

Body size and reproduction of a non-native lizard are enhanced in an urban environment

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Growth and body size are influenced by the environment and each have consequences for reproduction and, thus, fitness. Anthropogenically altered habitats (i.e. cities) create novel conditions that may enhance or reduce fitness via environmentally induced changes in growth or body size. By comparing urban and natural habitats, we can quantify the effects of human-modified landscapes on fauna and increase our general understanding of responses to novel environments. We collected lizards, *Anolis cristatellus* (Duméril & Bibron, 1837), from adjacent urban and forested areas, bred them in the lab under common conditions, measured body size, latency of oviposition, fecundity and egg size for each female and measured growth of hatchlings over 3 months. Female lizards from the city were larger, had a greater body condition index at the beginning of the breeding season and started laying eggs sooner than those from the forest, which increased their fecundity. Females from the forest, but not the city, improved their body condition during the study, so we infer that urban environments maximize body condition of anoles. Moreover, hatchlings from urban mothers had higher growth rates than those from the forest suggesting that body size differences may be due to intrinsic factors. Thus, we conclude that urban environments can enhance growth and reproduction in some vertebrate ectotherms.

ADDITIONAL KEYWORDS: body condition – fecundity – growth rate – reproductive phenology – urbanization.

INTRODUCTION

Growth rates and body size are largely determined by genetic factors and, thus, can be shaped by selection; however, the environment can make substantial contributions to these phenotypes via phenotypic plasticity. For ectotherms, growth and development are highly sensitive to environmental conditions (i.e. temperature), and body size often covaries with fecundity and mating success (Honěk, 1993; Shine, 2005; Monroe, South & Alonzo, 2015). Thus, the relationships among the environment, growth and reproduction are important for fitness in these species (Semlitsch, 1987; Adolph & Porter, 1996; Sokolovska, Rowe & Johansson, 2000). Natural selection should shape reproductive strategies to match the environment in ways that optimize fitness (Giesel, 1976; Angilletta Jr, Oufiero & Leaché, 2006); however, novel environments, like those created by anthropogenic disturbance, have the

potential to reduce fitness (Robertson, Rehage & Sih, 2013; Meillère *et al.*, 2015).

Human-modified habitats create a diversity of novel conditions to which organisms must respond to survive. In urban environments, abiotic conditions (i.e. light, moisture and temperature) can differ markedly from adjacent natural areas. Average temperatures tend to be higher in urban areas than in adjacent non-urban habitats due to the urban heat island effect (Arnfield, 2003), moisture levels can be greater in cities because of supplemental watering of lawns and gardens (Pickett *et al.*, 2001) and artificial lighting increases the intensity of light during evening hours (Perry *et al.*, 2008). These conditions can directly influence development and growth of animals (Perry *et al.*, 2008; Zhang *et al.*, 2016; Tiatragul *et al.*, 2017); however, they can also have indirect effects by altering the urban biotic environment (Shochat *et al.*, 2006). For example, urban populations often differ from their non-urban counterparts in population density (Fernández-Juricic, 2001), home range size (Lowry, Lill & Wong, 2013), community composition (Beissinger &

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Osborne, 1982; McIntyre *et al.*, 2001), predation pressure (Fischer *et al.*, 2012; Tyler, Winchell & Revell, 2016), mortality rate (Koenig, Shine & Shea, 2002; Glista, DeVault & DeWoody, 2008), food abundance (McIntyre *et al.*, 2001; Chamberlain *et al.*, 2009) and behaviour (Lowry *et al.*, 2013; Chejanovski *et al.*, 2017). Each of these have the potential to impact growth. For example, decreased predation pressure and increased food abundance allow for more time to accrue vital resources and result in faster growth. Obviously, many factors in urban habitats can potentially impose novel selection pressures on growth and body size, or induce changes in these phenotypes via plasticity.

Many of these novel conditions are similar across urban landscapes, and, thus, their impacts are somewhat generalizable across the globe (McKinney, 2002; but see Littleford-Colquhoun *et al.*, 2017). For example, urban habitats are often characterized by a reduction in canopy cover and an increase in impermeable surfaces (asphalt, concrete). These conditions result in higher average ambient temperatures and higher thermal fluctuations in urban landscapes than in adjacent rural or natural areas (Arnfield, 2003). As a result, city populations can evolve greater heat tolerance (Angilletta *et al.*, 2007; Brans *et al.*, 2017; Diamond *et al.*, 2017) when compared to adjacent non-urban congeners. However, for many animals, like insects and vertebrate ectotherms, rates of growth and development are highly sensitive to changes in temperature; therefore, urban environments have the potential to influence fitness via plastic changes in growth rates and body size as well (Kaiser, Merckx & Van Dyck, 2016; Diamond *et al.*, 2017). Though many researchers have sought to understand the various interactions between urban landscapes and wildlife (McIntyre, 2000; McKinney, 2008; Chamberlain *et al.*, 2009), the extent to which urban habitats influence fitness through alterations in body size is not well established (Brans *et al.*, 2017).

