The impact of urbanization on learning ability in an invasive lizard

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The process of urbanization brings about striking shifts across all levels of an ecosystem from habitat structure, resource availability, predator–prey relationship and climatic condition. As these ecological alterations are typically drastic and rapid, presenting wildlife with selective pressures that differ dramatically from those under which they naturally evolved, individuals must be either adjusted or excluded. One factor hypothesized to facilitate the successful exploitation of urban areas is cognition. It is predicted that enhanced cognitive function is strongly selected as it mitigates the presumably novel and often unpredictable conditions within cities by enabling the rapid perception of, and response to, changes in environmental cues. There is much evidence in support of this notion. However, this research focuses almost entirely on avian species. Here, we compared the learning performance between urban and natural populations of a widespread reptile species in eastern Australia, the delicate skink (*Lampropholis delicata*), to determine whether the positive relationship between cognitive ability and urbanization is a broader phenomenon. Lizards were exposed to a standard Y-maze designed to measure their ability to learn to discriminate between safe and unsafe artificial refuges, a key problem that delicate skinks are likely to confront in urban environments. Counter to our predictions, no differences in any learning metric between urban and natural lizard populations were detected. We propose that similarity in environmental conditions in both habitat types may have resulted in a lack of selection for enhanced cognitive function in urban lizards.

ADDITIONAL KEYWORDS: behavioural flexibility – cognition – colour association – *Lampropholis* – reptile.

INTRODUCTION

The world is urbanizing at an unprecedented rate (Faeth, Saari & Bang, 2012). The process of urbanization brings about striking shifts across all levels of an ecosystem, as man-made infrastructure replaces and fragments natural vegetation (Sol *et al.*, 2011; Faeth *et al.*, 2012; Lowry, Lill & Wong, 2013; Sol, Lapiedra & González-Lagos, 2013). Resources such as food and refuges become artificial and often spatially concentrated, anthropogenic disturbances (e.g. human presence, pollution, light, noise) increase and predator–prey dynamics change (Sih, Ferrari & Harris, 2011; Miranda *et al.*, 2013; Sol *et al.*, 2013). As these ecological alterations are typically drastic and rapid, presenting wildlife with selective pressures that differ dramatically from those under which they naturally evolved, urban environments are considered to be

novel (Lowry *et al.*, 2013). Animals must either adjust to these novel challenges or be excluded from urbanized areas.

The ultimate outcome, when confronted with such novel challenges, varies greatly among and within species. Some seem to not only be unaffected by the urbanization process, but rather use urban habitats as ecological opportunities that allow them to proliferate and expand their range (Sol *et al.*, 2013). While others are either unable to cope with the altered ecological conditions or avoid cities altogether (Sol *et al.*, 2013). The key question, therefore, is as follows: what facilitates the successful exploitation of urban areas? Hypotheses range from ecological niche breadth to life-history traits (Kark *et al.*, 2007). However, these do little in the way of explaining intraspecific differences in the success or failure of city living. One factor that has recently been posited as an important determinant towards individual variation in fitness and survival within the urban–natural context is cognition (Niemela *et al.*, 2013; Sol *et al.*, 2013). Cognition

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refers to the mechanisms by which animals acquire, process, store and respond to information from their environment (Shettleworth, 1998). It is thought that the novel and often unpredictable conditions within cities can be mitigated for those who are capable of rapidly perceiving changes in environmental cues and able to learn to use that information to modify their behaviour adaptively (Sol *et al.*, 2008; Wright *et al.*, 2010; Niemela *et al.*, 2013). Learning enables such individuals to identify unfamiliar food sources and predators and to discriminate between suitable and non-suitable habitats (Galef, 1988; Segura *et al.*, 2007; Brown *et al.*, 2013). For example, populations of common mynas (*Acridotheres tristis*) varied in using novel food items across an urbanization gradient (Sol *et al.*, 2011). Birds inhabiting cities exhibited higher number of feeding innovations than those from less urbanized sites. Similarly, bird species having larger brain size (a common proxy of cognitive function) and a lowered perception of risk towards humans were more prone to invading urban habitats than those restricted to rural habitats (Carrete & Tella, 2011).

