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Shrinking into the big city: influence of genetic and environmental factors on urban dragon lizard morphology and performance capacity

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Abstract

Urban wildlife faces a novel set of challenges resulting in selective pressure that can lead to population-level changes. We studied Australian water dragons (*Intellagama lesueurii*) from urban and natural populations to test if urban populations differed in body size, shape, and performance capacity. If urban-derived morphology has arisen through selection, we predicted distinct morphological differences between wild dragons from urban and natural areas in both adult and hatchling life-stages. Urban hatchlings were morphologically distinct (shorter body lengths and longer limbs) from natural populations, while urban adult males continued this trend but only for body size (shorter body lengths). We then experimentally reared hatchlings originating from urban and natural populations within urban- and natural-style enclosures (2×2 factorial design) for a year to determine if differences in morphology and performance capacity (sprint speed, endurance, and clinging ability) were related to either the individual's origin population or developmental environment. Yearlings reared in urban-style enclosures, irrespective of population origin, had smaller body sizes compared to those from natural-style enclosures, suggesting developmental environment was affecting their morphology. Despite this difference in body size, yearling dragon performance capacity was not significantly different between treatments. Overall, this study provides evidence of a complex relationship driving urban-divergent morphology – whereby urban dragons emerge as smaller hatchlings with longer limbs (innate traits) and are then further influenced by the urban environments that they develop in (phenotypic plasticity); however, and potentially owing to behavioral, ecological, and demographical differences, these changes appear to be sex-specific.

Keywords Adaptation · HIREC · Natural selection · Phenotypic change · Phenotypic plasticity · Reptile · Urban evolution

Introduction

Suitable habitat isolated within urban areas can be thought of as 'islands' and are exceptional crucibles for studying the evolution of species adapting to, and persisting within, them (Alberti et al. 2017; Johnson and Munshi-South 2017; Ouyang et al. 2018). Novel environments create selective pressures within urban landscapes that may have a strong effect on remnant populations, resulting in physiological (French et al. 2008; Atwell et al. 2012; Bonier 2012) and morphological traits (Marnocha et al. 2011; Winchell et al. 2016, 2018; Putman et al. 2019) that are divergent from conspecifics living in natural areas (i.e., urban-derived phenotypes). As such, there is a growing body of evidence that urban landscapes have resulted in phenotypic differentiation. For example, urban-dwelling birds and lizards exhibit a decreased physiological stress response when compared to natural-living counterparts (French et al. 2008; Atwell et al. 2012), while urbanized ants and lizards have increased their

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heat tolerance (Angilletta Jr et al. 2007; Campbell-Staton et al. 2020). Urban-derived morphology has been observed in several species of lizard (French et al. 2008; Marnocha et al. 2011; Iglesias et al. 2012; Littleford-Colquhoun et al. 2017), songbirds (Evans et al. 2009; Brown and Bomberger Brown 2013; Hutton and McGraw 2016), mice (Slábová and Frynta 2007), and spiders (Lowe et al. 2014). Despite these insights, however, studies examining if urban-derived phenotypes are arising through heritable adaptation remain relatively rare for wildlife (but see: spider behavior, Kralj-Fišer and Schneider 2012; lizard morphology, Winchell et al. 2016; thermal tolerance, Diamond et al. 2017, Campbell-Staton et al. 2020; lizard behavior, Baxter-Gilbert et al. 2019). As interest in this topic increases, there is evidence of globally widespread divergent phenotypes (Alberti et al. 2017; French et al. 2018; Ouyang et al. 2018) and marked genetic divergence between urban and natural-living populations (Delaney et al. 2010; Harris et al. 2013; Littleford-Colquhoun et al. 2017) which supports the idea that anthropogenic landscapes are capable of altering the evolutionary trajectories of urban species (i.e., urban evolution; Johnson and Munshi-South 2017).

Comparative examinations of the morphology and performance capacity of urban wildlife and their native counterparts provides a promising avenue for determining the contributions environmental factors and selection have on promoting urban-derived phenotypes. There is a close association between environmental factors and morphology (Collette 1961; Arnold 1983) and measures of whole-organism performance can demonstrate how variation in morphology, physiology, and fitness interrelate (Huey et al. 1984; Garland Jr and Losos, 1994; Irschick et al. 2008; Lailvaux and Husak 2014). The effects of habitat structure on morphology and performance capacity have been well documented in lizards (Losos 1990; Losos et al. 2000; Irschick et al. 2005; Kolbe and Losos 2005) and performance capacity is a heritable trait in several species (Garland et al. 1990; Le Galliard et al. 2004; Irschick et al. 2008). For example, variation in *Anolis* spp. body size and limb morphology provides both sprinting and jumping performance advantages relating to the size and shape of perching substrates (Losos and Sinervo 1989; Losos 1990; Irschick et al. 2005), which can drive morphological evolution during periods of ecological change (Stuart et al. 2014).