Reptiles make excellent models for studying the relationships among urban habitats, body size and reproduction because their activity patterns and growth are highly correlated with abiotic conditions (Andrews, 1982), their fecundity and mating success are often a function of body size (Trivers, 1976; Brandt & Navas, 2011) and many species have invaded and thrive in urban areas (Ackley *et al.*, 2015). Several studies have quantified the influence of urban environments on reptiles (French, Fokidis & Moore, 2008; Perry *et al.*, 2008; Kolbe, Battles & Avilés-Rodríguez, 2015), but few have explored the association between urban habitats and reproduction (Burger *et al.*, 2007; Endriss *et al.*, 2007; Lucas & French, 2012). This information will provide insight into the impact of landscape modifications on ectotherm populations, as well as the potential for individuals to respond to these novel habitats.

To understand the relationships among urban environments, body size and reproduction, we studied naturalized populations of the Puerto Rican crested anole (*Anolis cristatellus*, Duméril & Bibron, 1837) in south Florida. This lizard species has invaded urban areas both within and outside its native range on multiple, independent occasions (Kolbe *et al.*, 2012), and its reproductive ecology has been well studied (Gorman & Licht, 1974). Additionally, past studies have demonstrated that this species is responding to urban environments through morphological adaptation (Kolbe *et al.*, 2015; Winchell *et al.*, 2016) and behaviour (Chejanovski *et al.*, 2017). These studies have quantified the effects of urban environments on morphology or performance; however, such phenotypes only indirectly correspond to fitness as proxies for survival. More direct measures of fitness (i.e. fecundity) will be useful to fully understand how urban environments influence ectotherms.

Previous work on *Anolis* lizards suggests that body condition, a comparison of mass to length that signifies overall robustness, is greater in human-modified habitats (Chejanovski *et al.*, 2017), and that environments typical of such habitats (i.e. reduced canopy cover, increased temperatures) increase fecundity (Otero, Huey & Gorman, 2015). Because greater body condition is associated with greater fecundity in anoles (Warner *et al.*, 2015), urban environments have the potential to enhance fitness via increased fecundity. Therefore, we predicted that female *A. cristatellus* from urban areas would have enhanced body condition and reproduction compared to those from natural habitats. To test this, we measured female anoles from an urban site and an adjacent forested site in Miami, FL and bred a subset of animals in the laboratory for 6 months to observe aspects of their reproduction in a controlled environment.

MATERIALS AND METHODS

DATA COLLECTION

Body size

Adult lizards [females ≥ 36 mm snout-vent length (SVL); males ≥ 45 mm SVL; Philiposian, 1975] were collected from an urban site (Red Road – henceforth ‘city’) and a forested site (Matheson Hammock Park – henceforth ‘forest’) ~1 km apart in Miami, FL during the spring (29 April to 4 May) and fall (10–12 November) of 2016 and the summer (1–5 June) of 2017. From the forest, we collected 48 females and 20 males during spring, 37 females during fall and 87 females during the summer of 2017. From the city, we collected 40 females and 23 males during spring, 43 females during

fall and 101 females during summer of 2017. Each lizard was visually sexed per external morphology, and we measured SVL to the nearest mm and mass to the 100th gram with a digital scale on the day of capture. A subset of lizards ($n = 25$ females, 13 males from the forest; $n = 26$ females, 13 males from the city) collected in the spring were brought to Auburn University, bred over the summer (details below) and remeasured on 23 September 2016.

Reproduction

We housed females in single cages ($29 \times 26 \times 39$ cm; height \times width \times depth) illuminated with Reptisun 5.0 UVB bulbs (Zoo Med Inc.) and plant grow bulbs (model F40; General Electric Co.) with a 12:12 h light/dark cycle and maintained an ambient room temperature of 25.6 °C. Cages included two bamboo perches, an artificial plant, a nesting pot (plant pot filled with a mixture of soil and peat moss) and reptile cage carpet (Zoo Med Inc.) as a floor substrate. We fed lizards three crickets each (dusted with vitamins and calcium) three times per week and misted cages with water daily.

Because we had half as many males as females, each male was shared by two females and was rotated between them approximately once every 2 weeks. We paired males and females haphazardly, but individuals were not mixed between sites (i.e. males from the city were kept with females from the city). We collected eggs from nest pots three times per week from 5 May to 23 September 2016. We assume this period constitutes most of the breeding season (Fig. 1).

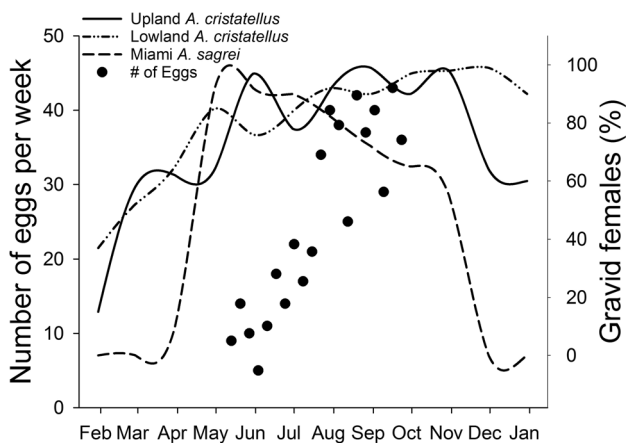


Figure 1. Weekly egg production for our lab colony of 51 females (closed circles) in comparison to the seasonal reproduction of upland and lowland populations of *Anolis cristatellus* in Puerto Rico (adapted from Gorman & Licht, 1974) and *A. sagrei* in Miami (adapted from Lee *et al.*, 1989). There are currently no field data describing the seasonality of reproductive cycles for *A. cristatellus* in Miami, but we assume it is truncated like *A. sagrei*.