High cognitive performance has the benefit of enabling innovative and plastic behavioural responses, yet this benefit comes at a cost in terms of maintaining energetically expensive neural structures or the time needed to evaluate environmental conditions (Lefebvre & Sol, 2004; Niemela *et al.*, 2013; Kotrschal *et al.*, 2015). It stands to reason then, for those inhabiting natural habitats that are relatively more predictable and familiar than urban areas, the energetic costs associated with enhanced learning ability would be higher than the advantages it would provide. Much evidence does indeed support the theory that cities have selectively favoured enhanced cognitive function (Maklakov *et al.*, 2011; Sol *et al.*, 2011, 2013; Papp *et al.*, 2014; Audet, Ducatez & Lefebvre, 2016; Preiszner *et al.*, 2017). Yet, nearly all have focused on avian species with most other taxa, particularly reptiles, being ignored. Reptiles have been shown to exhibit intraspecific variation in cognitive ability (Day, Crews & Wilczynski, 1999; Amiel & Shine, 2012; Leal & Powell, 2012; Carazo *et al.*, 2014; Clark *et al.*, 2014), but whether this variation has promoted different cognitive phenotypes to emerge in urban vs. natural sites is yet to be determined. To this end, we compared the learning performance between urban and natural populations of a widespread reptile species, the delicate skink (*Lampropholis delicata*). The delicate skink occurs in habitats ranging in levels of urbanization from low to high and its behaviour varies along this gradient (Moule *et al.*, 2016). Lizards were exposed to a standard Y-maze designed to measure their ability to learn to discriminate between safe and unsafe artificial refuges. The delicate skink naturally has a high tendency to find and stay within refuges (Chapple,

Simmonds & Wong, 2011b). Thus, identifying secure shelter sites is a key problem that this species is likely to confront in urban environments.

METHOD AND MATERIALS

STUDY SPECIES AND FIELD COLLECTION

The delicate skink is a small [35- to 55-mm adult snout–vent length], heliothermic, lizard species that is locally abundant and geographically widespread in eastern Australia (Chapple *et al.*, 2011a). Its native distributional range spans 26° of latitude from north Queensland to southern Tasmania (Chapple *et al.*, 2011a). In addition, this species has become introduced to Hawaii, New Zealand and Lord Howe Island (Chapple *et al.*, 2013a, b, 2014; Chapple, Reardon & Peace, 2016; Tingley *et al.*, 2016). Within both its native and introduced range, delicate skinks occur in moist habitats, including rainforests, wet sclerophyll forests, woodlands and heaths, but also use urban settings (Chapple *et al.*, 2014).

Seventy-four adult male lizards with complete tails were captured by hand from four sites within the Sydney (NSW, Australia: 27°38 S, 153°05 E) during October 2014. Two sites were on developed lands with a high level of human disturbance and were defined as urban sites. The other two sites were on national park land and were thus defined as natural sites. Each lizard was individually marked with a unique Visible Implant Elastomer (Northwest Marine Technology) colour code and transported back to the animal housing facility. Groups of five lizards were kept in large plastic tubs (425 mm × 315 mm × 220 mm) and maintained at 22 °C with a 14 h light:10 h dark cycle (0600–2000 h). Basking lamps 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, skinks were not fed in the 24 h preceding each experimental trial (Shine, 2003). The project was conducted in accordance with our Animal Ethics Committee approvals (BSCI/2012/17, BSCI/2013/19, BSCI2014/11, BSCI/2014/26, BSCI 2015/01), associated scientific research permits (NSW: SL101203; VIC: 10006866, 10006867) and under special permission from Lane Cove National Park. All lizards were kept in captivity after the completion of the study to be used for future experiments.

ASSOCIATIVE LEARNING

Apparatus and general design

To assess the relationship between urbanization and cognitive ability, we used a standard Y-maze (Orchid Scientific & Innovative India Pty Ltd) as this is an

established experimental paradigm for testing learning in a range of taxa, including the delicate skink (Waldman, 1985; Burger *et al.*, 1991; Amiel, Lindström & Shine, 2014; Bezzina, Amiel & Shine, 2014). Mazes were constructed from opaque white plastic with each arm (L: 3750 mm × W: 650 mm × H: 1300 mm) connecting to a central decision point (CDP). The start arm was fitted with an opaque guillotine door, and the two remaining arms were designated as the decision arms. Both decision arms were painted with either blue or yellow horizontal stripes. These colours were selected as a skink's visual system is capable of distinguishing between them (Fleishman, Loew & Whiting, 2011; Clark *et al.*, 2014). A refuge (D: 57 mm × H: 43 mm) was placed at the end of each decision arm, with the refuge matching the colour of the arm. Skinks were observed from behind a black curtain and recorded using a Panasonic HC-V130 video camera placed above the maze. All equipment was cleaned between trials with soap and water to remove olfactory cues. Lizards that had lost all or a portion of their tails were removed from the study as tail autotomy has been shown to influence learning or behaviour (Downes & Shine, 2001; Cromie & Chapple, 2012; Carazo *et al.*, 2014).

