Inherent behavioural traits enable a widespread lizard to cope with urban life

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Abstract

The global human population is increasing at a staggering rate, and more than half of that population resides in urban areas. As urbanization spreads across the landscape, animals are often confronted with a vast number of unfamiliar stimuli. Existing evidence from studies of birds and mammals suggests that increased boldness, arising either through behavioural plasticity or an intrinsic risk-taking ability, can provide a fitness advantage in urban environments. What is less clear, is if these same patterns are prevalent in other taxa. Accordingly, we measured the expression of boldness in two contexts, novelty and anti-predatory behaviour, in a successful urban lizard, the delicate skink (*Lampropholis delicata*). Lizards from genetically related urban and non-urban populations were exposed to a novel object, scent and noise as well as a simulated predator attack. Contrary to much of the current research, we found no behavioural variation between urban and non-urban populations, as all lizards exhibited similarly high levels of risk-taking behaviour in their antipredator response as well as neophobia towards the novel object, scent and noise. Our results suggest that the delicate skink is able to cope with the challenges of urban conditions through its inherent traits. As urbanization becomes more widespread, we need to better understand which animals are able to cope with altered environmental conditions and how that is achieved. This will be critical if we are to fully grasp the impacts of anthropogenic change on faunal communities globally.

Introduction

Due to the rapid rate of human population growth, the natural environment is undergoing irreversible changes worldwide (Prosser, Hudson & Thompson, 2006; Lowry, Lill & Wong, 2013). Urbanization is a global issue, with the population of the Earth growing at least 1% every year and more than 50% of the world's population already residing in metropolitan areas (McKinney, 2008; Buczkowski & Richmond, 2012; Norra, 2014). As more people move into cities, the boundaries of urban environments expand, with extensive industrial, commercial and residential developments breaking up the landscape. This can cause fragmentation of natural ecosystems (Hamer & McDonnell 2010), or complete loss of natural habitats (Threlfall, Law & Banks, 2013; Galbreath *et al.*, 2014). This urban encroachment, referred to as urban sprawl (Jaeger *et al.* 2010), disrupts natural ecosystems, alters community composition and influences the population dynamics of animals (Anderies, Katti & Shochat, 2007; Rutz, 2008; Sol, Lapiedra & González-Lagos, 2013). Given the projected increase in the incidence of permanently altered landscapes, it is vital that we understand the influence of urbanization on biological communities (Sol *et al.*, 2013).

As urbanization spreads across the landscape, animals are often confronted with a vast number of unfamiliar stimuli which they have never encountered (Miranda *et al.*, 2013). Human-built structures and litter act as novel objects and scents. Artificial lighting disrupts natural cycles of day and night, and vehicles, humans, domestic animals and pollutants must be recognized as potential new threats. Behaviour has been found to play a key role in dealing with such novel environmental conditions (Sih, Ferrari & Harris, 2011; Wong & Candolin, 2015). One behavioural trait that is particularly important for successfully coping with novelty is boldness (Lowry *et al.*, 2013). High levels of this trait may provide a fitness advantage for urban wildlife as they are better able to deal with novel stimuli through a reduced fear response (neophilia). Less fear increases the expression of risky behaviour and thus enables individuals to approach and explore novel objects or situations which would otherwise be avoided by those that are more fearful. Anthropogenic resources, such as food and shelter, can then be exploited in place of natural sources and be used as ecological opportunities (Cook *et al.*, 2017). This has been demonstrated in several species of birds where urban individuals have increased survival from the use of novel food sources, like bird feeders and litter, as a means

of supplementing their diet (Evans *et al.*, 2015; Plummer *et al.* 2015). Additionally, bolder animals also tend to exhibit a reduced anti-predatory response both towards novel as well as natural threats (Greggor *et al.*, 2016; Myers & Hyman, 2016). By investing less time engaged in anti-predatory behaviour, more time can, instead, be put towards other important activities such as foraging and reproduction, furthering the fitness benefit of being bold.