Within an urban context, recent research has documented urban-derived morphology in several species of lizard, resulting in urban populations showing: an increase in limb length (brown anoles, *Anolis sagrei*, Marnocha et al. 2011; swamplands lashtails, *Tropicagama temporalis*, Iglesias et al. 2012; Puerto Rican crested anoles, *A. cristatellus*, Winchell et al. 2016, 2018), a decrease in limb length (western fence lizards, *Sceloporus occidentalis*; Putman et al. 2019), and an increase in body length (brown anoles, Marnocha et al., 2011; swamplands lashtails, Iglesias et al., 2012). These changes in body size and shape related to urbanization are likely to impact a species' performance capacity. For example, urbanization increases the amount of flat impervious surfaces (hardscape) within a habitat (Dale and Frank 2014; Barnett 2015) and longer limbs have been associated with the use of broader surfaces in several lizard taxa (Losos and Sinervo 1989; Kohlsdorf et al. 2001), including urban hardscape (Marnocha et al. 2011; Iglesias et al. 2012). Furthermore, the divergent morphology observed in urbanized Puerto Rican crested anoles not only provides an ecologically relevant performance advantage for running on natural and anthropogenic substrates, but also represents a heritable trait (Winchell et al. 2016, 2018). Increased sprint speed may be ecologically important as it can enhance escape ability from common mortality sources found in urban landscapes (e.g., domestic/novel predators, like cats and dogs; Koenig et al. 2002). Adaptation favoring specific morphological traits or performance capabilities may also result in trade-offs (i.e., negative correlation between traits; Lailvaux and Husak 2014). As such, if an urban-derived morphology (e.g., longer limbs) result in performance advantages in sprint speed or clinging ability, then this may come at a cost to other traits (e.g., endurance). Urban environments tend to have limited suitable habitat and space, resulting in urban lizards having decreased home range sizes (e.g., common wall lizards, *Podarcis muralis*; Brown et al. 1995). With smaller home ranges, territories to patrol, and distances between mates, selection for endurance capacity may be relaxed; with increased sprint speed and clinging ability on hard flat surfaces, related to increased limb length, being favored instead.

We studied Australian water dragons (*Intellagama lesueurii*) to test: 1) if urban-derived and therefore divergent, morphological phenotypes (body size and limb lengths) have arisen in urban environments in Sydney, Australia; 2) if they are a result of selection or plasticity; and 3) if any altered morphology may impact individual performance. Recent studies have shown that water dragons from urban populations are undergoing rapid genetic and morphological diversification (Littleford-Colquhoun et al. 2017), as well as shifts in innate behavior (Baxter-Gilbert et al. 2019) – suggesting this species may be a promising model for studying urban evolution in lizards. We first examined if differences in adult and hatchling dragon morphology exist between urban and natural populations, and predicted that urban lizards would have a larger body size and longer limbs; mirroring the trend seen in other urbanized lizard taxa (Marnocha et al. 2011; Iglesias et al. 2012; Winchell et al. 2016, 2018). If differences in morphology are detectable at hatching it may suggest a heritable/genetic mechanism behind urban-derived divergent traits. We also experimentally reared hatchlings from urban and natural origin populations within urban- and natural-style enclosures (2×2 factorial design) for a year to test if any morphological differences were related directly to either the individual's origin population type (heritable traits) or rearing environment

(phenotypic plasticity). We predicted that if any urban-derived morphology was a result of adaptation, then trait expression would be significantly related to an individual's origin population type (urban vs natural). Last, we examined three measures of a dragon's performance (sprint speed, endurance, and clinging ability on concrete and tree bark) for the experimentally reared yearling dragons. Based on our previous prediction of increased limb length, we predicted that dragons from urban-origin populations would show an increase in sprint speed and clinging ability on anthropogenic surfaces, while also having a decreased endurance capacity (due to known trade-offs between sprint speed and endurance; Vanhooydonck et al. 2001, 2014; Lailvaux and Husak 2014).

Methods

Study species and field collection

Australian water dragons are large agamid lizards (maximum snout-vent length: 304 mm, Thompson 1993) with a lifespan of 28–40 years (Harlow and Harlow 1997; Griffiths 2006) and a generation time of 5 years (Littleford-Colquhoun et al. 2017). Found across much of eastern Australia, they are common around bodies of freshwater and are typically associated with forested riparian zones (Cogger 2014). They are also found within several major cities and are frequently found in many human-dominated landscapes (e.g., urban greenspaces, botanical gardens, zoos, and backyards; Littleford-Colquhoun et al. 2017; Baxter-Gilbert and Whiting 2018). These dragons are adept at swimming, but they are also skilled at climbing and sprinting (Baxter-Gilbert et al. 2018a).

We collected dragons from seven sites (four urban and three natural) within a 50 km radius within the greater Sydney area in New South Wales, Australia, from October 2015 to March 2017. Urban areas had a dense local human population and a landscape that was widely human-modified (e.g., concrete, gardens, roads, buildings). Natural areas, although not free from human disturbance, were generally riparian greenspaces consisting of waterways with wooded shorelines, native vegetation, and a comparatively low human presence (see Supplementary Material for site-specific details).

All adult dragons were captured by hand or lizard lasso (i.e., a loop of string with a sliding knot affixed to the end of a pole), and gravid females were palpated (i.e., gently squeezing their abdomen) to feel for the presence of shelled eggs. For the field component of our study, adult females (n = 123 females) and males (n = 74) were weighed, measured (see below), and released at their site of capture. During the nesting season (October/November) gravid females were collected, induced to oviposit with an injection of calcium gluconate and synthetic oxytocin, and then post-oviposition released at their site of capture (for details see Baxter-Gilbert et al. 2018b). Clutches of eggs were identically incubated in the lab at a constant temperature of 26.5 °C (for details see Baxter-Gilbert et al. 2018b) and, upon emerging, a random subset of the hatchlings were measured (n = 200) and released back at the mother's site of capture. For the 2 × 2 factorial experiment, we used a subset of the retained hatchlings (n = 97) and they were housed on-site at Macquarie University and regularly measured over their first year of life (see details below).

