each season, insect abundance was significantly greater in urban habitat compared to bush habitat (dry: $F_{(1,10)} = 6.18$, $P = 0.032$; dry–wet transition: $F_{(1,10)} = 5.82$, $P = 0.037$; wet: $F_{(1,14)} = 5.14$, $P = 0.040$; wet–dry transition: $F_{(1,6)} = 8.56$, $P = 0.026$).

Soil Moisture.—A two-factor ANOVA of soil moisture, with habitat and season as factors, showed that there was a significant effect of habitat ($F_{(1,136)} = 78.16$, $P < 0.001$) and season on water availability ($F_{(3,136)} = 12.50$, $P < 0.001$). The habitat \times season interaction was also significant ($F_{(3,136)} = 5.61$, $P = 0.001$). Although soil moisture did not vary with season in urban habitat, soil moisture did vary significantly with season in the bush habitat. In bush habitat, soil moisture was highest during the wet–dry transition and lowest during the dry season (Fig. 2).

DISCUSSION

Lophognathus temporalis in urban sites were larger than those in bush sites. Urban males were, on average, 71.2% heavier and

TABLE 5. Results of two-factor ANCOVA (habitat and sex as factors) of log-transformed linear body measurements of *Lophognathus temporalis*, with log SVL as a covariate.

Dependent variable	Source	df	F	P
Log HL	Habitat	1	<0.01	0.994
	Sex	1	9.63	0.002
	Habitat \times sex	1	0.25	0.621
Log HW	Habitat	1	3.58	0.059
	Sex	1	<0.01	0.858
	Habitat \times sex	1	8.53	0.004
Log FLL	Habitat	1	8.39	0.004
	Sex	1	37.03	<0.001
	Habitat \times sex	1	0.01	0.916
Log HLL	Habitat	1	12.41	<0.001
	Sex	1	48.14	<0.001
	Habitat \times sex	1	<0.01	0.952
Log TL	Habitat	1	0.17	0.683
	Sex	1	17.07	<0.001
	Habitat \times sex	1	0.05	0.817

13.9% longer than were bush males, and urban females were on average 37.4% heavier and 9.5% longer than were bush females (Table 4). Body condition was similar between urban and bush females; however, body condition in urban males was better than in bush males. *Lophognathus temporalis* from urban sites have longer FLL and HLL than their bush counterparts do relative to their SVL. HW, HL, and TL however are not significantly different, suggesting that with the exception of limb length, body shape is similar between urban and bush lizards. Food is directly linked to growth, and for most lizards, limited food availability corresponds to a reduction in growth (Griffiths and Christian, 1996; Zúñiga-Vega et al., 2005). Insect abundance in bush habitat was affected by season, with the greatest abundance occurring during the wet season and the least during the dry season. This result is consistent with those of a previous study of invertebrate abundance conducted in Darwin (Griffiths and Christian, 1996) and with other studies conducted in similar tropical systems (Denlinger, 1980; Woinarski and Tidemann, 1991). Invertebrate abundance was greater in urban habitat compared to bush habitat during each season. Also, although invertebrate abundance was affected by season in bush habitat, invertebrate abundance was seasonally stable in urban habitat. Our results suggest that food availability may play a role in the observed size differences between urban and bush populations of *L. temporalis*.

TABLE 6. Results of three-factor ANCOVA (habitat, sex, and season as factors) of the amount of feces excreted by *Lophognathus temporalis* during their first four days of captivity, with log body mass as a covariate.

Dependent variable	Source	df	F	P	
Log feces	Habitat	1	8.05	0.005	
	Season	3	4.57	0.004	
	Sex	1	1.95	0.164	
	Season \times habitat	3	4.14	0.007	
	Habitat \times sex	1	1.467	0.227	
	Sex \times season	3	0.33	0.802	
	Sex \times habitat \times season	1	0.17	0.683	
	Error		250		