Our study focused on a single functional component of cognition, associative learning. Measuring associative learning involves discrimination between two alternative stimuli presented simultaneously. The stimuli used in the present study were a 'safe' refuge and an 'unsafe' refuge. Refugia rather than food were selected as the reward because (1) refuge has been experimentally demonstrated to be an ecologically relevant reinforcement for this species given its high propensity to seek shelter (Chapple *et al.*, 2011b) and (2) the value of food declines across multiple trials in small lizards due to rapid satiation. The safe refuge was that in which lizards were permitted to remain inside without being disturbed, while lizards were removed from the unsafe refuges. A local cue (colour) was provided to enable lizards to discriminate between the two stimuli and reinforce the association between cue and stimuli (positive or negative).

Lizards were exposed to a two-phase learning paradigm where each phase differed in cue relevance, in this case the safe refugia. The first phase (training phase) served to train lizards to discriminate between the two stimuli, while the second phase (learning) was meant to determine whether the colour association was established and used to locate the safe refuge. As refuges used in the study were similar to those provided within their housing containers, no pre-training was conducted to familiarize lizards with their use.

Phase 1: training

Prior to the onset of the training phase, experimentally naive lizards were randomly assigned a safe goal colour (blue or yellow) that was held constant for the entire experiment. Goal allocation was counter-balanced among regions (urban/natural) and population to control for possible colour or side biases. The spatial location (i.e. left or right) of the goal remained constant for all trials during the training phase thereby enabling lizards to use either position and/or colour cues to navigate to the goal. Lizards were subjected to up to two training trials per day for a total of 15 trials or until the training criterion of five correct trials within six consecutive trials was met (Clark *et al.*, 2014; Noble, Byrne & Whiting, 2014). Lizards not reaching criterion were considered untrained and removed from the experiment, whereas all trained lizards continued onto the learning phase (phase 2).

At the start of each trial, lizards were individually placed behind the guillotine door for 5 min of acclimation. The gate was then lifted allowing them to move freely throughout the maze. Each lizard was given up to 5 min to enter half of its body into the goal shelter. Lizards remaining motionless for 15 continuous seconds were gently tapped on their dorsal surface near the base of the tail with a small paint brush to instigate movement. However, tapping provided no directional cue as the movement of the brush was perpendicular to the lizard's body. When lizards entered the incorrect (unsafe) shelter, they were chased out with the brush and allowed to continue manoeuvring the maze for the remaining time. If the goal was not reached within the allotted 5 min, the lizard was then chased into the goal shelter as a reinforcement. Trials were only scored as correct if the lizard initially turned into the goal arm and entered the goal shelter without leaving that arm. All other choices were scored as incorrect. The trial at which the criterion was achieved was designated as the training trial and served as a measure of learning speed. Additional metrics recorded during each trial were the number of incorrect turns (into non-goal arms from the CDP) as a measure of learning accuracy (Mamuneas *et al.*, 2014), as well as the position of the goal and colour cue to investigate potential side and colour biases. Lizards not entering the goal by the end of the trial were assigned 5 min as their time.

Phase 2: learning

In phase 2, the methods, criteria and metrics remained the same as that of the training phase described above. However, the maze colour layout changed randomly between trials. By changing the position of the goal, the use of colour vs. spatial cues could thus be deciphered. Lizards correctly finding the goal in five of six consecutive trials were considered to have learned the associative task, while those that did not meet the criteria were designated as non-learners.

STATISTICAL ANALYSES

To assess whether urbanization influenced cognitive performance, we used generalized linear models using SPSS v. 20.0. Learning metrics were assessed separately for each phase, and because cue colour and position were thought to be confounding effects, they were also included in the models. Population (urban or natural), colour cue position (training phase analyses only) and colour cue as well as their interaction were included as fixed effects, and criterion success (binary: 'yes' or 'no'), number of trials to reach criterion (count) and number of incorrect turns (count) were included as response variables. Only data associated with lizards reaching training criterion were included in models testing for number of trials to reach criterion and number of incorrect turns. Models predicting criterion success used the binary response 'negative binary logistic' that assumes a binomial distribution while those predicting number of trials to reach criterion (speed) and number of incorrect turns (accuracy) used a Tweedie distribution and 'log' link function. Pearson chi square was used as the scaling parameter to adjust for over-dispersion. Significance was determined by the Wald χ^2 statistic.