Morphological measurements

We measured snout-vent length (SVL), upper forearm length (UFL), lower forearm length (LFL), upper hindlimb length (UHL), lower hindlimb length (LHL), and total hindlfoot length (HFL), similar to previous water dragon research (see Littleford-Colquhoun et al. 2017). All measurements (except SVL) were made with digital Vernier calipers (± 0.01 mm), and SVL was measured with a clear plastic ruler (± 1 mm). For adults and released hatchlings, these morphometric measurements were taken either post-capture or post-hatching (before release), respectively. Hatchlings in the rearing treatments were measured six times over their first year of life (beginning after the hatching season and every 60 days thereafter; Table S4). For analyses, we combine UFL and LFL to get an overall measure of forearm length, as well as UHL and LHL for an overall measure of hindlimb length. Before statistical analysis we log-transformed all of these variables (Lleonart et al. 2000); this ensured allometric relationships were linear.

2 × 2 factorial experiment

We used outdoor enclosures at Macquarie University to replicate the weather and climate they would naturally experience around Sydney, Australia. Enclosures were 5 × 2.5 m and constructed within a netted predator exclusion area. Natural-style enclosures were outfitted with natural vegetation (e.g., grasses, weeds, and shrubs), wooden perches of varying diameter (5–50 mm), a shaded area, and a 150 L plastic pool (i.e., Fig. 1a). Urban-style enclosures were outfitted with hard, flat surfaces (paving stones, concrete blocks, steel sheets, and roofing tiles), eucalypt mulch, a shaded area, and the same type of plastic pool as the natural treatment (i.e., Fig. 1b). Both the natural- and urban-style enclosures were replicated three times, for a total of six enclosures. Each enclosure held individuals from natural origin populations (n = 8) and urban origin populations (n = 8), for a total of 16 dragons per enclosure. Siblings were split equally into natural- and urban-style enclosures, thereby controlling for maternal and clutch effects. Each enclosure experienced the same husbandry procedures (e.g., provided with water and crickets, *Acheta domesticus*, ad

Fig. 1 The setup for the 'natural' (**a**) and 'urban' (**b**) treatments. All replicates were identical in design

libitum and having access to free-living invertebrates inhabiting their enclosures). Dragons were housed in these enclosures for their first year of life.

Performance measures

We recorded each dragon's SVL (mm) (same methods as above) before performance trials, and their body temperature (± 0.1 °C) immediately prior to each individual's performance trial (following Baxter-Gilbert et al. 2018a). All performance trials were conducted by the same researcher (JBG) to ensure consistency.

Endurance and Sprint speed

Both endurance and sprint speed followed similar methods as described in Noble et al. (2014), with the exception that dragons were given a five day rest period between repeated measures. Each measurement was repeated three times. The sprint speed trial was measured on a 1.5 m running track lined with a textured rubber mat, marked at 0.25 m intervals (Noble et al. 2014). Dragons were placed at the starting line and stimulated to run by pinching the base of the tail with a blue nitrile gloved hand. We recorded sprint speed using a Panasonic HD video camera (120 fps) and quantified the maximum speed during each trial by determining the shortest time it took the individual to cross between the 0.25 m intervals, which was then transformed into m/s.

The endurance trial immediately followed the sprint speed trial and measured the time (s) it took a dragon to tire during continuous running (Noble et al. 2014). The endurance arena was constructed from a clear plexiglass box (1.1 × 0.08 m) with an open bottom placed on a human treadmill set to a fixed running speed of 1.0 km/h (Garland and Else 1987; Noble et al. 2014). During the trial dragons were placed in the first third (0.36 m) of the treadmill, so that as they tired there would be enough time to pinch the base of the tail 10 consecutive times before the dragon was carried along the track and pushed off the end (Garland and Else 1987; Baxter-Gilbert et al. 2018a).

Clinging ability

We conducted two clinging trials with one rest day between trials. A trial consisted of three measures of a dragon's ability to grip and hold on to the horizontal surface (i.e., a concrete slab and a section of tree bark) while being pulled backward at a steady pace until it detached. A Pesola spring dynamometer fitted with a slide marker to record maximum force (N; medio-line, model #40006) was attached to the dragon by a 0.5 m length of cotton string tied in a harness anterior to the pelvic girdle. The direction of the pulling was kept level to the substrate (preventing upward and downward pulling forces) and directly to the rear of the dragon (preventing lateral forces). The testing arenas were 0.6 × 0.2 m with a 0.3 m black plastic wall around three of the four sides. The concrete base was an aerated concrete brick (Hebel, PowerBlock). The tree bark base was a 0.6 × 0.2 m section of turpentine (*Syncarpia glomulifera*), a tree species found throughout the Australian water dragon's distribution. Although both flat surfaces, this measure examined the dragon's ability to adhere to natural and anthropogenic substrates.

Statistical analyses

All statistical tests were conducted in R version 3.2.3 (R Core Team, 2016). Before starting analyses, we explored each dataset following the protocol outlined in Zuur et al. (2010). We did not find any unexplainable outliers or strong collinearity between our predictor variables. For all models, prior to interpretation, we verified the assumptions of normality and homoscedasticity of residuals. Data are presented as mean ± standard error (*SE*) in the text, unless otherwise specified, and α was set at 0.05 for all models.

Morphology: Adults

We measured 197 adult dragons (123 females and 74 males) from seven sites in the greater Sydney area (four urban and three natural; for details see Supplementary Material). We used linear mixed effect models (LMMs) to examine differences in morphology between urban and natural populations with the R package *'lme4'* (Bates et al. 2015). Identical LMMs were performed separately for both sexes, because this species is sexually dimorphic (Baird et al. 2012). Supporting this, in preliminary analyses, we found that males were larger in SVL than females ($\beta = 0.083$, $SE = 0.005$, $t_{2,\ 192} = 17.353$, $p < 0.001$). Also, males were larger than females in forearm length ($\beta = 0.029$, $SE = 0.005$, $t_{2,\ 191} = 5.336$, $p < 0.001$), hindlimb length ($\beta = 0.034$, $SE = 0.006$, $t_{2,\ 191} = 5.944$, $p < 0.001$), and hindfoot length ($\beta = 0.040$, $SE = 0.005$, $t_{2,\ 191} = 7.911$, $p < 0.001$) when controlling for SVL (see Table S1 for model outputs). So, separately for each sex, we used LMMs to examine differences in SVL (response variable) between origin populations (categorical variable with two levels: urban or natural), and these models included a random intercept of site to incorporate dependency among observations of lizards from the same location. Models examining differences in the other morphological traits (forearm, hindlimb, and hindfoot lengths) contained the same fixed and random factors, but also included the additional fixed factor of SVL to standardize this variable with respect to body length.

