

The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity–exploratory behavioural syndrome

H. Moule¹, M. Michelangeli¹, M. B. Thompson² & D. G. Chapple¹

¹ School of Biological Sciences, Monash University, Clayton, Vic., Australia

² School of Biological Sciences, University of Sydney, Sydney, NSW, Australia

Keywords

activity; basking site selection; behavioural syndromes; exploratory behaviour; lizard; urbanization.

Correspondence

David G. Chapple, School of Biological Sciences, Monash University, Clayton Victoria 3800, Australia. Tel:

+61 3 9905 3015

Email: David.Chapple@monash.edu

Editor: Mark-Oliver Rödel

Received 20 April 2015; revised 16 July 2015; accepted 20 July 2015

doi:10.1111/jzo.12288

Abstract

Urbanization is rapidly converting natural landscapes into habitats dominated by man-made structures. Urbanized areas possess a range of novel stressors such as increased human disturbance, different suites of predators, new food types and altered habitats and complexity. Species may need to adjust aspects of their behaviour to cope with these novel stressors and persist in areas following urbanization. Sydney, Australia's largest city, has undergone rapid population and geographic expansion over two centuries, but remains a mosaic of natural and heavily urbanized habitats. We adopted a behavioural syndrome approach to investigate whether urbanization has influenced the behaviour of the delicate skink *Lampropholis delicata* in the Sydney region. Lizards from one of the urban populations were more active, and more likely to forage for food, than individuals from the other three populations, but there was no difference in activity or foraging behaviour between urban and non-urban populations overall. Skinks from urban and non-urban habitats did not differ in their exploratory or basking behaviours. Activity, exploratory behaviour and foraging behaviour were all repeatable, and a behavioural syndrome linking high activity with increased exploration was evident. Our study documents the impact of urbanization on an understudied taxonomic group in the Southern Hemisphere, where urbanization has occurred relatively recently, and suggests that the influence on behaviour might be related to the degree of urbanization that has occurred.

Introduction

Human-induced rapid environmental change (HIREC) is having drastic effects on biodiversity (Sih, 2013; Sol *et al.*, 2014). Urbanization, the modification of natural landscapes to accommodate high densities of buildings and humans, is a permanent form of HIREC that can have profound impacts on animals (McKinney, 2006; Lowry, Lill & Wong, 2012; Sol, Lapiedra & González-Lagos, 2013; Sol *et al.*, 2014). Species that fail to adjust to urbanization (e.g. increased human disturbance, presence of artificial structures and increased traffic and introduction of novel predators and foods) may become locally extinct around cities (Atwell *et al.*, 2012; Sol *et al.*, 2013). Such 'urbanophobes' are often native animals that have specialist lifestyles reliant on native resources (McKinney, 2006). Those that thrive in cities (i.e. 'urbanophiles') tend to be cosmopolitan species that have generalist lifestyles suited to scavenging in cities and utilizing human resources (McKinney, 2006).

Morphology and physiology play a role in the adaption of animals to urban regions (Atwell *et al.*, 2012; Helm *et al.*, 2013), but behavioural changes are the easiest way to adjust to

urbanization (Lowry *et al.*, 2012; Sol *et al.*, 2013). Dark-eyed juncos *Junco hyemalis* take more risks in human-occupied regions than individuals from natural regions (Atwell *et al.*, 2012). Additionally, animals can adjust their foraging behaviour. Coyotes *Canis latrans* have modified their home range to accommodate the increased food created by humans, and forage later at night when human disturbance is reduced (Grinder & Krausman, 2001).

A behavioural syndrome approach to understanding the impacts of urbanization on behaviour allows (1) examination of variation among individuals (Bell, 2007), which helps identify mechanisms through which populations adapt to urbanization; (2) a focus on behaviours that are repeatable over time (Bell, 2007); and (3) consideration of suites of correlated traits, rather than simply individual behaviours (Sih *et al.*, 2004, 2012). This approach can enhance our understanding of the behavioural response to urbanization. For example, house sparrows *Passer domesticus* exhibit correlations between boldness and aggression (Evans, Boudreau & Hyman, 2010) and object neophobia, boldness and activity (Bókony *et al.*, 2012). However, behavioural studies of the impacts of urbanization are biased towards birds and mammals, and the Northern

Hemisphere where urbanization is an older and more ubiquitous phenomenon (Sol *et al.*, 2013). We use a behavioural syndrome approach to investigate the behavioural consequences of urbanization in an underrepresented taxon (a reptile; the delicate skink *Lampropholis delicata*) from a recently urbanized region in the Southern Hemisphere (Sydney, Australia).

Sydney is Australia's largest city (population 4.5 million), and has undergone urbanization over the last two centuries (Shea, 2010). Yet, urbanization in Sydney is relatively young compared with European cities (Duh *et al.*, 2008). Sydney is a complex mosaic of land, with heavily and continuously urbanized areas, patches of natural landscape and semi-urbanized areas all present within the same region (Shea, 2010), enabling comparison of urban and non-urban populations within the same geographic area. The delicate skink [35–50 mm adult snout-vent length (SVL)] occurs in high densities in all habitat types throughout the Sydney region (Shea, 2010; Wilson & Swan, 2013). Delicate skink populations in the Sydney region fall within the same genetic lineage (Chapple *et al.*, 2011a), allowing for control of phylogenetic history. Importantly, the delicate skink shows inter-individual variation in behaviour (Chapple, Simmonds & Wong, 2011b; Cromie & Chapple, 2012), meaning that behavioural syndromes may be present in the species.