Being less fearful can clearly enable an animal to establish and persist within urban environments. In this regard, behavioural plasticity is one potential mechanism that could enable individuals in urban populations to rapidly adjust their behaviour to become bolder as a means of coping with the repeated exposure to novel objects, scents and predators. If this is the case, then elevated expression of boldness among individuals inhabiting urban sites would lead to population differences in behaviour (Sol *et al.*, 2011; Cook *et al.*, 2017). Evidence of behavioural plasticity in response to novelty has indeed been well-documented (Adams, Lengas & Bekoff, 1987; Prosser *et al.*, 2006; McCleery, 2009; Møller, 2009; Seress *et al.*, 2011; Atwell *et al.*, 2012; Chapman, Rymer & Pillay, 2012; Miranda *et al.*, 2013; Wong & Candolin, 2015; Greggor *et al.*, 2016; Myers & Hyman, 2016; Cook *et al.*, 2017). In a review conducted by Miranda *et al.* (2013), for example, half of the 14 studies investigating population variation in boldness indicated that the expression of bold behaviour was highest in urban versus rural populations.

Alternatively, it could be that successful urban living arises instead from a species having innate fearlessness and risk-taking ability, independent of experience, that predisposes them to coping with novelty. Under this premise, no population differences in behaviour would be evident as a high level of boldness would already exist within the natural populations. This would result in relatively consistent behaviour across the rural–urban gradient. Few studies have actually examined this concept or considered it as a potential mechanism for explaining the lack of observable differences between urban and natural populations and, among these exceptions, they have tended to focus on differences across species, rather that differences at the intra-specific level (Hu & Cardoso, 2009; Møller, 2009; Wright *et al.*, 2010; Crates, French & McLean, 2011; Skandrani *et al.*, 2016).

Identifying the mechanisms that enable animals to cope with novelty and determining the generality of these patterns is important to our understanding of the impacts of urbanization. Yet, this understanding is limited as most studies to date have focused almost entirely on birds or mammals (but see Prosser *et al.*, 2006 and Altermatt & Ebert, 2016). This is true despite the fact that a wide range of taxonomic groups can occur in, and are impacted by, urban environments. Accordingly, we examined the behavioural responses in two broad contexts, exposure to novel stimuli and anti-predatory behaviour, among urban and non-urban populations of a common species of reptile, the delicate skink (*Lampropholis delicata*). Our aim was to determine if the success of this species within urban environments has arisen either through behavioural plasticity or instead by having inherently high levels of boldness

which predispose them to coping with the challenges of urbanization.

The delicate skink is a small diurnal lizard that is highly abundant in both urban and natural habitats throughout the Sydney region (Chapple *et al.*, 2011a; Wilson & Swan, 2017) and whose behaviour has been extensively studied (Chapple, Simmonds & Wong, 2011b; Cromie & Chapple, 2012; Moule *et al.*, 2016; Michelangeli, Wong & Chapple, 2016a; Michelangeli, Chapple & Wong, 2016b; in press; Goulet *et al.*, 2017). Sydney represents a relatively young urban system as well as it being located in the southern hemisphere which is an underrepresented model in urbanization studies (Sol *et al.*, 2013). Furthermore, as all delicate skink populations within the Sydney region are part of the same genetic sub-lineage (Chapple *et al.*, 2011a), any observed behavioural differences between populations can potentially be attributed to behavioural flexibility rather than the result of genetic differences.

Materials and methods

Animal collection and husbandry

Eighty delicate skinks were collected from two urban sites (St Stephens Cemetery, Newtown: 33°53′40.82″S, 151°10′47.17″E, *n* = 20; Sydney Park: 33°54′37.76″S, 151°10′55.95″E, *n* = 20) and two non-urban sites (Ku Ring Gai Chase National Park: 33°39′35.41″S, 151°9′29.06″E, *n* = 20; Lane Cove National Park: 33°47′17.85″S, 151°8′44.29″E, *n* = 20) in the Sydney region in October 2014. Lizards were captured either by hand or by 'mealworming.' All individuals were sexed (through eversion of hemipenes), weighed (±0.1 g) and measured (±0.1 mm) for both tail length (TL) and snout–vent length (SVL: measured from the tip of the snout to the cloacal opening). To avoid potential confounding behavioural differences between the sexes (Michelangeli *et al.*, 2016b), and the possibility of females being gravid during the study period (Shine, 2003), only adult males (with SVL > 35 mm) with full tails were retained for the study.