Morphology: Hatchlings

We sampled 200 hatchlings from 40 unique clutches across four populations (two urban [$n = 84$] and two natural [$n = 116$]). Models examining differences in hatchling SVL included the fixed factor of origin population (categorical with two levels: urban or natural), and the random intercepts of site and clutch to incorporate dependency among observations of lizards from the same location or the same clutch, respectively. Models examining differences in the other morphological traits (forearm, hindlimb, and hindfoot lengths) contained the same fixed and random factors, but also included the additional fixed factor of SVL to standardise the response variable with respect to body length.

Morphology: 2 × 2 factorial experiment

Juvenile dragons were sampled after approximately one year in captivity. On average, juveniles sampled were 371.53 days old (*SE* = 0.99 days, range = 351 to 386 days). We were able to sampled 77 yearlings from 23 unique clutches from six populations (three urban [$n = 38$] and three natural [$n = 39$]), which were raised in a total of six enclosures (three natural- and three urban-style). Linear mixed effects models that examined differences in juvenile SVL included the fixed factors of age (days; continuous), origin population (categorical with two levels: urban and natural), and rearing treatments (categorical with two levels: urban and natural). An interaction effect between origin population and rearing treatments was also included in models. The model also included random intercepts of clutch, site, and rearing enclosure to incorporate dependency among observations from the same clutch, the same location, and the same captive rearing enclosure, respectively. Models examining differences in yearling morphological traits (forearm, hindlimb, and hindfoot length) contained the same fixed and random factors, but also included the additional fixed factor of SVL to standardize the response variable with respect to body length.

If the interaction between origin population and rearing treatment was significant, then we used the function '*lsmeans*' in the '*lsmeans*' R package (Lenth 2016) to statistically compare among all origin population and rearing treatment combinations (6 comparisons in total). The *p*-values generated for these comparisons were corrected using Tukey's HSD multiplicity adjustment (Lenth 2016). If the interaction effect was not significant, then it was removed from the model and the model was re-run in order to allow interpretation of main effects.

Performance: 2 × 2 factorial experiment

The performance trials were limited to a subset of the yearling dragons within our experiment. In total we sampled performance from 59 yearlings from 22 unique clutches and from six sites (three urban [$n = 30$] and three natural [$n = 29$]) that were raised in a total of six enclosures (three natural- and three urban-style). We examined if dragon performance metrics varied across experimental treatments using four separate, identical LMMs for each response variable. The response variables were endurance (s), sprint speed (m/s), clinging force on concrete (N), and clinging force on tree bark (N). We analyzed clinging ability separately for each substrate, because it was significantly lower on concrete than tree bark (Table S5). We included repeated measures of each performance trait, instead of using only maximal values, within our LMMs to account

for within-individual variation in our study (Careau and Wilson 2017; Baxter-Gilbert et al. 2018a).

Fixed factors were trial order (continuous), SVL (continuous, log-transformed), body temperature (continuous), origin population (categorical with two levels: urban and natural), rearing treatment (categorical with two levels: urban and natural), as well as the interaction between origin population and rearing treatment. Post-hoc assessment and treatment of the interaction effect was the same as described above. There were significant trial order effects in our data (specifically for endurance and sprint speed; Tables S7 and S8), potentially due to training effects, and inclusion of them in our models statistically controlled for this potentially confounding variable (Baxter-Gilbert et al. 2018a). Models also included the random intercepts of juvenile identity, clutch, site, and rearing enclosure to incorporate dependency among observations of the same individual, clutch, location, and captive rearing enclosure, respectively.

Results

Morphology: Adults

Females did not significantly differ in SVL ($\beta = -0.049$, $SE = 0.049$, $t_{2,\ 120} = -0.987$, $p = 0.324$) between urban and natural sites. Female forearm length ($\beta = 0.003$, $SE = 0.005$, $t_{2,\ 119} = 0.591$, $p = 0.555$), hindlimb length ($\beta = 0.029$, $SE = 0.035$, $t_{2,\ 119} = 0.810$, $p = 0.418$), and hindfoot length ($\beta = 0.040$, $SE = 0.044$, $t_{2,\ 119} = 0.900$, $p = 0.370$), relative to SVL, were not significantly different between natural and urban sites. All morphological traits (forearm, hindlimb, and hindfoot length) were significantly and positively related to SVL (see model output in Table S2).

Contrary to our prediction, male SVL was smaller in urban than natural populations (Table 1, Fig. 2b). Based on a summary of raw data, urban males were smaller by 10.3 mm (average SVL for urban males = 222.3 ± 3.4 mm, and natural males = 232.6 ± 2.5 mm) than males from natural habitats. Male forearm, hindlimb, and hindfoot length, relative to SVL, did not differ between urban and natural populations (Table 1). The models for limb and foot lengths controlled for SVL, since SVL was significantly and positively related to all these traits (Table 1). This being said, because males in urban populations were significantly smaller than males in natural populations, this trend also applied to the absolute length of forearms, hindlimbs and hindfeet of dragons. In fact, based on raw absolute values, urban male forearms, hindlimbs, and hindfeet were smaller, on average by 0.485 mm (0.7% decrease), 3.337 mm (2.9% decrease), and 3.381 mm (4.3% decrease) respectively, compared to natural-living males.