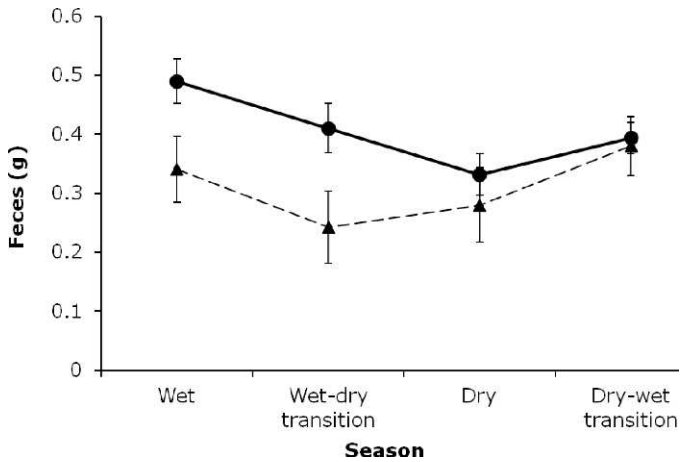


FIG. 1. Least-square means of feces excreted (dry weight, mass corrected using ANCOVA) by *Lophognathus temporalis* ± SE, during four tropical seasons. Solid lines represent all lizards from urban habitat and dashed lines represent all lizards from bush habitat.

When mass effects were taken into account, the amount of feces excreted by urban *L. temporalis* was greater than that excreted by bush *L. temporalis* (Table 6). This result further supports our hypothesis that food availability may be an important factor contributing to the size differences between urban and bush populations of *L. temporalis*.

Other factors contributing to the observed size differences between urban and bush populations of *L. temporalis* may be related to seasonal water availability. The natural bush environment in the tropics undergoes dramatic changes in water availability during the wet and dry seasons (Griffiths and

Christian, 1996; Christian et al., 1999a,b). By comparison, the urban environment with its year-round access to artificial watering systems is less variable in terms of seasonal fluctuations in water availability. This was reflected in our soil moisture results, which showed that soil moisture in urban habitat did not vary seasonally and was consistently higher than in bush habitat except during the wet-dry transition when soil moisture was similar in both habitats. It should be noted that, in the year in which we conducted our soil moisture measurements, the rainy season occurred late, and heavy rains fell during March and April (i.e., between the end of the wet season and the start of the wet-dry transition). In most other years, soil moisture in city and bush sites is likely to be most similar during the wet season (December through March) only.

We encountered *L. temporalis* with much greater frequency in urban sites than in bush sites, and this is reflected in the number of animals caught in each habitat (Table 4). Although we did not measure capture effort directly, we do know that we typically spent much less time collecting equal or greater numbers of *L. temporalis* in urban sites (30 min to 1 h) than in bush sites (2–4 h). This difference suggests that urban populations of this lizard may be denser than bush populations. Larger body size is sometimes favored in high density populations because of the enhanced competitive ability afforded by large body size (Calsbeek and Smith, 2007). This trend is especially pronounced when resources (food and water) are not a limiting factor. Thus, higher population densities in urban *L. temporalis* may also be a factor contributing to their larger body size compared to those from bush populations.

It is interesting to note that urban *L. temporalis* had longer limbs than did bush *L. temporalis*. Lizards from open terrestrial habitats tend to have longer limbs than do those from more densely vegetated habitats (Melville and Swain, 2000; Herrel et