For each egg ($n = 398$), we recorded the mass, date of oviposition and maternal identity. Eggs were then allocated to incubation treatments for another study (results not reported here). Because we wanted to accurately measure fecundity (total # of eggs) and the latency of oviposition (# of days until first egg was laid), we also collected eggs laid outside of nesting pots ($n = 110$). However, because these eggs were often desiccated when found in the cage, their mass was not measured. Additionally, six females laid eggs in their collection bags in the field just after capture. Oviposition dates for these eggs were recorded and used in our analyses.

We housed hatchling lizards ($n = 117$ from the forest; $n = 118$ from the city) in cages identical to those described for the adults and provided them with the same light cycle, thermal conditions and feeding regime; however, we kept 6 hatchlings per cage such that each cage represented hatchlings from multiple incubation treatments.

STATISTICAL ANALYSES

All statistical analyses were performed in R 3.1.3 (R Development Core Team, 2015). To assess the influence of males on females and offspring, we built models that included male as a random effect and compared these via AICc to models that did not include males (Supporting Information, Table S1). Including males only improved model fit for latency of oviposition; therefore, for this model only, we included male SVL as a covariate and male identity as a random effect.

Body size

For adult females, we used ANOVAs with season (spring, fall, summer) nested within site (city vs. forest) as an independent variable to test for differences in SVL and body condition. Each female's body condition was her residual score from a second-degree polynomial regression of log mass and log SVL of all females collected from both sites during all three sampling periods. This index of body condition is a proxy for the robustness of individuals (Schulte-Hostedde *et al.*, 2005; Hoare *et al.*, 2006) and provides a rough indication of body fat mass and lean mass in anoles (Warner, Johnson & Nagy, 2016).

To calculate body condition residuals for females bred in the lab, we combined initial SVL and mass (at capture) and final SVL and mass (at end of study) of each female into one data set and performed a second-degree polynomial regression between log mass and log SVL; therefore, each female was represented twice in the regression. We analysed SVL and body condition using mixed-model ANOVAs with season (initial vs. final) nested within site and individual as a random

effect. All post hoc, pairwise comparisons were made with the *lsmeans* package using a false discovery rate *P*-value correction.

All eggs were equally distributed among five incubation treatments for another study, but hatchlings were raised in common conditions for ~3 months. Each incubation treatment consisted of a daily thermal cycle from temperatures measured at either the urban or forest site (Tiatragul *et al.*, 2017). Although the effect of incubation treatment was not a focus of this study, we included it in our models as a potential source of variation; however, incubation treatment had no effect on hatchling size, body condition, growth or survival (all *P*-values > 0.11).

Lizards were measured upon hatching and we used mixed-effects linear models to assess differences in SVL and body condition according to maternal site of origin; initial egg size, hatch date and incubation treatment were covariates, and maternal identity was a random effect. To assess changes in SVL and body condition, we used mixed-effects linear models to test for differences in final SVL and final body condition of all hatchlings that survived to 3 months ($n = 67$ from the forest; $n = 62$ from the city); these analyses included maternal site of origin as the independent variable and hatching SVL or body condition (respectively), hatch date and incubation treatment as covariates. Enclosure was considered a random effect because lizards were housed communally (6 per cage). We analysed hatchling survival with a generalized linear mixed-effects model (GLMM) using a binomial distribution. We included maternal site of origin, hatch date, incubation treatment and hatching SVL in the model and used cage as a random effect. To achieve model convergence, we utilized the Nelder Mead optimizer and rescaled and centred all continuous covariates at zero by subtracting the mean from each value (Bolker *et al.*, 2009).

Reproduction

We performed generalized linear models with a Poisson distribution to explain fecundity and latency as a function of site using initial residual body condition and initial SVL as covariates. For fecundity, we also included each female's latency and average egg size. The model for latency included male SVL and male identity as a random effect (Supporting Information, Table S1). Fecundity was the total number of eggs each female laid, including eggs laid outside the nesting pot. Latency was the time from the day of collection (days) to oviposition of the first egg for each female. For egg size, we used a mixed-model ANCOVA with egg mass as the response variable and site as the independent variable. Female body condition, initial SVL and fecundity were considered as covariates, and maternal identity was a random effect.

For these analyses, we calculated body condition residuals using only females bred in the laboratory; thus, body conditions were not relative to those of females collected in the fall. Because we were interested in the effects of site, initial SVL and body condition on reproduction, we did not include final measures of body condition or SVL in our analyses. For the six females that laid eggs in the collection bags soon after capture, we accounted for egg mass by subtracting 0.24 g (average egg mass during our study) from these females' mass prior to calculating body condition residuals, because their mass was measured just prior to oviposition.