Morphology: Hatchlings

Urban hatchlings had a smaller SVL at birth than hatchlings from natural populations (Table 2, Fig. 2a). Hatchling forearm and hindlimb length, relative to SVL, was larger in urban than natural populations (Table 2). Hatchling hindfoot length, relative to SVL, did not differ between urban and natural populations (Table 2). The models for limb and foot lengths controlled for SVL, since SVL was significantly and positively related to all these traits (Table 2).

Morphology: 2 × 2 factorial experiment

Yearling water dragon SVL was not significantly related to origin population, but dragons raised in urban treatments had smaller SVLs than those raised in natural treatments (Table 4). Based on a summary of raw data, yearlings raised in urban enclosures were smaller by 4.3 mm than yearlings raised in natural enclosures (average SVL for urban-reared yearlings = 88.1 ± 1.3 mm, and natural-raised yearlings = 83.8 ± 1.0 mm; Table 3). The interaction effect between origin population and rearing treatment was not significant ($\beta = 0.004$, $SE = 0.011$, $t_{4,67} = 0.397$, $p = 0.692$; Table 4).

Yearling forearm, hindlimb, and hindfoot length, relative to SVL, also did not differ significantly between origin population or rearing treatments, and there was no significant interaction between these factors either (Table S3). All models controlled for dragon age, since age was significantly and positively related to SVL (Table 4), but age was not signficantly related to any other morphological trait (Table S3). The models for limb and foot lengths also controlled for SVL, and SVL was significantly and positively related to all these traits (see model outputs in Table S3). This being said, as yearlings in urban enclosures were significantly smaller than yearlings in natural enclosures, this trend also applies to the absolute length of forearms, hindlimbs, and hindfeet (Table 3). In fact, based on raw absolute values, urban-raised yearling forearms, hindlimbs, and hindfeet were smaller, on average, by 1.083 mm (4.1% decrease), 1.932 mm (4.5% decrease), and 1.413 mm (4.4% decrease) respectively, than those of natural-raised yearlings.

Performance: 2 × 2 factorial experiment

Dragon endurance (Table S6), sprint speed (Table S7), and clinging ability on concrete (Table S8) and tree bark (Table S9) did not differ significantly between origin populations, rearing treatments, and in all cases there was not a significant interaction between these two factors. All performance measures were significantly and positively related to dragon SVL (Table S6-S9).

Table 1 Outcomes of linear mixed effect models examining differences in male Australian water dragon morphological traits (from top to bottom: snout-vent, forearm, hindlimb, and hindfoot lengths) between urban and natural populations. All morphological traits were log-transformed before analyses. Model estimates (β) of fixed effects are presented with their corresponding standard errors (*SE*), variance estimates (σ^2) are supplied for residuals and random effects. Test statistics (*t*) are presented and all significant values ($p < 0.05$) are presented in bold. Reference levels for categorical variables are given in brackets following the variable name

	Variable Names	Model Output			
Snout-vent Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	**2.366**	**0.007**	**328.571**	**<0.001**
	Population (Urban)	**−0.021**	**0.010**	**−2.155**	**0.031**
	Random Effects	σ^2			
	Site	<0.001			
	Residuals	0.001			
Forearm Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	**−0.338**	**0.164**	**−2.058**	**0.040**
	Snout-vent Length	**0.922**	**0.069**	**13.288**	**<0.001**
	Population (Urban)	0.012	0.008	1.519	0.129
	Random Effects	σ^2			
	Site	<0.001			
	Residuals	<0.001			
Hindlimb Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	−0.069	0.152	−0.452	0.651
	Snout-vent Length	**0.903**	**0.064**	**14.066**	**<0.001**
	Population (Urban)	0.002	0.009	0.169	0.866
	Random Effects	σ^2			
	Site	<0.001			
	Residuals	<0.001			
Hindfoot Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	**0.378**	**0.151**	**2.502**	**0.012**
	Snout-vent Length	**0.640**	**0.064**	**10.041**	**<0.001**
	Population (Urban)	−0.004	0.008	−0.507	0.612
	Random Effects	σ^2			
	Site	<0.001			
	Residuals	<0.001			

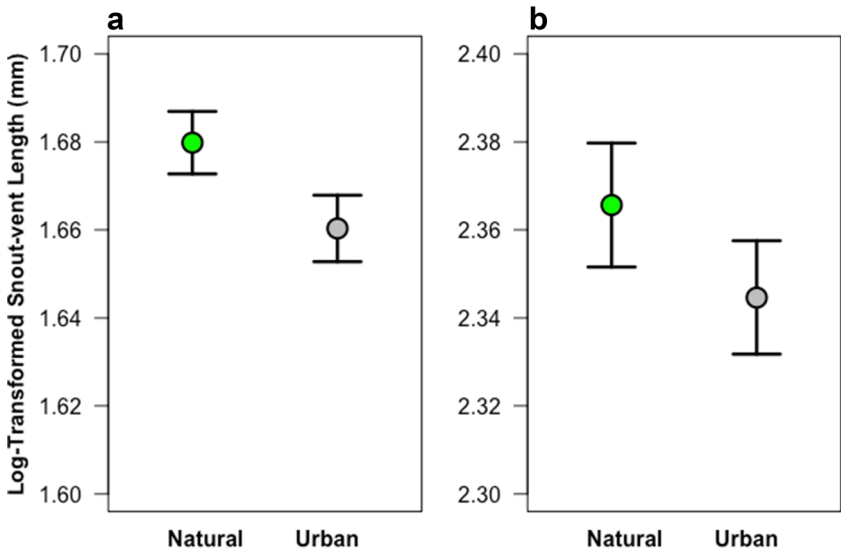

Fig. 2 Urban populations (grey circles) of (**a**) hatchling and (**b**) adult male Australian water dragons have smaller mean snout-vent lengths (SVL) than natural populations (green circles). SVL was log-transformed before statistical analyses. Circles are predicted fitted means, and error bars reflect predicted 95% confidence intervals