We conducted five behavioural assays to compare three of Reale's behavioural axes (activity, exploration, boldness) among two urban and two non-urban populations. These three axes were selected to investigate some of the common behavioural changes exhibited by wildlife in urban areas as summarized by Sol *et al.* (2013). We predicted that urban skinks would be more active due to release from natural predators, show increased exploratory behaviour in order to take advantage of novel resources and be bolder in their basking site choices than skinks from non-urban populations due to pre-disposal of bold animals to inhabit urban environments (Lowry *et al.*, 2012; Sih *et al.*, 2012). We also predicted that there would be correlations between several key behavioural traits. Such behavioural syndromes have been seen in the rockpool prawn *Palaemon elegans*, where activity, exploration and boldness were correlated (Chapman, Hegg & Ljungberg, 2013).

Materials and methods

Animal collection

Delicate skinks were collected from four locations within the greater Sydney region during October 2013. Lizards were collected from two urban locations (UP1 and UP2) and two areas of natural habitat (NP1 and NP2; Supporting Information Table S1). Skinks were hand captured using unbiased active search methods (Michelangeli, Wong & Chapple, 2015). Only adult males (SVL >35 mm) with long tails (TL > SVL) were studied because tail loss (Downes & Shine, 2001; Cromie & Chapple, 2012) and gravidity (Shine, 2003) can influence behaviour in *Lampropholis* skinks. Skinks from urban regions

were larger than skinks from non-urban populations (analysis of variance: $F_{3,56} = 5.614$, $P = 0.0002$; Supporting Information Table S1).

Lizards were transported to Monash University, uniquely marked using Visual Implant Elastomer (Northwest Marine Technology, Shaw Island, WA, USA) and housed in a temperature-controlled room ($\sim 22^{\circ}\text{C}$), lit from 07:00 AM to 09:00 PM daily. Groups of five lizards, mimicking natural groups sizes (Downes & Hoefer, 2004), from the same population were housed in large plastic containers ($300 \times 230 \times 370$ mm) as outlined in Cromie & Chapple (2012).

Behavioural experiments

We conducted five behavioural assays (trials) to examine skink activity, exploration and basking behaviour. To minimize the risk of carry-over effects confounding the detection of a behavioural syndrome, skinks were placed through the trials in a fixed order, outlined below, where trials that would have the greatest impact upon behaviour were at the end of the experimental schedule (Bell, 2012). Skinks completed each trial twice, with at least 3 days between trials, to assess repeatability of behaviour (Bell, Hankison & Laskowski, 2009).

Trials were conducted in opaque-walled experimental arenas ($550 \times 320 \times 240$ mm), in a temperature-controlled room (22°C). Skinks were allowed to acclimatize to the arena under transparent containers for 10 min prior to the start of each trial. The transparent containers were removed at the commencement of the trial and the skink was allowed to move freely for the duration of the trial (45 min). The trials were recorded using JVC Everio GZ-E100 video cameras (JVC, Yokohama, Japan). All equipment was thoroughly washed between trials to prevent scent contamination among trials.

Are activity and exploratory behaviours different between urban and non-urban populations?

Non-directed activity

Skinks were allowed to roam freely in the arena marked with 20 equal grid squares, with no obstacles, and the number of transitions between grid squares was used as a measure of activity. This assay measured activity as the lizard acclimated to the arena prior to the trial and there were no novel areas for the animal to explore (Réale *et al.*, 2007; Carter *et al.*, 2013). This trial was conducted as per Chapple *et al.* (2011b).

Exploratory behaviour

Skinks were presented with a trapezium-shaped barrier that divided the arena in two, around which the skink could crawl to reach the novel compartment. Whether skinks reached the far compartment, and the time taken to do so, was recorded as the measure of exploration (Réale *et al.*, 2007; Carter *et al.*, 2013).

Is foraging activity different between urban and non-urban populations?

Skinks were presented with four different food choices (*c.* 0.2 g), each in a Petri dish in different corners of the arena. Both natural (a live mealworm and blackberry segments) and urban food choices (mashed banana and cat food) were provided. Time spent in each food zone and whether the food was tasted was recorded. Tasting was defined as active consumption of the food by the lizard and foraging behaviour was encouraged by a 48-h starvation period before trials.

Is basking site use different between urban and non-urban populations?

The arenas were divided into three areas: a central no-choice zone and two basking sites at each end of the arena. In the first trial the basking site choices were urban (weed mat found in urban areas) or rural sites (shredded paper; after Howard, Williamson & Mather, 2003), surrounding a terracotta tile placed under a basking light. A second trial assessed boldness using an open terracotta tile, and a terracotta tile half covered by a shelter site under basking lights. We examined whether skinks spent more time basking in a risky zone (the open site) or a safe zone (the sheltered site). The time spent in each zone, the number of transitions between zones and the overall zone preferences were determined during video playback.

Statistical analyses

All data were analysed using the statistical program R (R Development Core Team, 2012). Statistical significance was assigned at $\alpha = 0.05$.