Lizards were transported back to Monash University and individually marked with a unique visible implant elastomer (Northwest Marine Technology) colour code. Lizards were housed by collection site in groups of five within opaque plastic containers (300 × 230 × 370 mm) and maintained at 22°C with a 14 h light:10 h dark cycle (0600–2000 h). Basking lamps in each container created a thermal gradient of 22–35°C to promote natural thermoregulatory behaviour. Lizards were fed crickets (*Acheta domesticus*) three times weekly and provided water *ad libitum*. However, given that digestion has been shown to affect behaviour, lizards were not fed in the 24 h preceding each experimental trial (Shine, 2003). Lizards were provided up 2 weeks to acclimate to laboratory conditions prior to the onset of experiments. The project was conducted in accordance with our Animal Ethics Committee approvals (BSCI/2014/12), associated scientific research permits (NSW: SL101425; VIC: 10007279) and under special permission from Lane Cove National Park.

Experimental procedures

Each of the four populations of lizards were put through a series of behavioural trials involving exposure to novel stimuli (object, scent, sound) and a simulated predator attack. Experiments were conducted between October 2014 and January 2015. To minimize the potential impact of carry-over effects, which may influence behavioural responses across successive experiments, assays were conducted in a fixed order where those trials assumed to cause the biggest change in behaviour were placed last in the order of experiments (Bell, 2013).

Each experiment was conducted in a large opaque-walled experimental arena (550 mm × 320 mm × 240 mm), with the set-up of the arena modified according to the behaviour being tested. Before the commencement of each trial, individual lizards were placed under a transparent container and left to acclimate for 10 min. Following the acclimation period, the plastic container was lifted and each individual was then free to explore the test arena for 30 min. Each trial was recorded on a Panasonic HCV130 camcorder suspended from above. Experimental arenas and associated equipment were thoroughly washed between trials to avoid cross contamination between individuals. Behavioural measurements were analysed to the nearest second using the quantitative analysis program JWatcher version 1.0 (Blumstein, Evans & Daniel, 2006). To minimize observer bias, blinded methods were used when all behavioural data were recorded and interobserver reliability was maintained by having a single observer performing all trials and behavioural measurements.

Novel stimuli experiments

To assess the level of neophilia expressed by lizards, individuals were exposed to three novel stimuli: object, noise and scent. For the novel object assays, the experimental arena was divided into two equal compartments with an opaque partition extending the entire length and height of the arena. In one compartment, a novel object (100 × 400 mm) was placed on the surface of the arena within a buffer zone (200 mm diameter). The object was unfamiliar to the lizards but otherwise neutral as it did not resemble any predator, competitor or conspecific (Supporting Information Figure S1). Lizards were placed on the other side of the partition unable to view the novel object. Following the acclimation period, the opaque partition was removed, and the lizard was left to explore the arena and novel object. Exploration of the novel object was defined as lizards either entering the buffer zone and/or coming into contact with the object. Within each trial the following measurements were recorded: time taken for the lizard to cross the centre of the arena, time spent outside the buffer zone, time spent in the buffer zone surrounding the object but not in contact with the object and time spent in contact with the object. Lizards not crossing the centre line were assigned the maximum time (1800 s). Faster time to approach the side of the arena having the object as well as greater amount of time spent within the buffer zone and/or inspecting the object would be indicative of neophilia.

Behavioural response towards a novel scent was evaluated by exposing lizards to the smell of clove oil. This scent was selected as it is an unfamiliar but neutral odour that does not elicit any chemosensory cues resembling a predator, competitor or conspecific. Two drops of oil were placed on a piece of paper towel that was then wrapped around a small tile to secure its position within the arena. The experimental arena was divided into two equal compartments with an opaque partition. In one compartment a novel scent was placed on the surface of the arena within a buffer zone (200 mm diameter). To ensure the lizards were not reacting to the presence of the paper towel but rather responding to the scent itself, each lizard was exposed to an unscented towel to familiarize them with the object prior to onset of the experiments. The habituation experiments were conducted using the same methodology yet with an unscented towel. Within each trial the following measurements were recorded: time taken for the lizard to cross the centre of the arena, time spent in the outside of the buffer zone, time spent in the buffer zone but not in contact with the scent and time spent in contact with the scent. Lizards not crossing the centre line were assigned the maximum time (1800 s). Faster time to approach the side of the arena having the scent as well as greater time near and/or inspecting the scent would be indicative of neophilia.