RESULTS

BODY SIZE

In the field, we found significant interactions between site and season for female SVL and body condition (Table 1): females from the city were larger and had higher body condition than those from the forest during the spring and summer, but there was no difference between groups in the fall (Table 2; Fig. 2).

For females kept in the lab, we also found significant interactions between site and season for SVL and body condition (Table 1). Females from the city were greater in both initial and final SVL than those from the forest; however, body condition was only higher for city lizards initially (Table 2; Fig. 3). Laboratory conditions allowed females from the forest to improve their body condition while females from the city experienced no change (Fig. 3B).

For hatchlings, there were no differences between sites in SVL or body condition at hatching (Table 3). However, after being raised in standard conditions for 3 months, hatchlings from the city had a final SVL 1.32 mm (± 0.53 SE) greater than those from the forest (Fig. 4). Final body condition, however, did not differ between sites (Table 3). The only factor that influenced hatchling survival in the laboratory was hatch date: lizards that hatched earlier had better survival than those that hatched later. Survival did not differ according to maternal site of origin (Table 3).

REPRODUCTION

Latency to oviposit differed between sites and covaried with female SVL and body condition (Table 4). We found a negative relationship between latency and both body condition and SVL: smaller females (lower in body condition and SVL) took longer to start laying eggs (Fig. 5A). Even after controlling for body condition and SVL, we observed a difference in latency between sites (Table 4); females from the forest had an average

Table 1. Effect of site (city vs. forest) and site by season interaction on body size and condition of females in the field and lab

	Fixed effects	Site			Site × season		
		d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Field	SVL	1,349	1.67	0.197	4,349	15.85	<0.0001
	Body condition	1,349	2.55	0.111	4,349	24.74	<0.0001
Lab	SVL	1,49	17.88	<0.0001	2,49	32.08	<0.0001
	Body condition	1,49	0.93	0.339	2,49	7.64	0.0013

For field data, season refers to collection periods during spring and fall 2016 and summer of 2017. For lab data, season refers to the initial (spring) and final (fall) measures during the study period. Bold typeset denotes statistical significance. Associated mean values and SEs are reported in Table 2. SVL, snout-vent length.

Table 2. Estimates of body condition and SVL of females from both the forest and city during each sampling period

	Site	Field			Lab		
		Sample date	Mean	SE	Time of study	Mean	SE
Body condition	Forest	April 2016	0.0266	0.0152	Initial	-0.0584	0.0192
		November 2016	-0.115	0.0173	Final	0.0382	0.0192
		June 2017	-0.0378	0.0113			
	City	April 2016	0.0723	0.0166	Initial	0.0072	0.0189
		November 2016	-0.0769	0.0162	Final	0.0121	0.0189
		June 2017	0.0653	0.0105			
SVL (mm)	Forest	April 2016	42.52	0.34	Initial	42.56	0.436
		November 2016	44.89	0.38	Final	44.92	0.436
		June 2017	45.14	0.25			
	City	April 2016	45.4	0.37	Initial	45.5	0.427
		November 2016	45.57	0.36	Final	47.5	0.427
		June 2017	47.11	0.23			

SVL, snout-vent length.

latency of 49.88 days (± 7.13 SE) while those from the city had a latency of only 34.5 days (± 7.03 SE).

Fecundity did not differ between sites or covary with body condition, average egg mass or female SVL (Table 4). The most important predictor of fecundity was latency of oviposition: females that started laying eggs sooner produced more eggs than those that started later (Fig. 5B). However, because latency and body condition differ between sites, when they were removed from the model, fecundity also differed between sites ($X^2 = 5.06$; d.f. = 1; $P = 0.024$): city females produced an average of 10.46 eggs each compared to only 8.84 eggs per forest female. This indicates that the difference in fecundity between females from the city and forest is driven by body condition and latency.

Variation in egg mass was not explained by body condition, fecundity or site; however, females with larger initial SVL produced larger eggs (Table 4; Fig. 5C). For each 1-mm increase in initial SVL, egg mass increased by 0.003 g (± 0.0012 SE). Therefore, the average egg mass for our largest females (~50 mm)

was as much as 15% larger than that from our smallest females (~38 mm).

DISCUSSION

Because urban areas differ from natural sites in ways that influence growth and reproduction, female lizards from urban and natural habitats should differ in size and possibly reproduction. We predicted that *A. cristatellus* females would have higher body condition in the city in ways that could influence reproduction. Our results support this prediction in that females from the city were larger at the onset of breeding and started laying eggs sooner; hatchlings from the city were also larger than those from the forest after 3 months.