Table 2 Outcomes of linear mixed effect models examining differences in hatchling Australian water dragon morphological traits (from top to bottom: snout-vent, forearm, hindlimb, and hindfoot lengths) between urban and natural populations. All morphological traits were log-transformed before analyses. Model estimates (β) of fixed effects are presented with their corresponding standard errors (*SE*), variance estimates (σ^2) are supplied for residuals and random effects. Test statistics (*t*) are presented and all significant values ($p < 0.05$) are presented in bold. Reference levels for categorical variables are given in brackets following the variable name

	Variable Names	Model Output			
Snout-vent Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	**1.680**	**0.004**	**462.61**	**<0.001**
	Population (Urban)	**−0.020**	**0.005**	**−3.683**	**<0.001**
	Random Effects	σ^2			
	Site	<0.001			
	Clutch	<0.001			
	Residuals	<0.001			
Forearm Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	−0.060	0.132	−0.456	0.649
	Snout-vent Length	**0.725**	**0.078**	**9.240**	**<0.001**
	Population (Urban)	**0.019**	**0.007**	**2.598**	**0.009**
	Random Effects	σ^2			
	Site	<0.001			
	Clutch	<0.001			
	Residuals	<0.001			
Hindlimb Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	−0.083	0.125	−0.663	0.507
	Snout-vent Length	**0.860**	**0.074**	**11.566**	**<0.001**
	Population (Urban)	**0.018**	**0.004**	**4.309**	**<0.001**
	Random Effects	σ^2			
	Site	<0.001			
	Clutch	<0.001			
	Residuals	<0.001			
Hindfoot Length	*Fixed Effects*	β	*SE*	*t*	*p*
	Intercept (Natural)	0.093	0.096	0.973	0.331
	Snout-vent Length	**0.717**	**0.057**	**12.551**	**<0.001**
	Population (Urban)	0.003	0.005	0.647	0.518
	Random Effects	σ^2			
	Site	<0.001			
	Clutch	<0.001			
	Residuals	<0.001			

Table 3 Average ± standard error of raw (i.e., not log-transformed) (a) morphological traits and (b) performance measures of yearling Australian water dragons for each origin population and rearing treatment combination (urban origin with urban rearing [uU], natural origin with urban rearing [nU], natural origin with natural rearing [nN], and urban origin with natural rearing [uN]) within our 2 × 2 factorial experiment

(a) Morphological Traits (mm)	**nN** ($n = 17$)	**nU** ($n = 21$)	**uN** ($n = 21$)	**uU** ($n = 18$)
Snout-vent Length	90.353 ± 1.867	85.667 ± 1.308	86.286 ± 1.815	81.556 ± 1.534
Forearm Length	26.735 ± 0.542	25.958 ± 0.655	25.820 ± 0.522	24.201 ± 0.527
Hindlimb Length	44.149 ± 0.971	42.224 ± 0.783	42.140 ± 0.778	39.804 ± 0.754
Hindfoot Length	33.070 ± 0.693	32.009 ± 0.588	31.695 ± 0.609	29.601 ± 0.564
(b) Performance Measures	**nN**	**nU**	**uN**	**uU**
	($n = 14$)	($n = 16$)	($n = 15$)	($n = 14$)
Endurance (s)	138.810 ± 4.925	126.971 ± 5.040	127.136 ± 4.100	117.141 ± 4.525
Sprint Speed (m/s)	1.202 ± 0.027	1.252 ± 0.037	1.161 ± 0.028	1.204 ± 0.032
Concrete – Clinging Ability (N)	2.860 ± 0.098	2.613 ± 0.088	2.734 ± 0.119	2.508 ± 0.104
Bark – Clinging Ability (N)	3.383 ± 0.090	3.194 ± 0.098	3.114 ± 0.129	2.880 ± 0.123

Table 4 Outcomes of linear mixed effect models examining difference in yearling Australian water dragon snout-vent length between origin populations and rearing treatments. Snout-vent length was log-transformed before analyses. Model estimates (β) of fixed effects are presented with their corresponding standard errors (*SE*), variance estimates (σ^2) are supplied for residuals and random effects. Test statistics (t) are presented and all significant values ($p < 0.05$) are presented in bold. Reference levels for categorical variables are given in brackets following the variable name. The interaction between origin population and rearing treatment was not significant ($\beta = 0.004$, $SE = 0.011$, $t_{4,67} = 0.397$, $p = 0.692$), and it was removed and the model re-run. This is indicated with a "na" below

Variable Names	Model Output			
Fixed Effects	β	*SE*	t	p
Intercept (Natural Population, Natural Treatment)	**1.207**	**0.198**	**6.088**	**<0.001**
Age	**0.002**	**0.001**	**3.723**	**<0.001**
Origin Population (Urban)	-0.021	0.014	-1.500	0.134
Rearing Treatment (Urban)	**-0.019**	**0.006**	**-3.401**	**0.001**
Origin Population*Rearing Treatment (Urban Population, Urban Treatment)	na	na	na	na
Random Effects	σ^2			
Site	<0.001			
Clutch	<0.001			
Housing Enclosure	<0.001			
Residuals	0.001			

Discussion

Urban Australian water dragons were morphologically distinct from their natural-living counterparts. As we predicted, urban hatchlings had proportionally longer limbs, however, contrary to our expectations, urban hatchlings and adult males were smaller (SVL) when compared to natural populations. Adult females showed no significant morphological differences between urban and natural populations. These findings were generally antithetical to our predictions (i.e., representing smaller urban body sizes), but also suggest that although urban-derived morphology was innate at hatching, either through genetic or maternal effects, the continued expression over time required additional factors (e.g., sex- and/or habitat-specific influences across ontogeny).