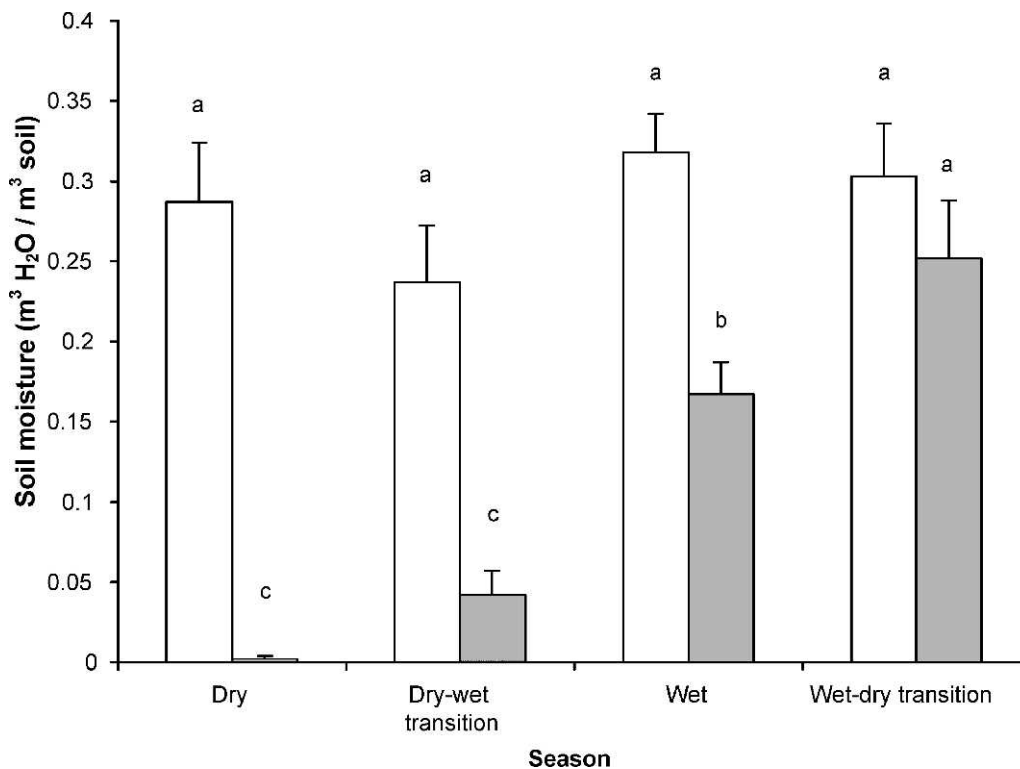


FIG. 2. Seasonal soil moisture in urban (unshaded) and bush habitats (shaded). Values are means ± SE, and units of soil moisture are m³ of H₂O per m³ of soil. Equivalent lowercase letters indicate no significant difference at the *P* < 0.05 level using ANOVA and Fisher's LSD posthoc tests.

al., 2002; Schulte et al., 2004). This difference may represent adaptive plasticity, because locomotor ability benefits from long legs in open terrestrial habitats and from short limbs in dense vegetation (Melville and Swain, 2000). Urban sites in this study were more open and less densely vegetated than bush sites; thus, habitat differences in vegetation may help explain the difference in limb lengths observed between urban and bush *L. temporalis*.

Darwin is a relatively young city, having been founded in 1869. Assuming that (a) the modern urban habitat in Darwin is approximately 100 years old (although in reality it is probably less, with respect to widespread irrigation) and (b) that *L. temporalis* becomes sexually mature after one year (K. A. Christian, pers. obs.) then we can also assume that any changes observed in urban dwelling *L. temporalis* have occurred over 100 generations or fewer. Thus, urban *L. temporalis* may represent another example of an animal rapidly evolving (Phillips et al., 2006; Carroll et al., 2007; Witte et al., 2008). Further work on this species, such as common garden and translocation experiments, are encouraged and will go a long way toward helping us to determine whether the differences in size between urban and bush populations of *L. temporalis* have their origins in genetics or phenotypic plasticity.

In summary, *L. temporalis* is a sexually dimorphic lizard that can be found in both urban and natural bush habitats. Urban populations of this lizard have greater mass, longer SVL, and longer FLL and HLL than do bush populations. Urban males also have better body condition than do bush males, although females from both habitats have similar body condition. Habitat effects on morphology are most pronounced and readily observed in males. The reason behind the differences in size we observed between urban and bush populations of this lizard remain unclear; yet the answer may be related to differences in food and water availability, which were more abundant and seasonally stable in urban habitats compared to bush habitats. High population densities of this lizard in urban sites may also be a contributing factor to the observed size differences; however, these explanations, which are not an exhaustive list, remain as hypotheses to be tested in additional studies.

Urbanization of the natural environment impacts on native wildlife (Dickman, 1987; Dickman and Doncaster, 1987; Fearn et al., 2001; Shine and Koenig, 2001; Prosser et al., 2006). However, the impact is not always negative, and some animals actually benefit from living in the modified urban environment (Fearn et al., 2001). Given that *L. temporalis* is larger and possibly more numerous in urban populations than in bush populations, then *L. temporalis* can be considered yet another example of a successful invader of the urban environment.

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