Many studies reveal that ectotherms attain increased body size in urban habitats (French *et al.*, 2008; Kaiser *et al.*, 2016; Chejanovski *et al.*, 2017); however, other studies find no relationship or the opposite of that found here (Niemelä *et al.*, 2002;

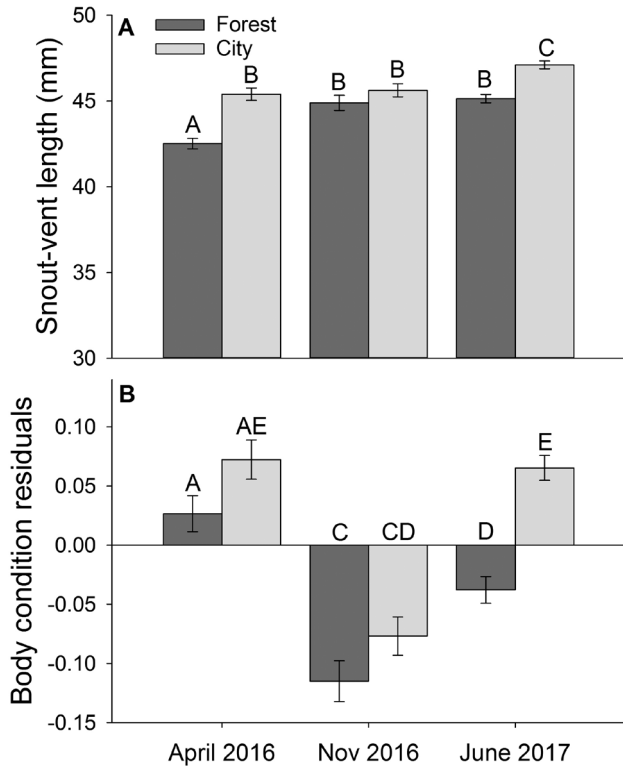


Figure 2. Mean SVL (A) and body condition (B) of females from the forest and city during three, temporally separated sampling efforts. Body condition was calculated as the residual score from a mass/length regression that includes all data from both sites and all three sampling efforts. Bars represent ± 1 SE. Letters above bars denote groups that were statistically different from one another after false discovery rate correction of *P*-values for 15 comparisons. SVL, snout-vent length.

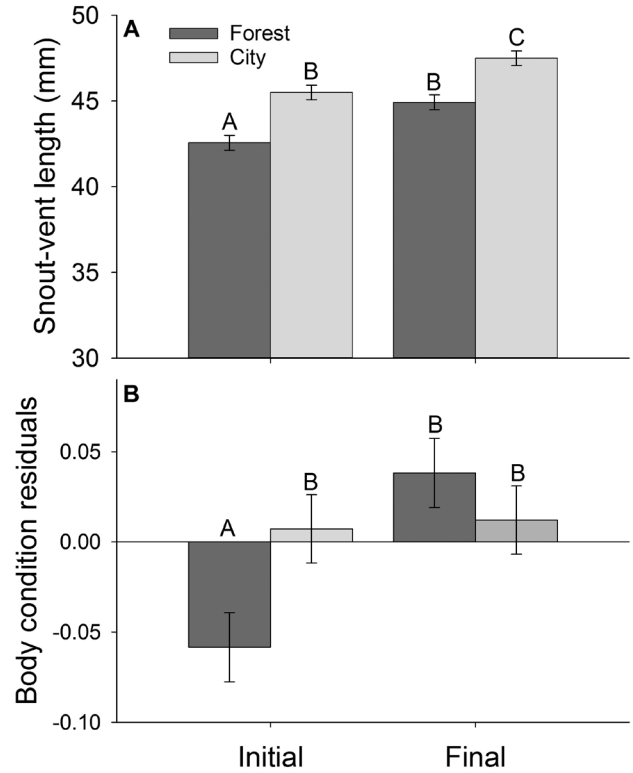


Figure 3. Initial and final SVL (A) and body condition (B) of females collected in the spring and bred in the lab for 6 months. Body condition was calculated as the residual score from a mass/length regression that includes all data from the beginning and end of laboratory breeding; therefore, each female is included twice in this regression. Bars represent ± 1 SE. Letters above bars denote groups that were statistically different from one another after false discovery rate correction of *P*-values for 6 comparisons. SVL, snout-vent length.

Table 3. Effect of site (city vs. forest) and covariates on offspring phenotypes at hatching and after 3 months of being reared in the lab

	Site	Hatch date	Incubation treatment	Initial egg mass	Initial SVL	Initial body condition
Hatching SVL	$F_{1,46} = 2.82$; $P = 0.0997$	$F_{1,207} = 0.64$; $P = 0.425$	$F_{4,207} = 0.26$; $P = 0.905$	$F_{1,207} = 28.43$; $P < 0.0001$	-	-
Hatching body condition	$F_{1,46} = 0.56$; $P = 0.458$	$F_{1,207} = 1.02$; $P = 0.314$	$F_{4,207} = 1.41$; $P = 0.233$	$F_{1,207} = 36.67$; $P < 0.0001$	-	-
Final SVL	$F_{1,38} = 6.05$; $P = 0.0186$	$F_{1,38} = 2.22$; $P = 0.145$	$F_{4,38} = 2.01$; $P = 0.112$	-	$F_{1,38} = 4.58$; $P = 0.0388$	-
Final body condition	$F_{1,38} = 3.44$; $P = 0.0714$	$F_{1,38} = 16.88$; $P = 0.0002$	$F_{4,38} = 0.83$; $P = 0.513$	-	-	$F_{1,38} = 1.12$; $P = 0.296$
Hatchling survival	$F_{1,177} = 0.05$; $P = 0.817$	$F_{1,177} = 4.80$; $P = 0.0144$	$F_{4,177} = 0.89$; $P = 0.469$	-	$F_{1,177} = 0.82$; $P = 0.441$	-

Bold typeset denotes statistical significance. SVL, snout-vent length.