To evaluate behavioural responses towards a novel sound, a speaker which would be delivering the noise was placed beside one end of the test the experimental arena out of view from the lizards. The arena was divided into three zones: Zone 1 was furthest from the sound, Zone 2 was the central zone and considered the neutral zone and Zone 3 was closest to the sound. Lizards were placed in the neutral zone and allowed to acclimate. After the acclimation period, an industrial pressing machine sound, similar to that used by Lowry, Lill & Wong (2011), was played from the speaker for 40 s at 40 db (Wever, 1978). The novel sound covered a variety of frequencies so it was assumed that it fell within the hearing range of this species. Time spent in each of the three zones following exposure to the sound was recorded where greater time in Zone 1 was considered a neophobic response while greater time spent in Zone 3 was considered a neophilic response.

Anti-predatory behaviour experiments

Boldness within the context of anti-predatory behaviour was evaluated using a simulated predator attack. The experimental arena was comprised of a basking site at one end of the arena and a shelter site at the opposite side. Lizards were given 10 min to freely explore the test arena then a bird model (50 × 70 cm) was flown over the test arena. The model was made of black plastic cut in the silhouette of a crow, a natural predator of skinks. It operated on a pulley system and was passed over the test arena five times at 0.5 m s^{-1} to ensure the model was detected by the lizards. Behavioural responses were assessed for 30 min following the flyover and boldness evaluated based on initial reaction (flee or freeze), time spent in the shelter, time spent in the open and time spent basking.

High levels of boldness would be indicated by a greater amount of time spent active following the simulated attack.

Statistical analyses

Generalized linear models were constructed to test for population differences of behavioural responses between urban and non-urban populations towards the novel object and noise as well as the simulated predator attack using SPSS v 23.0 (IBM Corp., Armonk, NY, USA). For each model, population type (urban or non-urban) and site nested within population were fixed effects and lizard body size (SVL) was included as a covariate. Collection method was not included as a factor as previous research indicated that the capture technique does not result in sampling bias towards a particular behavioural type (bold vs. neophobic; Michelangeli *et al.*, 2016a). Because time spent within the buffer zone of the novel object was heavily zero inflated, the data were changed to a binary response of yes or no. For the novel scent experiment where lizards were exposed to two trials, linear mixed effects models were used to test for population differences. Lizard ID was included as a random effect while phase (control or test), population type and site nested within population were fixed effects and SVL was included as a covariate. All main effects in each of the models were kept in the model even when not significant to avoid the probability of Type 1 errors as well as oversimplifying the models (Forstmeier & Schielzeth, 2011). And finally, a one-way ANOVA was used to test for differences in the time expressing bold versus neophobic behaviour in response to the simulated predator attack. Bold behaviour was derived from the time spent basking while neophobic behaviour consisted of the time spent within the refuge.

Results

No differences were detected between urban and non-urban delicate skinks in response to the novel stimuli (Tables 1 and 2). All lizards expressed similar levels of neophobia as indicated by a greater time spent outside of the buffer zones surrounding the object ($F = 1047.85$, df = 1, $P < 0.00$) and scent ($F = 2106.52$, df = 1, $P < 0.00$) as well as within the zone furthest from the sound ($F = 26.83$; df = 1; $P < 0.00$; Fig. 1a–c). This was further suggested by the time taken to cross the centre line towards the object (non-urban: $\sigma = 967.88$ s $\pm$ 113.23; urban: $\sigma = 735.18$ s $\pm$ 98.14). However, for the novel scent, population did influence the amount of time taken to cross the centre line ($F = 1.19$, df = 1, $P = 0.03$) where urban lizards crossed at a higher rate (Test Phase: non-urban: $\sigma = 688.64$ s $\pm$ 131.67; urban: $\sigma = 442.08$ s $\pm$ 86.64). Behavioural responses towards any novel stimuli also did not differ between sites (Tables 1 and 2).