Our 2 × 2 factorial experiment supports the assertion that, after hatching, water dragon morphology is likely mediated by environmental factors. After being reared for a year in our experimental environment, individuals from urban-style enclosures were significantly smaller in body size (SVL) compared to those raised in natural-style enclosures, irrespective of their origin population. This suggests that the persistence of urban-derived morphology is related to environmental cues (e.g., increased broad, flat, or hard surfaces) triggering phenotypic plasticity for a smaller overall body size. Phenotypic plasticity of body size and shape related to differences in developmental environment or ecological events has been previously documented in lizards, like anoles (*Anolis* spp., Losos et al. 2000; Donihue et al. 2018), common lizards (*Lacerta vivipara*, Sorci et al. 1996), eastern garden lizards (*Calotes versicolor*, Ammanna et al. 2018), and eastern fence lizards (*Sceloporus undulatus*, Wild and Gienger 2018). Many of these studies observed changes in limb morphology, which we did not observe in our study, but rather, we saw an urban-related reduction in body size. Our finding is contrary to other differences between urban-dwelling lizards and their natural-living counterparts (e.g., brown anoles, Marnocha et al., 2011; swamplands lashtails, Iglesias et al., 2012); however, these studies were not able to determine if their observed increase in urban body size was related to natural selection, phenotypic plasticity, or ecological factors (e.g., increased resources or longevity). If phenotypic plasticity is a major driver of divergent body size in water dragons across ontogeny, as suggested by our 2 × 2 factorial experiment, then this raises three key questions: 1) why does it result in a reduced body size for adult males and not females; 2) does it have a functional purpose; and 3) how does this relate to the presence of divergent body size at the time of hatching (i.e., without environmental cues)?

In wild adult water dragons the presence of urban-derived morphology differs demographically, which may be related to sex-specific differences in habitat use and social behavior across ontogeny (Baird et al., 2012, Gardiner et al., 2014; Strickland et al. 2014; Piza-Roca et al. 2018). Adult water dragons are sexually dimorphic, with a male bias toward a longer SVL, heavier mass, enlarged head, and sex-specific differences in social behavior (Baird et al. 2012, 2014; Strickland et al. 2014). Males are often combative and defend territories or adopt a satellite (non-territorial) reproductive tactic (Baird et al. 2012, 2014). These aggressive interactions are energetically demanding and likely come with a substantial physiological cost (Baird et al. 2014). Female water dragons

do not defend territories, although they can be aggressive, and tend to be more aggregative, with home range's frequently overlapping with multiple males and females (Strickland et al. 2014). Female water dragons also tend to form strong non-random social associations between individuals (i.e., strong social bonds; Piza-Roca et al. 2019). Furthermore, reductions in female body size may be constrained by the need to maintain a natural optimum for egg production, however more research into urban reproductive biology and how this can impact morphology is needed. Given these ecological and behavioral sex-specific differences, it may be expected that phenotypic plasticity would mediate the expression of urban-derived morphology differently. Similar findings, albeit sex-reversed, have been seen in green anoles (*Anolis carolinensis*), whereby females exhibit a stronger plastic response in relation to habitat type (i.e., longer limbs in areas with wider perches) compared to males; a finding seen in both wild populations (Dill et al. 2013) and laboratory-reared individuals (Kolbe and Losos 2005). Previous research on Australian water dragons has also identified sex-specific differences in adult body shape (SVL, limb length, and head shape) between isolated urban populations, which were attributed to localized genetic divergences (Littleford-Colquhoun et al. 2017). Our results do not counter the assertion that rapid localized adaptation is occurring within some urban water dragon populations, but rather serve to outline the complex nature of how different urban areas impact specific populations through a suite of potential mechanisms, including rapid genetic differentiation (Littleford-Colquhoun et al. 2017), phenotypic plasticity (our study), or possibly a combination of both (e.g., heritable phenotypic plasticity, Lande 2009; Chevin and Lande 2011) depending on the location and population.

Habitat-related phenotypic plasticity in lizard morphology has typically been associated with conferring performance advantages within the novel or altered landscape (Losos et al. 2000; Dill et al. 2013; Winchell et al. 2018), yet we were unable to detect any significant difference in sprint speed, endurance, or clinging ability on tree bark or concrete between our experimentally-reared treatments of yearling dragons. Although we found this surprising, these findings may have stemmed from several factors relating to limb morphology, sex, or experimental design. Our 2 × 2 factorial experiment did result in altered body size for urban dragons, yet we did not see a difference in limb morphology; which has previously been attributed to altered performance capacities in lizards (Losos et al. 2000; Dill et al. 2013; Winchell et al. 2018). Furthermore, a factor that could limit the interpretation of results from our experimentally reared yearlings is their sex. Unfortunately, we did not determine the sex of the yearlings; as sexual maturity in Australian water dragons occurs at approximately 4–5 years of age (Thompson 1993; Harlow and Harlow 1997; Hosking 2010). If we had been able to tease apart variances in performance capacity related to sex it may have provided notable differences - or at least clearer insights. We recommend future work identify juvenile sex as early as possible, regardless of the age of sexual maturity. Lastly, there is the distinct possibility that the metrics we used to measure performance capacity (sprint speed, endurance, and clinging ability) were not the attributes that a reduction in urban body size was acting upon. Instead, the reduced body size seen in urban-reared yearlings may be related to factors such as thermal biology (Sinervo and Adolph 1994; Sorci et al. 1996) or water loss (Gunderson et al. 2011), which may be impacted substantially in urban landscapes (e.g., altered thermal regimes and water availability). We suggest further investigations also examine the potential physiological factors that may explain a plastic response favoring a smaller dragon body size in urban landscapes, particularly in relation to the urban heat island effect (i.e., reduced vegetation and increased hardscape increasing urban environmental temperatures; Arnfield 2003).