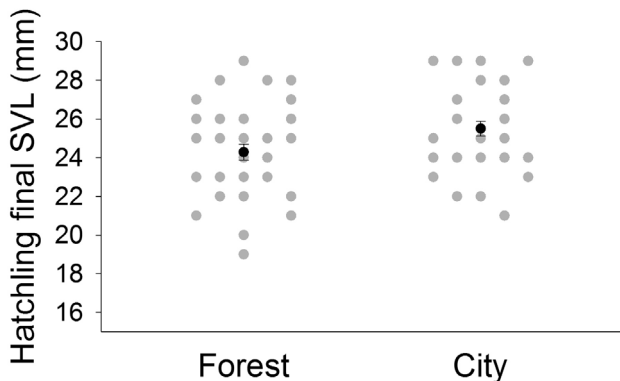


Figure 4. Final SVL of hatchling lizards whose mothers came from the forest and city. Eggs were incubated and hatched in the lab. Lizards were raised under common conditions for 3 months. Grey dots represent raw data, black dots represent the mean and bars are ± 1 SE. SVL, snout-vent length.

Weller & Ganzhorn, 2004; Battles *et al.*, 2013; Winchell *et al.*, 2016; Brans *et al.*, 2017). Very likely, the factors that determine body size across urban–rural gradients are both species and location dependent (Niemelä & Kotze, 2009). There are several possible explanations for the increased body size of city animals: (1) intrinsic (genetic) differences between sites, (2) plastic differences in growth rates or (3) differences in phenology such that city animals hatch earlier in the year and mature earlier in the subsequent year.

We found some evidence to support intrinsic differences: laboratory-hatched individuals from the city had higher growth rates in a common environment (Fig. 4), and females from the city were greater in SVL even after being fed in the lab for 6 months (Fig. 3). Phenotypic plasticity, however, could still be responsible. During development, the environment can have lasting effects into adulthood and even into the next generation in lizards (Goodman, 2008; Warner, Uller & Shine, 2013). For example, the maternal diet during reproduction can influence how offspring grow and survive in response to their own diet during early life (Warner *et al.*, 2015). Thus, we cannot rule out the possibility that these size differences are due to maternal or environmental effects without longer-term experiments in the laboratory. Furthermore, our study period (~6 months) might not have been long enough for forest females to reach the same size as city females, were they able to do so.

Moreover, growth rates in lizards are positively correlated with environmental factors like temperature and food availability (Adolph & Porter, 1996). Temperatures are much higher at our city site than the forest, partially due to the urban heat island effect (Tiatragul *et al.*, 2017). This could contribute to the

Table 4. Effects of site (city vs. forest) and covariates on reproduction of females maintained in the lab

	Site	SVL	Initial body condition	Average egg mass	Latency	Fecundity	Male SVL
Latency of oviposition	$F_{1,45} = 11.00$; $P = 0.0019$	$F_{1,45} = 35.61$; $P < 0.0001$	$F_{1,45} = 90.00$; $P < 0.0001$	-	-	-	$F_{1,45} = 1.56$; $P = 0.211$
Fecundity	$F_{1,45} = 1.03$; $P = 0.311$	$F_{1,45} = 2.33$; $P = 0.127$	$F_{1,45} = 0.38$; $P = 0.536$	$F_{1,45} = 0.07$; $P = 0.798$	$F_{1,45} = 33.39$; $P < 0.0001$	-	-
Egg size	$F_{1,42} = 3.39$; $P = 0.0724$	$F_{1,42} = 6.81$; $P = 0.0125$	$F_{1,42} = 1.34$; $P = 0.253$	-	-	$F_{1,42} = 3.20$; $P = 0.0807$	-

Bold typeset denotes statistical significance. SVL, snout-vent length.