We used generalized linear mixed effects models with appropriate error distributions (Bolker *et al.*, 2009) to (1) determine if there were any behavioural differences between skinks from urban and non-urban regions ('lme4' package: Bates, Maechler & Bolker, 2012) and (2) if behaviour differed between the four populations ('MCMCglmm' package: Hadfield, 2010). We used Markov chain Monte Carlo models to assess differences between populations to more appropriately deal with uncertainty over both the fixed and random effect parameters. We used non-informative priors (mean = 0; variance = 1000), after we determined that models with more informative priors had no effect on the model outcome. Posterior distributions were used to confirm homogeneous variances (i.e. no overdispersion; Gelman and Hill 2007). Models were run for 13 000 iterations with a burn in of 3000 iterations and mixing of chains was assessed (Gelman and Hill 2007).

Consistency of behaviour across time was assessed using non-parametric Kendall's tau bivariate correlations. We also calculated adjusted repeatability values by extracting the variance components (between individual variance and residual variance; see Dingemanse & Dochermann, 2012). Significance of the random effect (i.e. between-individual variation) was assessed using likelihood ratio tests by comparing models with and without the random factor (i.e. SkinkID; Bolker *et al.*, 2009). Any experiments that did not demonstrate test-

retest consistency were excluded from further analysis for behavioural syndromes, as they were not repeatable (Bell, 2007; Bell *et al.*, 2009).

Principal component analysis (PCA) was conducted to assess correlations between behavioural scores of individuals across repeats, to determine the presence of a behavioural syndrome within the delicate skink, for the full dataset and for individual populations (McEvoy *et al.*, 2015). Behavioural syndromes can be defined in this way by identifying principal components that correlate different factors, or behaviours (Carter *et al.*, 2013).

Results

Are activity and exploratory behaviours different between urban and non-urban populations?

Non-directed activity

Activity was repeatable between trials ($r = 0.210$, $P = 0.019$), and there was between-individual variation in activity ($\chi^2 = 4.90$, $P = 0.027$). There was no difference in activity between urban and non-urban regions ($z = 0.7$, $P = 0.46$); however, individuals from Padstow (UP2) were more active than the other three populations (Table 1; Fig. 1a).

Exploratory behaviour

Exploratory behaviour was repeatable between trials ($r = 0.232$, $P = 0.01$), and individuals varied in their time to complete the obstacle ($\chi^2 = 1.90$, $P < 0.01$). Exploratory behaviour did not vary between urban and non-urban regions ($z = 1.50$, $P = 0.13$; Fig. 1b) or populations (Table 1; Fig. 1b).

Is foraging activity different between urban and non-urban populations?

Foraging activity, as a proportion of time spent tasting foods, was repeatable ($r = 0.50$, $P < 0.01$), and varied between individuals ($\chi^2 = 3.23$, $P < 0.01$). Urban and non-urban skinks did not differ in how long they tasted food ($z = 1.57$, $P = 0.117$; Fig. 2a). However, skinks from UP2 were more likely to taste food (five of 11 individuals tasted food vs. only four individuals from the other sites combined tasted food; Table 1). Skinks showed no preference for or avoidance of the urban food zone between regions ($z = 1.54$, $P = 0.12$) or populations ($z = 0.90$, $P = 0.37$; Fig. 2b).

Is basking site use different between urban and non-urban populations?

Selection of the urban or rural basking site was not repeatable ($r = -0.11$, $P = 0.27$). Boldness in basking site choice was also not repeatable ($r = 0.09$, $P = 0.31$) and did not vary between individuals ($\chi^2 = 1.06$, $P = 0.41$). Urban and non-urban skinks

Table 1 Population differences in activity (number of transitions), exploratory behaviour (time taken to pass obstacle), foraging activity (number of times food was tasted) and boldness (time spent in open area) analysed using generalized linear mixed effects models (GLMMs)

	Coef	CIs (2.5%, 97.5%)	<i>P</i>	BI Var	Resid Var	Adj repeat
Activity	–	–	–	0.17	0.40	0.30
Intercept (NP1-Lane Cove)	5.02	(1.60, 8.23)	<0.01	–	–	–
NP2 – Kuring-gai	0.09	(–0.32, 0.53)	0.67	–	–	–
UP1 – St. Stephens	0.07	(–0.34, 0.51)	0.75	–	–	–
UP2 – Padstow	0.56	(0.03, 1.05)	0.03	–	–	–
SVL	–0.03	(–0.12, 0.06)	0.49	–	–	–
Exploratory behaviour	–	–	–	1.30	2.21	0.37
Intercept (NP1-Lane Cove)	2.93	(–6.97, 11.84)	0.57	–	–	–
NP2 – Kuring-gai	–1.05	(–2.35, 0.32)	0.12	–	–	–
UP1 – St. Stephens	0.29	(–0.79, 1.70)	0.63	–	–	–
UP2 – Padstow	–0.25	(–1.77, 1.31)	0.75	–	–	–
SVL	–0.01	(–0.25, 0.26)	0.93	–	–	–
Foraging activity	–	–	–	0.54	0.50	0.52
Intercept (NP1-Lane Cove)	–2.48	(–3.78, –1.19)	<0.01	–	–	–
NP2 – Kuring-gai ^a	–16.82	(–20.32, 20.45)	0.99	–	–	–
UP1 – St. Stephens	0.34	(–1.15, 1.84)	0.65	–	–	–
UP2 – Padstow	1.34	(–0.27, 2.69)	0.05	–	–	–
SVL	–0.56	(–2.34, 1.02)	0.32	–	–	–
Boldness	–	–	–	0.02	0.64	0.03
Intercept (NP1-Lane Cove)	3.15	(2.66, 3.62)	<0.01	–	–	–
NP2 – Kuring-gai	0.49	(–0.24, 1.22)	0.18	–	–	–
UP1 – St. Stephens	–0.02	(–0.71, 0.67)	0.96	–	–	–
UP2 – Padstow	0.07	(–0.71, 0.85)	0.86	–	–	–
SVL	0.21	(–0.54, 0.92)	0.43	–	–	–