While the experimentally reared yearlings provided an explanation for the reduced body size of adult males (phenotypic plasticity), it does not directly address the reduced body size and proportionally longer limbs observed in urban water dragon hatchlings (innate trait). Since this trend is restricted to the hatchling life-stage - being absent at one year of age (as seen in our 2 × 2 factorial experiment) - if it is adaptive, this phenotype may only be advantageous over this short time period; or else it may merely be a by-product of parental effects driven by urban ecological factors (e.g., diet, physiological stress, pollution, thermal landscape, Shine and Downes 1999; de Solla et al. 2002; Lorioux et al. 2012). Based on the inferences from mark-recapture data (Thompson 1993), large clutch sizes (up to 17 eggs, Baxter-Gilbert unpubl. data) and frequency (up to three clutches per year, Doody et al. 2006), and a wide array of known predators (Doody et al. 2014), we can predict that juvenile water dragon mortality rates are reasonably high. As such, urban dragons experiencing altered ecosystems (e.g., novel predators and habitat structure) may have undergone differential selective pressures or maternal effects (e.g., physiological priming of offspring; Shine and Downes 1999) resulting in smaller SVL and proportionally longer limbs during this early life-stage to better evade predation. If this early-life phenotype is adaptive it may be temporally limited. Differences in limb-body proportions can change during development because of different physiological and kinematic constraints arising across ontogeny. For example, American alligators (*Alligator mississippiensis*) decrease proportional limb length across ontogeny, as well as adjusting gait and limb posture, to compensate for the challenges of increased load stress on bones (Allen et al. 2010). If this is the case for urban water dragons, then the advantages of longer limbs may only be effective for smaller age-classes; with the costs of this trait outweighing the benefits as they mature. An alternative is that the differences seen in urban hatchling morphology are not

adaptive, but rather a result of circumstantial ecological maternal effects, such as diet. Investigations of other urban water dragon populations revealed a high fat and plant rich diet (from gut microbiome profiling) and incorporating anthropogenic food sources rich in protein (from stable isotope analysis, Littleford-Colquhoun et al. 2019a). These urban dragons also had several gut microbial taxa associated with obesity, which were occurring at a much higher frequency and abundance within urban populations compared to their natural conspecifics (Littleford-Colquhoun et al. 2019a). Although the maternal effects of anthropogenically-subsidized maternal diets on offspring morphology are widely understudied for reptiles, previous research has seen maternal diet quantity or quality affect offspring body size, growth, and performance capacity (Sorci and Clobert 1997; Warner and Lovern 2014; Wang et al. 2017; Horváth et al. 2019). Overall, we are unable to clearly delineate the mechanism driving the innate expression of the urban water dragon hatchling morphology, whether it be fixed and heritable or a result of adaptive or circumstantial maternal effects. We recommend future studies examine if these traits (shorter SVL and longer limbs at hatching) are repeatable over multiple generations in lab-reared colonies, as well as the impact urbanized diets have on water dragon physiology and reproduction.

Conclusion

In the face of rapid ecological change, such as urbanization, plastic responses may provide a stopgap allowing populations to temporarily persist under urban pressure, creating time for natural selection to act upon adaptive heritable traits (Price et al. 2003; Winchell et al. 2016). Our study provides support for the assertion that phenotypic plasticity can result in urban-derived morphological phenotypes in lizards - including sex-specific differences in expression occurring across ontogeny (Kolbe and Losos 2005; Dill et al. 2013). However, our study has also generated a suite of new questions. We suggest urban research further explore changes in urban-derived morphology across ontogeny and in different ecological contexts (e.g., urban vs natural); as body shape can relate to habitat-use and diet, which often varies across an individual's lifetime (Mushinsky et al. 1982, Irschick et al. 2000, Bouchard and Bjorndal 2005, Arthur et al. 2008, Purwandana et al. 2016). Also, additional research should focus on how interactions between sexual dimorphism and natural selection (Littleford-Colquhoun et al. 2019b) impact urban evolution and urban-derived phenotypes. Our research builds on the growing idea that although urbanization is a key factor imperiling biodiversity, there are certain wildlife populations capable of adapting to an increasingly human world.

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Authors' contributions JBG, CHF, and MJW conceived the idea for this study, JBG led the data collection, JLR led the statistical analysis, and JBG, JLR, CHF, and MJW contributed to the writing of the manuscript.

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Data Availability Data and R code are available from the Open Science Framework at https://osf.io/gk6jh/.

Compliance with ethical standards

Conflicts of interest We have not any conflicts of interest or competing interests.

Ethics approval Experimental protocols were approved by the Macquarie University Animal Ethics Committee (ARA # 2015/023), the Taronga Zoo Animal Ethics Committee (ARA # 3b/08/15), and New South Wales National Parks and Wildlife Services (scientific license # SL100570).

Consent for publication We consent to the publication of our research and manuscript.

Code availability Data and R code are available from the Open Science Framework at https://osf.io/gk6jh/.

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