Likewise, urban and non-urban populations of delicate skinks responded similarly following the simulated predator attack (Table 1). However, unlike the behavioural responses towards novel stimuli, all lizards expressed high levels of boldness (time spent active in the open arena and basking) was greater than that spent in the refuge ($F = 88.67$, df = 1, $P < 0.00$; Fig. 2). High expression of boldness was further indicated by a greater number of lizards from both populations

freezing (urban = 79%; non-urban = 85%) rather than fleeing after the simulated attack. And differences between sites were again not present (Table 1).

Discussion

Our study detected few population-level differences in anti-predatory behaviour or response towards novelty. In general, we found that both urban and rural lizards were equally neophobic, mostly avoiding all three types of novel stimuli. Nevertheless, the amount of time taken to cross the centre line towards the novel scent did vary in that urban lizards were faster. We also did not detect any variation in the expression of bold behaviour following a simulated predatory attack between urban and non-urban populations. However, in this case, most lizards initially froze during the flyover phase and, following the treatment, spent their time either basking or being active in the open, suggesting an equally high level of boldness across individuals. The overall results counter our own predictions and also contrast with the population differences in bold behaviour reported in several species of birds (Møller, 2008; Lowry *et al.* (2011); Scales, Hyman & Hughes, 2011; Sih *et al.*, 2011; Myers & Hyman, 2016; Cook *et al.*, 2017).

The similarity in the expression of bold behaviour between urban and non-urban populations of the delicate skink demonstrated here indicates an inherent neophobia towards novelty yet high levels of risk-taking behaviour within the context of an anti-predatory response. The divergent expression of boldness in either context (novel stimuli and anti-predatory behaviour) seems counter-intuitive as it would seem that an elevated level of risk-taking should be expressed by lizards within both the context of a potential predatory attack as well as towards novel stimuli. The mechanisms through which boldness subsides in the presence of unfamiliar objects, scents and noises is unknown. One possibility though, is that neophobia may provide a fitness advantage when inspecting novel stimuli as this behaviour may incur greater costs, even under natural conditions (Lima & Bednekoff, 1999; Higginson *et al.*, 2012; Trimmer *et al.*, 2017). Neophobia may also be more advantageous in urban areas as this behavioural response could protect lizards from dangers such as pollutants (Greggor *et al.*, 2016), or by reducing the time exploring novel stimuli which may impose greater vulnerability to unfamiliar predators (e.g. humans or domestic animals; Martin & Fitzgerald, 2005). High levels of object neophobia among urban populations have been reported among several species of birds (Echeverría & Vassallo, 2008; Miranda *et al.*, 2013). These studies suggest that stable food resources and thermal regimes within urban environments may decrease the need of neophilia while greater exposure to potentially dangerous novel situations would instead make heightened fear responses advantageous.

An intrinsic boldness in terms of anti-predatory behaviour may, however, be advantageous in that the elevated expression of boldness could offset the constraints that predation imposes on activity patterns and/or thermoregulatory requirements (i.e. increased basking to achieve high optimal body temperatures). Small skinks are highly vulnerable to several avian, mammalian and reptilian predators. Thus, time spent foraging,

Table 1 Results of the GLMs used to evaluate the effects of urbanization on behavioural responses towards novelty and a simulated predator attack among delicate skinks