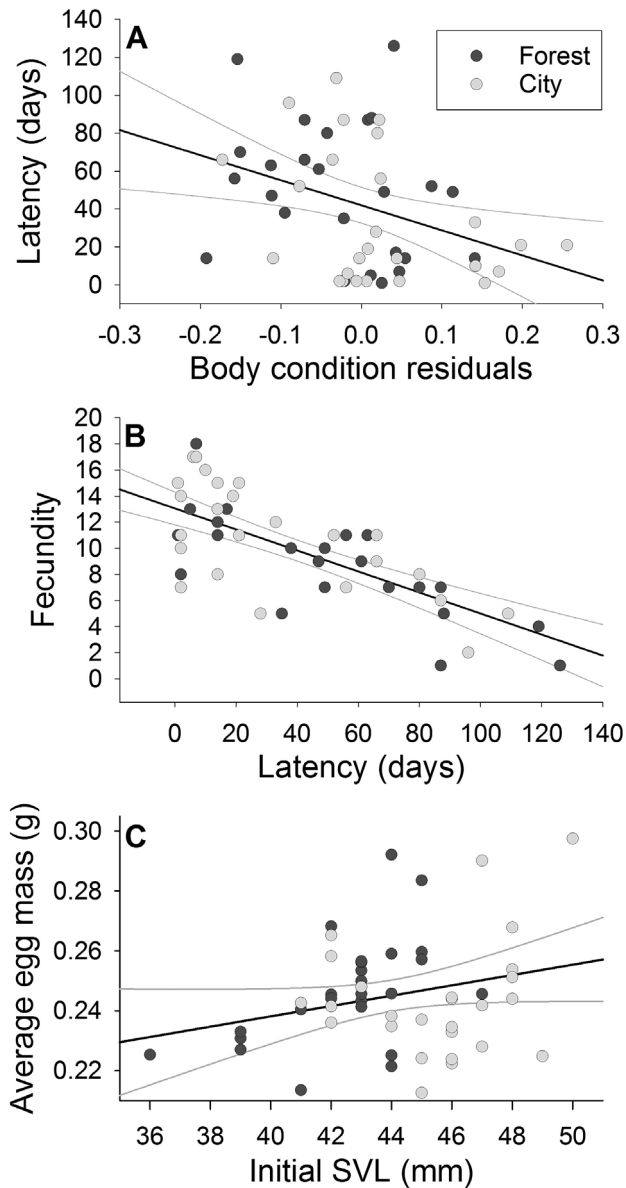


Figure 5. Regressions between (A) latency of oviposition and relative body condition for females from both sites, (B) fecundity (total # of eggs) and latency of oviposition for females from both sites and (C) the average egg mass for each female and her initial SVL. Grey lines represent 95% confidence intervals of raw data. SVL, snout-vent length.

larger size of lizards in the city vs. the forest; however, biotic factors may contribute as well. For example, food abundance may be greater for lizards living in the city since some insect species have greater abundance in urban areas (Raupp, Shrewsbury & Herms, 2010; Meineke *et al.*, 2013), and food resources are often more concentrated and predictable in urban habitats (Lowry *et al.*, 2013). Additionally, predation pressure is often lower in urban environments (Fischer *et al.*,

2012), and this would provide lizards with more time during the day to forage (Drakeley, Lapidra & Kolbe, 2015; Chejanovski *et al.*, 2017), increasing their growth.

Greater food abundance and lower predation pressure might also explain why city lizards consistently had higher body condition than those from the forest (Fig. 2B). A recent study found anoles can have higher body condition in urban habitats and determined that city lizards are more reluctant to feed when offered prey (Chejanovski *et al.*, 2017). This suggests they may be more satiated due to abundant invertebrate prey in the city (Raupp *et al.*, 2010; Meineke *et al.*, 2013). Furthermore, past studies demonstrate that experimentally increasing quality and quantity of food increases body condition of anoles (Lovern & Adams, 2008; Warner *et al.*, 2015). Individuals from the city may be better fed and have relatively greater fat reserves, which are important contributions to female reproduction (Price, 2017). However, we could not determine if higher body condition was due to fat reserves, lean mass, water content or other components of body composition (Warner *et al.*, 2016).

In general, *Anolis* species that reproduce seasonally decrease egg production during the cooler, drier months and concordantly increase fat reserves (Gorman & Licht, 1974; Lee *et al.*, 1989), which suggests their body condition should change through the year. Our data show that females in both the city and forest had higher body condition at the beginning of the breeding season (spring) than at the end (fall) (Fig. 2B), indicating they procured fat reserves during winter and subsequently depleted them across the summer. Previous studies have measured body condition of urban populations at only one time of year (i.e. Battles *et al.*, 2013; Chejanovski *et al.*, 2017) or made comparisons of animals collected at different times of year (Irschick *et al.*, 2005); therefore, these studies may not have captured the true difference of body condition between natural and human-modified habitats. We suggest that future studies account for seasonal variation. Moreover, we add to previous work by simultaneously measuring seasonal fluctuations of body condition between urban and non-urban habitats in the field and laboratory. In the laboratory, females from the city did not change their body condition after being well-fed for nearly 6 months, but forest females made significant gains in body condition (Fig. 3B). This suggests that food availability and/or foraging behaviour are likely mechanisms driving differences in body condition between urban and non-urban habitats. Merely describing patterns is far too common in studies of urban impacts on wildlife; however, unearthing mechanisms for these patterns is less common (Shochat *et al.*, 2006).