RESULTS

A total of 24 lizards (31%) met the criterion for the training phase, and eight of the 24 (33%) trained lizards successfully completed the learning phase (Table 1). Thirty-seven percent of natural lizards met the training criterion, while only 28% of urban lizards achieved six consecutive correct trials. Similarly, a greater percentage of natural vs. urban lizards were learners (natural: 38%; urban: 27%). No differences between urban and natural populations were evident in either phase for reaching criteria, learning speed (number of trials to reach criteria) or learning accuracy (number of incorrect turns) (Table 2). Goal colour, cue position or their interaction with urbanization also did not influence any of the metrics (Table 2).

DISCUSSION

Overall, a small percentage of delicate skinks were able to learn to associate a colour cue as it related to a safe shelter when presented with an associative learning task. However, no significant differences in any of the learning measures were detected in either phase between urban and natural populations. Learning speed, accuracy and the capacity to achieve criteria were the same across populations despite differences in the degree of urbanization. Our results contrast with much of the current research examining the cognitive effects of urbanization (Sol *et al.*, 2005; Carrete & Tella, 2011; Maklakov *et al.*, 2011; Papp *et al.*, 2014; Audet *et al.*, 2016; Cook *et al.*, 2017; Preiszner *et al.*, 2017). Urban populations have often been found to be better at problem solving, have greater feeding innovations and be more able to perceive the level of threat of unfamiliar predators. Collectively, these studies demonstrate that these differences in cognition arise in response to the higher amount of environmental variability and novelty characterizing urban habitats relative to those that are less affected by humans. Responsive cognitive types have a fitness advantage in variable environments as higher levels of behavioural flexibility and attention to changes in cues is favoured when resources, predators and ecological conditions change unpredictably or are unfamiliar (Niemela *et al.*, 2013). Learning enables new food items to be identified and handled, solutions to new problems to be developed and modified habitats to be utilized, thereby maximizing foraging opportunities and increasing availability of suitable habitat (Koenig, Shine & Shea, 2001; Schuck-Paim, Alonso & Ottoni, 2008; Roth, LaDage & Pravosudov, 2010; Sol *et al.*, 2011). Having the ability to perceive humans less as a predator and more as a potential food source also may have positive effects on urban dwellers. For instance, urban bird species have been shown to have lower flight initiation distances from humans than rural species enabling these individuals to approach novel food sources such as feeders and human waste more readily. Less time and energy may then be spent on anti-predator behaviours (e.g. vigilance, evasion, avoidance) among urban dwellers where valuable time and energy reserves can instead be devoted to other important activities such as foraging and reproduction (Carrete & Tella, 2011).

Table 1. Between-individual variation and repeatability of personality traits

	Activity	Exploration	Sociability
Inter-individual variation	254.73 ($F_{49,50}$ = 2.08)	155 130.9 ($F_{48,49}$ = 2.41)	35 115.6 ($F_{49,50}$ = 2.12)
ICC (95% CI)	0.35 (0.08, 0.57)	0.41 (0.15, 0.62)	0.36 (0.09, 0.58)
P	0.006	0.001	0.005

F-statistics are from one-way ANOVA, and ICC were used to assess repeatability. ANOVA, analysis of variance; CI, confidence interval; ICC, intraclass correlation coefficients.

Table 2. Results of LMMs examining the influence of trial number, batch and personality on learning metrics. Significant effects ($P < 0.05$) are in bold

Response	Predictor	$F_{d.f.}$	P
Number of incorrect turns phase 1	Intercept	$46.40_{1,138.85}$	**< 0.00**
	Batch	$0.71_{2,31.05}$	0.50
	Personality	$0.88_{1,167.49}$	0.35
	Trial number	$2.43_{15,197.42}$	**< 0.00**
	Personality × trial number	$1.85_{15,238.36}$	**0.03**
Latency phase 1	Intercept	$3661.19_{1,104.89}$	**< 0.00**
	Batch	$1.02_{2,38.23}$	0.37
	Personality	$0.65_{1,195.50}$	0.42
	Trial number	$1.06_{15,395.62}$	0.40
	Personality × trial number	$1.52_{15,369.90}$	0.10
Correct/incorrect trial phase 1	Intercept	$150.26_{1,104.76}$	**< 0.00**
	Batch	$0.26_{2,30.52}$	0.78
	Personality	$1.90_{1,198.44}$	0.97
	Trial number	$0.58_{15,355.11}$	0.89
	Personality × trial number	$1.02_{15,382.85}$	0.43
Number of incorrect turns phase 2	Intercept	$21.23_{1,37.01}$	**< 0.00**
	Batch	$0.07_{2,28.54}$	0.93
	Personality	$0.35_{1,167.49}$	0.85
	Trial number	$1.18_{19,160.722}$	0.28
	Personality × trial number	$0.61_{19,156.48}$	0.90
Latency phase 2	Intercept	$3578.57_{1,31.06}$	**< 0.00**
	Batch	$3.78_{2,31.05}$	**0.04**
	Personality	$0.38_{1,28.84}$	0.54
	Trial number	$2.50_{19,294.17}$	**< 0.00**
	Personality × trial number	$1.18_{19,282.20}$	0.27
Correct/incorrect trial phase 2	Intercept	$315.52_{1,24.18}$	**< 0.00**
	Batch	$2.89_{2,20.67}$	0.08
	Personality	$0.15_{1,20.96}$	0.71
	Trial number	$1.89_{19,265.17}$	**0.02**
	Personality × trial number	$1.82_{19,262.09}$	**0.02**