Stimuli	Response variable	Explanatory variable	df	X²	P
Novel object	Time outside buffer zone	Population	1	0.03	0.87
		Site	2	1.03	0.60
	Time to cross centre line	Population	1	0.14	0.71
		Site	2	0.42	0.81
	Time within buffer zone	Population	1	0.51	0.48
		Site	2	1.34	0.51
Novel sound	Time inside zone 1 (furthest from sound)	Population	1	0.61	0.44
		Site	2	0.79	0.67
	Time inside zone 2 (neutral zone)	Population	1	0.52	0.47
		Site	2	1.98	0.37
	Time inside zone 3 (closest to sound)	Population	1	0.25	0.62
		Site	2	0.09	0.98
Predator attack	Initial response	Population	1	0.42	0.52
		Site	2	0.43	0.81
	Time spent in refuge	Population	1	0.93	0.34
		Site	2	0.07	0.96
	Time spent active	Population	1	0.50	0.48
		Site	2	1.24	0.54
	Time spent basking	Population	1	0.01	0.92
		Site	2	0.91	0.63

Table 2 Results of the mixed effects models used to evaluate the effects of urbanization on behavioural responses towards a novel scent among delicate skinks. Significant effects ($P < 0.05$) are in bold

Stimuli	Response variable	Explanatory variable	df	f	P
Novel scent	Time outside buffer zone	Population	1	0.43	0.52
		Site	2	1.26	0.29
		Phase	1	36.41	**<0.00**
	Time to cross centre line	Population	1	5.15	**0.03**
		Site	2	1.19	0.31
		Phase	1	0.63	0.43
	Time inside buffer zone	Population	1	0.27	0.61
		Site	2	1.45	0.24
		Phase	1	37.19	**<0.00**

seeking mates or basking may be reduced under natural or artificial levels of predation. The trade-off between resource acquisition versus predator avoidance, by way of fleeing to and staying within refuges, may necessitate greater risk taking, as being too fearful would seemingly have detrimental fitness consequences. Thus, the delicate skink may need to be active under constant levels of threat in order to maximize foraging and reproduction, resulting in inherently high levels of boldness in this species. Reduced anti-predatory response, in terms of flight initiation response and re-emergence, would also enable delicate skinks to cope well in urban habitats where predation pressure is often greater than in natural sites (Møller, 2009; Myers & Hyman, 2016).

Inherent bold behaviour in the delicate skink is further evidenced by the fact that this species is invasive throughout the Pacific region (Lord Howe Island, New Zealand and Hawaii; Chapple *et al.*, 2013a,b, 2014; Chapple, Reardon & Peace, 2016; Tingley *et al.* 2016; Miller *et al.* 2017). Boldness has been found to be a key trait enabling individuals to successfully proceed through the invasion process and establish into novel environments (Chapple *et al.*, 2011b). An intrinsic boldness has also been demonstrated in other invasive species such as the mourning gecko (*Lepidodactylus lugubris*; Short & Petren, 2008). A high propensity towards bold behaviour in this lizard species has been shown to influence its invasive potential and allowed it to successfully forage in an environment with limited food resources.