Population and SVL were fixed factors and skink ID was included as a random factor. Significant results are indicated in bold.

^aNo individuals from this population tasted food.

BI Var, between individual variation; Cis, 95% credibility intervals; Coef, coefficients; *P*, *P*-values; Resid Var, residual variance (within-individual variance); SVL, snout-vent length.

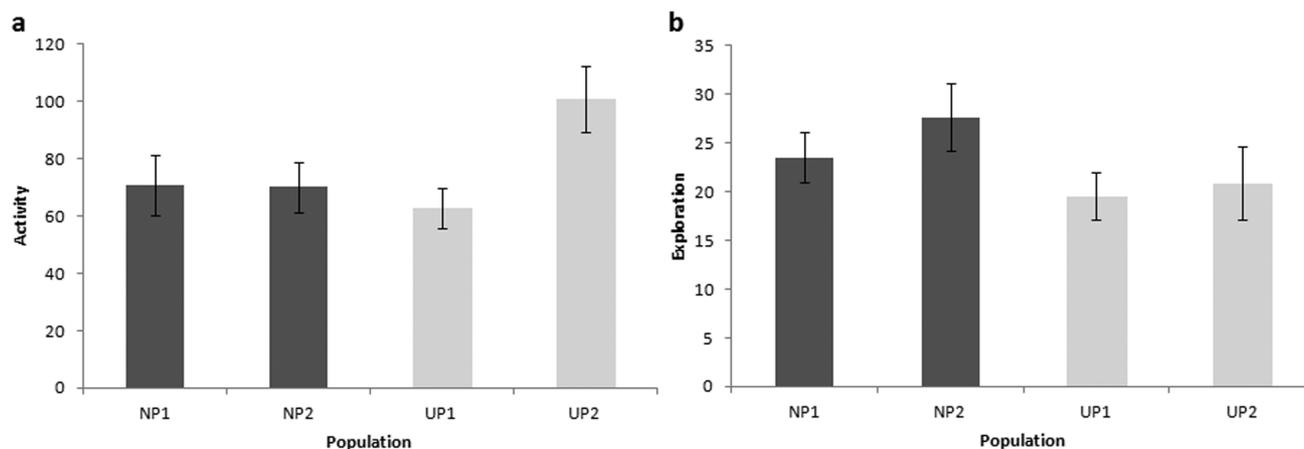


Figure 1 Delicate skink *Lampropholis delicata* non-directed activity and exploratory behaviour in urban and non-urban populations in the Sydney region. (a) Activity [number of grid squares crossed ± standard error (SE)]. (b) Exploratory behaviour (time taken to pass barrier ± SE). UP1 = St Stephens cemetery, Newtown, UP2 = Padstow, NP1 = Lane Cove National Park, NP2 = Ku-Ring-Gai Chase National Park.