Similar findings have also been demonstrated among natural populations of birds inhabiting harsh vs. benign environmental conditions (Roth *et al.,* 2010, 2012). In these studies, black-capped chickadees (*Poecile atricapillus*) from high latitudes who experience severe and unpredictable environmental conditions outperformed birds from lower latitudes in problem-solving and spatial memory tasks. The authors suggested that this variation in learning between bird populations was driven by selection as high cognitive function promotes greater foraging efficiency of unpredictable and spatial variable food resources. In addition, this assertion was further supported by their common garden experiments showing that cognitive traits were indeed heritable.

The lack of relationship between associative learning and urbanization shown in our study may be due, at least in part, to a similarity between the delicate skink's natural environment under which they evolved within and the urban environment in which some populations currently inhabit (Sih *et al.*, 2011). Perhaps the ecological conditions confronting urban lizards are equally variable or novel as those in its natural habitats. Many aspects of the natural environment, such as seasonal variation in food availability, predator abundance and climate could potentially be as heterogeneous as those in urban environments. In addition, microhabitat characteristics may have similar complexity in both habitat types. Naturally, this species tends to prefer sites with an open canopy and a high abundance of leaf litter and woody debris to behaviourally thermoregulate while still being in close proximity to refuge and prey (Howard, Williamson & Mather, 2003). These features are also characteristic of the microhabitats within selected urban sites, such as parks, gardens and trail edges. Perhaps then that in the absence of the differential selective pressures normally attributed to cities, higher cognitive traits may in fact not be favoured in urban populations of delicate skinks.

Alternatively, there may indeed be variation in cognition among delicate skinks across the urbanization gradient, although it may not be in colour associative learning. This notion is evidenced by the fact that our study lizards rapidly learned how to discriminate between safe and unsafe refuges when the test involved both colour and spatial cues (phase 1), but this ability dramatically declined when the position of the safe refuge alternated randomly between trials (phase 2), forcing lizards to rely only on colour in discriminating between refuges. Colour may not be an ecologically relevant cue in delicate skinks as it may not be as reliable as spatial positioning. Finding and recognizing key resources in the wild is likely to be related more to their location relative to other objects or visual information, such as shape or size, rather than colour. Having little value under natural conditions would then result in poor overall colour association ability no matter what level of urbanization the lizards experienced. Previous studies have also demonstrated that position rather than colour cues was more important to cognitive processes in reptiles (Bitterman, 1965; Grisham & Powers, 1990; Day, Ismail & Wilczynski, 2003).

Population differences in cognition among delicate skinks may instead arise in other mechanisms such as spatial memory or problem solving. Indeed, variation in cognitive traits other than colour association has been detected in several lizard species as a result of ecological factors (Paulissen, 2011; Amiel & Shine, 2012; Amiel *et al.*, 2014; Clark *et al.*, 2014; Dayananda & Webb, 2017). For instance, developmental temperatures were found to influence spatial learning and problem-solving abilities in three-lined skinks (*Bassiana duperreyi*) (Amiel & Shine, 2012; Clark *et al.*, 2014). Lizards from hotter nests had higher learning performance than those from colder nests. Future studies should investigate other cognitive traits to determine whether urbanization does indeed favour higher cognitive performance among delicate skinks in particular and lizards in general.

CONCLUSION

Our findings show that urbanization has no influence on colour associative learning in the delicate skink. This is the first study to investigate the cognitive effects of urbanization in a reptile. More research is needed to determine whether urban populations of reptiles have greater performance in other cognitive traits such as spatial discrimination or problem solving. Furthermore, quantifying the level of variability and novelty in urban habitats relative to their natural counterparts is also necessary to determine whether selective forces favouring enhanced cognitive traits

are actually at play. Together, this information would enable us to better understand the evolution of cognition and its ecological consequences.

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