Conclusion

The results of this study counter much of the previous research revealing behavioural shifts as a by-product of the urbanization process. Instead we have provided support for the hypothesis that inherent behavioural traits may have predisposed the delicate skink to successfully inhabiting both urban and non-urban environments. It is one of few studies to investigate the behavioural responses towards urbanization in a reptile species. Given that urbanized environments are overtaking much of the
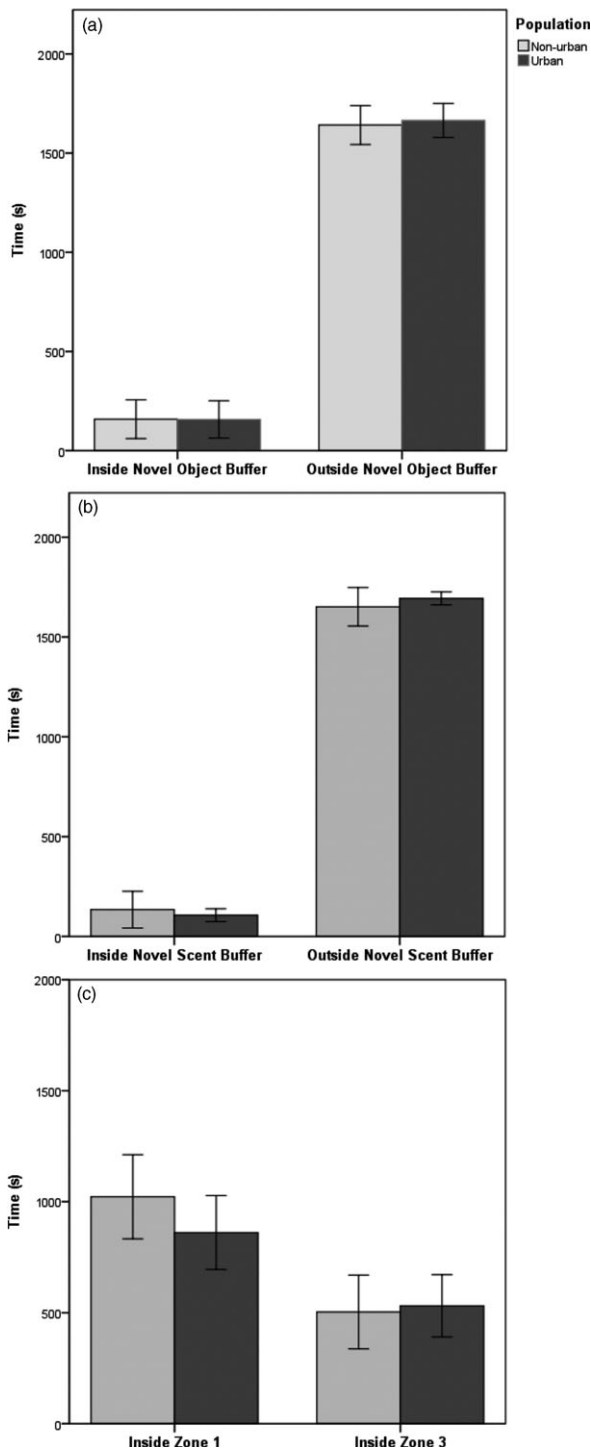
Figure 1 Behavioural responses towards novel object (a), scent (b) and noise (c) between urban and non-urban populations of delicate skinks. The level of neophobic behaviour expressed by lizards is presented by the average time spent outside the buffer zones surrounding the object and scent and away from the sound (zone 1). The level of bold behaviour expressed by lizards is presented by the average time spent within buffer zones and close to the sound (zone 3).
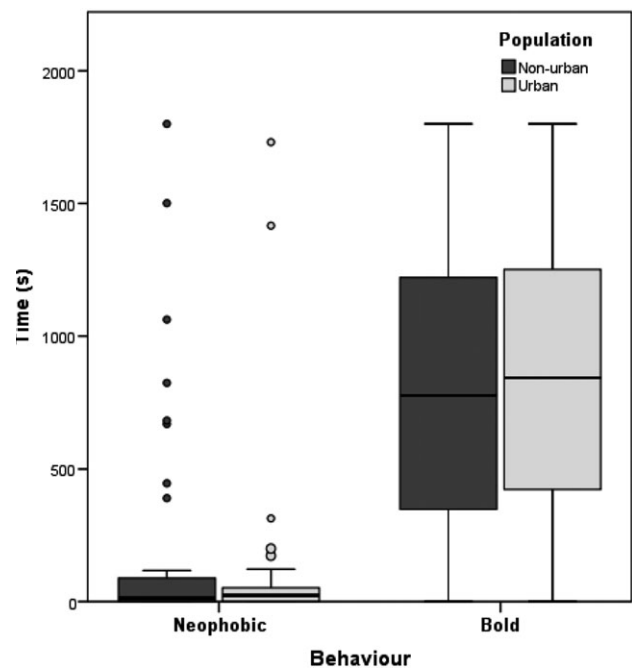

Figure 2 Behavioural responses following a simulated predator attack in urban and non-urban populations of delicate skinks. The level of neophobic behaviour expressed by lizards is presented by the average time spent hiding within the refuge after the attack, whereas the level of bold behaviour expressed by lizards is presented by the average time spent active and basking after the attack.

landscape, challenging wildlife with novel stimuli and predators that are dramatically different from their natural habitats, examining how different taxa either respond to, or are adapted for, novel environmental conditions is integral to understanding the impacts of urbanization on wildlife.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The novel object used in the behavioural trials.