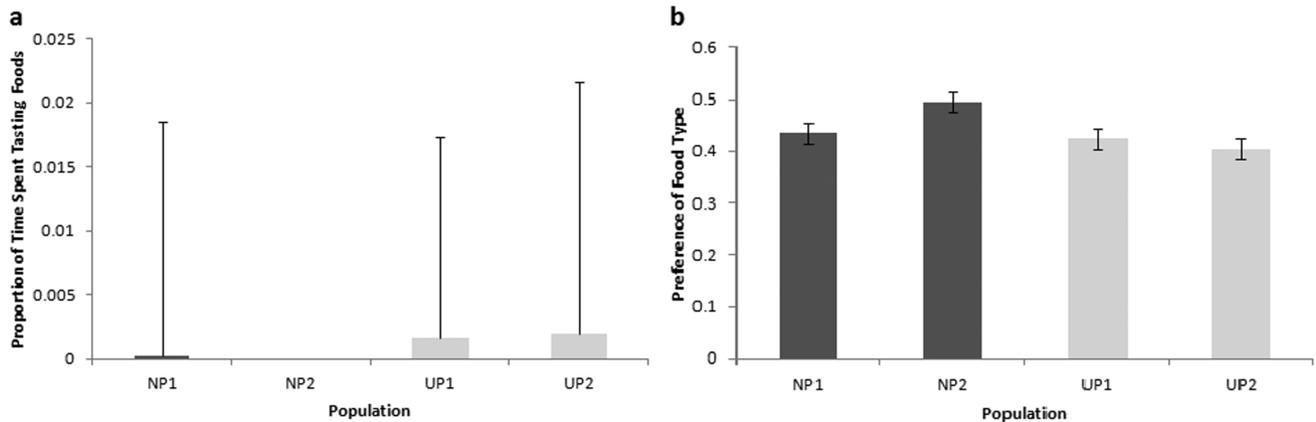


Figure 2 Delicate skink *Lampropholis delicata* foraging behaviour in urban and non-urban populations in the Sydney region. (a) Mean foraging exploration scores [proportion of time spent tasting foods \pm standard error (SE)] and (b) preference of food type (proportion of time spent in urban food zone \pm SE). UP1 = St Stephens cemetery, Newtown, UP2 = Padstow, NP1 = Lane Cove National Park, NP2 = Ku-Ring-Gai Chase National Park.

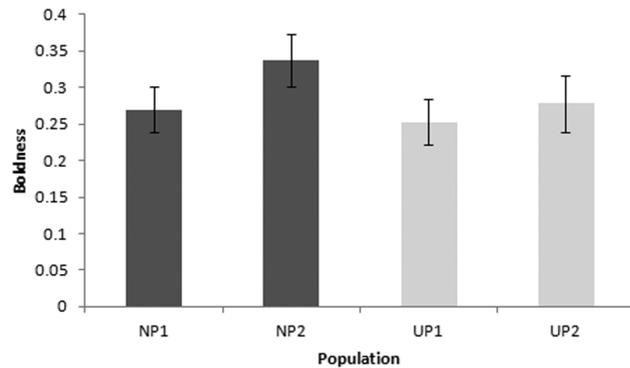


Figure 3 Delicate skink *Lampropholis delicata* basking site selection in urban and non-urban populations in the Sydney region. Boldness score (proportion of time spent in open habitat \pm standard error). UP1 = St Stephens cemetery, Newtown, UP2 = Padstow, NP1 = Lane Cove National Park, NP2 = Ku-Ring-Gai Chase National Park.

did not differ in the time they spent in the open area ($z = 0.83$, $P = 0.41$; Fig. 3). There were also no population differences (see Table 1).

Behavioural syndrome

Activity and exploratory behaviour were repeatable and were used in the behavioural syndrome analyses (Fig. 4). Tasting behaviour, while repeatable and variable, was not used in the PCA as inclusion of these data violated Bartlett’s sphericity test.

PCA of all populations revealed a principal component (PC1) that explained 64% of the variance. PC1 (eigenvalue = 1.13, 63.80% of the variance) included activity and exploration, and indicated that activity increases in association with higher exploratory behaviour (Supporting Information Table

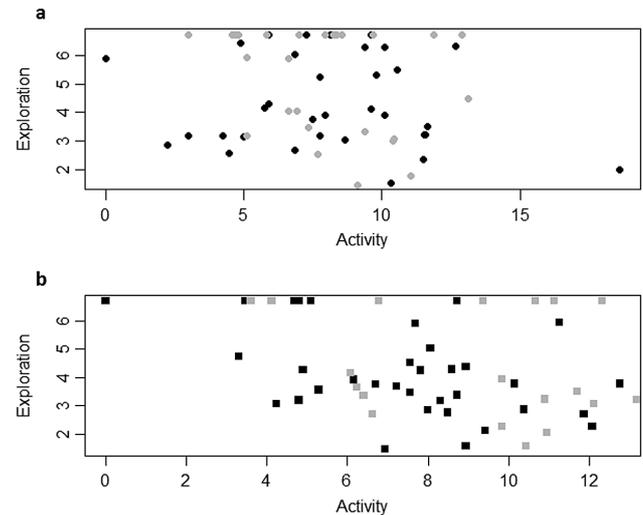


Figure 4 Delicate skink *Lampropholis delicata* square-root transformed activity and exploration scores for (a) NP1 and NP2 and (b) UP1 and UP2. UP1 (black squares) = St Stephens cemetery, Newtown, UP2 (grey squares) = Padstow, NP1 (black circles) = Lane Cove National Park, NP2 (grey circles) = Ku-Ring-Gai Chase National Park.

S2). However, the behavioural syndrome broke down at a population level, and a principal component (PC2) that explained 73% of the variance was only present in UP1. PC2 (eigenvalue = 1.2, 72.51% of the variance) also indicated that activity increases in association with higher exploratory behaviour (Supporting Information Table S2).

Discussion

A behavioural syndrome linking activity and exploratory behaviour was found in male delicate skinks. Skinks from the

highly modified and disturbed habitat of Padstow (UP2), a suburban backyard, were more active than skinks from the two natural populations and the less modified urban population (inner city parkland/cemetery), with some preliminary evidence that Padstow skinks were more likely to investigate novel foods.