Though genetic adaptation and plasticity likely contribute to the trends observed in body size, we know that urban populations often have a broader reproductive season than their non-urban analogs (Partecke, Van't Hof & Gwinner, 2004; Lowry *et al.*, 2013). Hatching early in the season can increase growth and survival in lizards (Warner & Shine, 2007; Pearson & Warner, 2016), and thus, individuals from the city may benefit from a shift in phenology. Even when controlling for SVL and body condition, city females started laying eggs sooner than those from the forest. Data on *Anolis* reproduction in adjacent urban and natural areas are lacking. However, there are data describing variation in reproduction across elevational and latitudinal gradients (Licht, 1967), across seasons (Ruibal, Philibosian & Adkins, 1972) and between areas that vary in microclimate (Otero *et al.*, 2015). Reproductive cycles appear to be driven by temperature, rainfall and day length (Ruibal *et al.*, 1972; Gorman & Licht, 1974; Otero *et al.*, 2015). Temperature, light and humidity are conditions that are often altered by urban habitats; thus, we should expect that reproductive phenology should be altered. We provide evidence that their reproductive season is likely more extensive in urban areas.

If anoles in urban environments initiate reproduction earlier in the season, they might attain maximum size earlier as well. Moreover, since potential nest temperatures are higher in the city (Tiatragul *et al.*, 2017), offspring may hatch sooner, compounding this result. Urban-induced shifts in reproductive phenology have been studied extensively in other organisms (i.e. birds – Partecke *et al.*, 2004; Chamberlain *et al.*, 2009; reviewed by Deviche & Davies, 2014); however, very little data have been collected for vertebrate ectotherms (Cook, Trenham & Northen, 2006), and little work has been done to unearth the mechanisms that drive these phenological shifts (Partecke *et al.*, 2004; Partecke, Van't Hof & Gwinner, 2005). We suggest this topic deserves more attention from researchers.

Breeding phenology is likely important for fitness because the primary determinant of fecundity is latency (Fig. 5B). When we remove latency and body condition from our model for fecundity, city females produced significantly more eggs than those from the forest. This suggests that fecundity may in fact differ between city and forest habitats due to differences in body condition and phenology; however, other unmeasured variables can influence fecundity (i.e. food availability; Andrews, 1982; Lovern & Adams, 2008), and additional research on this topic is warranted. One important caveat to consider is that females from the city may have been habituated to human presence and novel environments, generally (Irschick *et al.*, 2005; Lapiedra, Chejanovski & Kolbe, 2017). This might have made their transition from the field to the laboratory

less stressful and allowed them to start laying eggs sooner than females from the forest.

Egg mass did not differ between sites; however, we observed a positive relationship between initial SVL and egg mass (Fig. 5C) similar to that found in other studies of anoles (Lovern & Adams, 2008; Hernández-Salinas & Ramírez-Bautista, 2015; but see Vitt, Zani & Durtsche, 1995; Domínguez *et al.*, 2010). If lizards from urban environments attain larger body sizes than those from adjacent natural areas, one benefit might be the ability to produce larger eggs which, in many reptiles, produce larger hatchlings with greater survival (Janzen, 1993; Warner & Andrews, 2002; Mitchell, Maciel & Janzen, 2015).

We recognize that our study only examines a single population of lizards and we are cautious in making broad generalizations about the effects of urbanization on wildlife. However, relatively few studies explore the population ecology of vertebrate ectotherms in urban areas (Magle *et al.*, 2012), and our study has implications for various aspects of urban population ecology. For example, enhanced body size may indicate increased food supply or decreased predation pressure and these factors can influence mortality rates, population density, home range size and inter-/intraspecific competition (Schoener & Schoener, 1980; Guyer, 1988; Buckley & Jetz, 2007). Moreover, if females produce more eggs in urban habitats because of a lengthened reproductive season, this has consequences for population density, cohort recruitment and intraspecific competition during early life stages. Importantly, costs of enhanced body size and fecundity in urban habitats (i.e. increased physiological stress; French *et al.*, 2008) must also be considered. For example, city lizards may have greater fecundity during their first breeding season, but this might shorten their lifespan and reduce their lifetime reproductive success (Lucas & French, 2012).

Anolis lizards serve as excellent models for basic ecology and evolution, and now recent work highlights their utility as models in urban ecology. Indeed, numerous studies describe how populations vary between urban and non-urban habitats with respect to morphology, performance, behaviour, development, body size and reproduction (respectively, Kolbe *et al.*, 2015; Winchell *et al.*, 2016; Chejanovski *et al.*, 2017; Lapiedra *et al.*, 2017; Tiatragul *et al.*, 2017; this study). What we lack, however, are studies that determine the mechanisms driving these patterns and their population-level consequences. Such information would help to raise our understanding of urban adaptation to a broader scale and provide vital insight into the fitness consequences of human-induced habitat modification.

The urban landscape is predicted to grow rapidly over the next 50 years and numerous studies have documented its effects on various species (McIntyre *et al.*, 2001; Perry

et al., 2008; Winchell *et al.*, 2016). Here, we present results that suggest urban environments enhance body size and reproduction in an ectotherm. Moreover, our data show that growth rates might be relatively high for offspring from urban mothers. Overall, the positive effects of urban environments on size and reproduction may explain the success of some animals (i.e. anoles) in anthropogenically modified environments, and these findings could be generalized to other ectotherms that inhabit cities. Future research should further explore the relationships among urban environments, growth and reproduction in terrestrial ectotherms.

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SUPPORTING INFORMATION

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

Table S1. Results of comparing models that either did or did not include male as a random effect. In bold are the models we selected based on AICc weight.