Urban gradients

Contrary to our hypothesis, delicate skinks from the two urban populations did not exhibit similar behaviours. These populations were intended to replicate urban populations, but there are significant differences in activity and foraging behaviour between skinks from these sites. The extent to which a landscape is urbanized generally falls along a gradient, ranging from a highly modified and disturbed centre to a less modified city fringe (McKinney, 2002). Parks, with areas of natural vegetation and reduced traffic, could present refugia away from novel stressors (Yasuda & Koike, 2006). Animals in these areas would not need to modify their behaviour as strongly as animals in areas of higher urbanization, due to exposure to fewer novel stressors (McKinney, 2002; Sol *et al.*, 2013). The inner city parkland/cemetery (UP1) contained relatively untended vegetation and lower levels of human foot traffic compared with the Padstow garden (UP2; a suburban backyard). Thus, these urban populations fell on different areas of the urban gradient: a highly urbanized habitat (UP2) and a moderately urbanized habitat (UP1), potentially influencing how much modification of behaviour is required in these areas.

Does urbanization influence activity and exploratory behaviour?

Skinks from UP2 are the most active, which might be attributed to a release from natural predators (Sih, Kats & Maurer, 2003). In urban Sydney the closely related garden skink *L. guichenoti* allows human observers to approach closer, and basks further away from refuge, compared with populations from natural habitats (Prosser, Hudson & Thompson, 2006). Under natural predation pressures, active animals are more likely to be seen by predators. Thus, in areas of high predator density, low levels of activity are selected for (Sih *et al.*, 2012). However, under low predator density, animals with low activity will be outcompeted by animals with high activity that have increased foraging and mate-finding success (Sih *et al.*, 2012). Natural predators are often absent in urban areas, releasing native animals from predation pressure (Lowry *et al.*, 2012; Sol *et al.*, 2013). Thus, high activity in highly urbanized areas may be advantageous for delicate skinks.

Alternatively, the composition of urban populations could be due to a more active subset of individuals colonizing these landscapes (Evans *et al.*, 2010). As urbanization increases, it creates fragmented landscapes, thus only highly active animals are able to reach the urbanized area (McKinney, 2006). It is difficult to disentangle this possibility from predator release, as both will result in similar differences in behaviour between

urban and natural regions (Evans *et al.*, 2010). Nonetheless, increased activity will impact the ecology and evolution of urban skinks, and may lead to increased interactions between conspecifics (Sih *et al.*, 2012), which could influence aggression levels within populations. At high population densities, Zenaida doves *Zenaida aurita* decrease territorial aggression and feed in large communal flocks with no conspecific aggression (Carlier & Lefebvre, 1997). Changes in aggression in the delicate skink would impact its population demographics within cities (Sih *et al.*, 2012).

Contrary to our prediction, and the results of previous studies, exploratory behaviour did not differ among populations. Urban populations of common myna *Acridotheres tristis* demonstrate increased exploration compared with natural populations (Sol *et al.*, 2011). Exploration of the environment may confer a survival advantage, as animals with good knowledge of their habitat will fare better in species interactions, such as competition and predation (Verbeek, Drent & Wiepkema, 1994; Sih *et al.*, 2012). Iberian wall lizards *Podarcis hispanica* that explore more also habituate faster to their environment, allowing them to quickly assess the level of risk in the area (Rodríguez-Prieto, Martín & Esteban, 2011). The absence of such differences in our study could indicate that delicate skinks are already highly exploratory (Chapple *et al.*, 2011b). Indeed, the delicate skink was more exploratory than the closely related garden skink *L. guichenoti* (Chapple *et al.*, 2011b), and there may be limited potential for urbanization to further influence this trait.

Urbanization and foraging behaviour

Due to unbalanced sample numbers between populations, while more skinks from UP2 tasted more than other populations combined, this should be considered a preliminary result. Food preferences did not differ between non-urban and urban regions. A willingness to taste foods, including novel foods, has been seen previously in urban species such as grey squirrels *Sciurus carolinensis* (Bowers & Breland, 1996). Urbanized Pacific black ducks *Anas superciliosa* have adjusted to eating novel foods by altering their foraging behaviours when bread is offered (Chapman & Jones, 2012). Urban common mynas are more likely to explore and taste novel foods than their natural counterparts (Sol *et al.*, 2011). Such results are unsurprising as urban environments present animals with an opportunity to utilize many novel food resources, mainly created by human wastage or supplementary feeding (Lowry *et al.*, 2012; Sol *et al.*, 2013). The absence of such differences in the delicate skink may reflect a generalist diet, as is often seen in native animals that have adapted to urban environments (Lowry *et al.*, 2012; Sol *et al.*, 2013).

Basking site selection is not influenced by exposure to urbanization

Our basking site assay was not repeatable. This could be because the basking sites did not adequately represent urban and non-urban habitats, but shredded paper has been used

previously to mimic leaf litter (Howard *et al.*, 2003). The replacement of natural habitats with fragmented, urbanized habitats results in animals having to adapt to using these novel habitats. Urban coyotes *C. latrans* utilized larger amounts of urban areas than remnant patches of natural habitat (Grinder & Krausman, 2001). Likewise, the creation of novel human structures impacts behaviour. Human structures are used for dens by brushtail possums *Trichosurus vulpecula* and stone martens *Martes foina* (Statham & Statham, 1997; Herr *et al.*, 2010). The use of novel structures and habitats by urban animals may enhance survival (Lowry *et al.*, 2012), but future studies will be needed to explore this possibility in the delicate skink.

Similarly, our boldness assay was not repeatable. This may be because our laboratory-acclimated lizards did not fear the stimulus used (Bell, 2012). In previous studies, fear has been created using human disturbance or other stimuli, such as a fake predatory bird (Evans *et al.*, 2010; Bókony *et al.*, 2012). Skinks do show a fear response to predators and other risky situations (e.g. Downes, 2001; Carter *et al.*, 2012). Exposure to the same behavioural trials, or acclimation to laboratory conditions, can cause animals to become habituated to testing or lead to a loss of repeatability (Martin & Reale, 2008; Bell, 2012). Future studies of the delicate skink should measure boldness using predator chemical scent (e.g. Downes & Hoefler, 2004) or by simulating predator strikes.

A behavioural syndrome exists in the delicate skink

A behavioural syndrome, linking high activity and increased exploratory behaviour, was identified in male delicate skinks. Although it is possible that high levels of activity drive high levels of exploration (Chapman *et al.*, 2013), our use of Reale's axes to define activity as movement in a non-novel environment and exploration as movement in a novel setting enables us to separate these two behaviours (Reale *et al.*, 2007). This common syndrome receives much attention in the literature. Chipmunks *Tamias striatus* that are highly active are also more exploratory than chipmunks that display low activity (Martin & Reale, 2008). Invertebrates, such as the rock pool prawn, also show a similar response with individuals exhibiting a positive correlation between activity and exploration (Chapman *et al.*, 2013). However, the behavioural syndrome broke down at a population level, with only UPI displaying it. This has been reported previously in song sparrows (Scales, Hyman & Hughes, 2011), where a boldness–aggression syndrome was lost in urban populations, and damselfish *Stegastes leucostictus*, the same syndrome disappeared in high-quality habitats (Snekser *et al.*, 2009). Understanding how behavioural syndromes differ among populations represents an important area for future research (Sih & Bell, 2008).

Conclusion

The presence of a behavioural syndrome in the delicate skink will have impacts upon its ecology and evolution, as behaviour

will mediate its response to urbanization. As urbanization is predicted to increase with human population growth the understanding of behavioural syndromes in animals, both male and female, that are able to colonize urban environments will enable us to identify vulnerable species that may not be able to cope with urbanization, and hence allow us to intervene before urbanization impacts them. The study of behavioural syndromes on males and females will allow us a greater understanding of not just how species will react to urbanization, but also their reaction to all aspects of such human environmental change (Sih, 2013).

Acknowledgements

We thank C. Goulet, J. Herbert, J. Reid, S. Syme, J. Thompson, J. Van Dyke and C. Whittington for assistance during fieldwork. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the Monash University Animal Ethics Committee (BSCI/2013/12), and in accordance with the appropriate collection and research permits (New South Wales: SL101202; Victoria: 10006866).

References

- Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Campbell-Nelson, S., Roberstson, K.W. & Ketterson, E.D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol.* **23**, 960–969.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using Eigen and EigenR package, version 0.999375–39. Available from: <http://CRAN.R-project.org/package=lme4>
- Bell, A.M. (2007). Future directions in behavioural syndromes research. *Proc. Roy. Soc. Lond. Ser. B.* **274**, 755–761.
- Bell, A.M. (2012). Randomized or fixed order for studies of behavioral syndromes? *Behav. Ecol.* **24**, 16–20.
- Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783.
- Bókony, V., Kulcsár, A., Tóth, Z. & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS ONE* **7**, e36639.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135.
- Bowers, M.A. & Breland, B. (1996). Foraging of gray squirrels on an urban-rural gradient: use of the gird to assess anthropogenic impact. *Ecol. Appl.* **6**, 1135–1142.
- Carlier, P. & Lefebvre, L. (1997). Ecological differences in social learning between adjacent, mixing, populations of zenaida doves. *Ethology* **103**, 772–784.

- Carter, A.J., Heisohn, R., Goldzein, A.W. & Biro, P.A. (2012). Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* **83**, 1051–1058.
- Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlshaw, G. & Heisohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev.* **88**, 465–475.
- Chapman, B.B., Hegg, A. & Ljungberg, P. (2013). Sex and the syndrome: individual and population consistency in behaviour in Rock Pool Prawn *Palaemon elegans*. *PLoS ONE* **8**, e59437.
- Chapman, R. & Jones, D. (2012). Synurbanisation of Pacific Black Ducks *Anas superciliosa* in south-eastern Queensland: the influence of supplementary feeding on foraging behaviour. *Aust. Field Ornithol.* **29**, 31–39.
- Chapple, D.G., Hoskin, C.J., Chapple, S.N.J. & Thompson, M.B. (2011a). Phylogeographic divergence in the widespread delicate skink (*Lampropholis delicata*) corresponds to dry habitat barriers in eastern Australia. *BMC Evol. Biol.* **11**, 191.
- Chapple, D.G., Simmonds, S.M. & Wong, B.B.M. (2011b). Know when to run, know when to hide: can behavioral differences explain the divergent invasion success of two sympatric lizards? *Ecol. Evol.* **1**, 278–289.
- Cromie, G.L. & Chapple, D.G. (2012). Impact of tail loss on the behaviour and locomotor performance of two sympatric *Lampropholis* skink species. *PLoS ONE* **7**, e34732.
- Dingemanse, N.J. & Dochermann, N. (2012). Quantifying individual variation in behaviour: mixed effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54.
- Downes, S. (2001). Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* **82**, 2870–2881.
- Downes, S. & Hofer, A.M. (2004). Vigilance in lizards: interactions between group size and predation risk. *Anim. Behav.* **67**, 485–492.
- Downes, S. & Shine, R. (2001). Why does tail loss increase a lizard's later chances of being consumed by snake predators? *Ecology* **82**, 1293–1303.
- Duh, J.D., Shandas, V., Chang, H. & George, L.A. (2008). Rates of urbanisation and the resiliency of air and water quality. *Sci. Total Environ.* **400**, 238–256.
- Evans, J., Boudreau, K. & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* **116**, 588–595.
- Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge: Cambridge University Press.
- Grinder, M.I. & Krausman, P.R. (2001). Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *J. Wildl. Mgmt.* **65**, 887–898.
- Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Softw.* **33**, 1–22.
- Helm, B., Ben-Shlomo, R., Sheriff, M.J., Hut, R.A., Foster, R., Barnes, B.M. & Dominoni, D. (2013). Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proc. Roy. Soc. Lond. Ser. B.* **280**, 20130016.
- Herr, J., Schley, L., Engel, E. & Roper, T.J. (2010). Den preferences and denning behaviour in urban stone martens (*Martes foina*). *Mammal. Biol.* **75**, 138–145.
- Howard, R., Williamson, I. & Mather, P. (2003). Structural aspects of microhabitat selection by the skink *Lampropholis delicata*. *J. Herpetol.* **37**, 613–617.
- Lowry, H., Lill, A. & Wong, B.B.M. (2012). Behavioural responses of wildlife to urban environments. *Biol. Rev.* **88**, 537–549.
- Martin, J.G.A. & Reale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **75**, 309–318.
- McEvoy, J., While, G.M., Sinn, D.L., Carver, S. & Wapstra, E. (2015). Behavioural syndromes and structural and temporal consistency of behavioural traits in a social lizard. *J. Zool.* **296**, 58–66.
- McKinney, M.L. (2002). Urbanisation, biodiversity and conservation. *Bioscience* **52**, 883–890.
- McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260.
- Michelangeli, M., Wong, B.B.M. & Chapple, D.G. (2015). It's a trap: sampling bias due to animal personality is not always inevitable. *Behav. Ecol.* (Online DOI: 10.1093/beheco/arv123).
- Prosser, C., Hudson, S. & Thompson, M.B. (2006). Effects of urbanization on behaviour, performance, and morphology of the garden skink, *Lampropholis guichenoti*. *J. Herpetol.* **40**, 151–159.
- R Development Core Team (2012). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rèale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318.
- Rodriguez-Prieto, I., Martín, J. & Esteban, F.-J. (2011). Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proc. Roy. Soc. Lond. Ser. B.* **27**, 266–273.
- Scales, J., Hyman, J. & Hughes, M. (2011). Behavioral syndromes break down in urban song sparrow populations. *Ethology* **117**, 887–895.
- Shea, G.M. (2010). The suburban terrestrial reptile fauna of Sydney – winners and losers. In *The natural history of Sydney*: 154–197. Lunney, D., Hutchings, P. & Hochuli, D. (Eds). Mosman: Royal Zoological Society of NSW.
- Shine, R. (2003). Locomotor speeds of gravid lizards: placing 'costs of reproduction' within an ecological context. *Funct. Ecol.* **17**, 526–533.
- Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* **85**, 1077–1088.

- Sih, A. & Bell, A.M. (2008). Insights from behavioural syndromes for behavioural ecology. *Adv. Study Behav.* **38**, 277–281.
- Sih, A., Kats, L.B. & Maurer, E.F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim. Behav.* **65**, 29–44.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: an integrative overview. *Quart. Rev. Biol.* **79**, 241–277.
- Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecol. Lett.* **15**, 278–289.
- Snekser, J.L., Leese, J., Ganim, A. & Itzkowitz, M. (2009). Caribbean damselfish with varying territory quality: correlated behaviors but not a syndrome. *Behav. Ecol.* **20**, 124–130.
- Sol, D., Griffin, A.S., Bartomeus, I. & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS ONE* **6**, e19535.
- Sol, D., Lapiedra, O. & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Anim. Behav.* **85**, 1101–1112.
- Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecol. Lett.* **17**, 942–950.
- Statham, M. & Statham, H.L. (1997). Movements and habits of brushtail possums (*Trichosurus vulpecula* Kerr) in an urban area. *Wildlife Res.* **24**, 715–726.
- Verbeek, M.E.M., Drent, P.J. & Wiepkema, P.R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* **48**, 1113–1121.
- Wilson, S. & Swan, G. (2013). *A complete guide to reptiles of Australia*. 4th edn. Sydney: Reed New Holland.
- Yasuda, M. & Koike, F. (2006). Do golf courses provide refuge for flora and fauna in Japanese urban landscapes? *Landsc. Urban Plan.* **75**, 58–68.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Mean snout-vent length (SVL ± SD) of skinks collected from the urban and non-urban populations in the Sydney region, with sample size collected from, and location of, each site.

Table S2. Components matrix showing correlations between behavioural scores for the significant principal components (eigenvalue >1). Only loadings considered large (>0.5) were considered significant in this study.