Close encounters of the urban kind: predators influence prey body size variation in an urban landscape

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Abstract

Body size is a key trait linked to many aspects of an organism's life history, physiology, and behavior. Variation in body size can thus have important fitness consequences across a broad range of ecological contexts. We utilized the variation in multiple abiotic and biotic factors found among urban habitats to test simultaneously their relative effects on body size variation in urban populations of brown anole lizards (*Anolis sagrei*). These factors represent major hypotheses regarding body size variation in ectotherms and other animal groups: temperature, food availability, conspecific abundance and predator abundance. We also performed a tethered intruder experiment to determine whether the attack behavior of predatory curly-tailed lizards (*Leiocephalus carinatus*) depends on the body size of their brown anole prey. Lastly, we conducted a common garden experiment to assess whether brown anole body size differences between sites with and without curly-tailed lizard predators are genetically based. Predator abundance was the primary predictor of brown anole body size for both males and females. No other hypotheses were consistently supported. Brown anole body size increased along with increasing predator abundance, and predator abundance was negatively related to body size variation. Additionally, predators approached larger brown anoles less often and at longer latencies compared to smaller ones. Finally, male brown anoles from sites with predators had faster growth rates compared to those from sites without predators under common conditions in the lab. Brown anole body size differences among populations may result from higher survival of larger lizards during predatory confrontations, and this trait is at least partially heritable in males. Therefore, our results suggest that curly-tailed lizard predators may be important agents of evolution by natural selection for brown anole populations in urban habitats. To further investigate the ecological and evolutionary consequences of predator–prey interactions in urban habitats, future research should focus on measuring predator-induced selection in these novel environments.

Keywords *Anolis* lizards · Natural selection · Predator–prey interactions · Species interactions · Common garden

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Introduction

Body size is a key trait linked to many aspects of an organism's life history, physiology, and behavior. A number of important body size relationships generalize to a diverse array of taxa. For example, nearly every measure of fecundity is highly correlated with body size in most vertebrate and invertebrate groups (Blueweiss et al. 1978; Honěk 1993). Body size is also tightly linked to the daily energy requirements of many animals. In a study of hundreds of vertebrate species, body size explained over 70% of the variation in field metabolic rate (Nagy 2005). As such, larger individuals have higher food requirements. Body size also appears to play a role in determining consumer diets in that the majority of feeding interactions within a food web involve a larger predator consuming smaller prey (Cohen et al. 1993). Even in non-predator–prey systems, body size can influence the result of both intra- and interspecific interactions. Larger organisms often dominate and displace smaller ones, enabling better access to food, mates, and preferred habitat (Morse 1974; French and Smith 2005). Variation in body size can thus have important fitness consequences across a broad range of ecological contexts. Thus, a large research effort exists aimed at identifying the factors that may contribute to body size variation both within and between species (Peters 1986; Dmitriew 2011).

Both abiotic and biotic factors have been posited to drive patterns of body size variation at various geographic scales. Globally, studies have related latitudinal trends in body size with climatic factors, such as temperature and precipitation. Body size in temperate organisms is often larger compared to those inhabiting more tropical areas, perhaps owing to an increased ability of larger organisms to retain heat and thus persist in colder climates (e.g. Bergmann's Rule; Meiri and Dayan 2003). At the local scale, colder temperatures experienced by ectotherms during development can slow growth rates and increase size at maturity (Angilletta et al. 2004). Additionally, precipitation and temperature together may correlate with primary productivity, which may serve as a proxy for food availability (Yom-Tov and Geffen 2006). The dependence of growth on food availability is straightforward from an energy-acquisition perspective. However, when food is limited, organisms may face a trade-off between the energy allocated to somatic growth versus that devoted to other traits such as immune function or reproduction (Van Noordwijk and de Jong 1986; van der Most et al. 2011).

With regard to biotic factors, both competition and predation have been hypothesized to influence body size. For example, body size has often been considered in studies of ecological character displacement across taxa (Dayan and Simberloff 2005). Therefore, changes in body size can result from divergent natural selection generated by inter- or intraspecific competition between similarly sized individuals. Additionally, when competition is high and food resources are limited, this may favor smaller individuals with lower energy requirements (Peters 1986). Predators can also mediate competition for limited resources by depressing population densities through prey consumption and thus indirectly influence competition-driven selection on body size (Wootton 1994). Predators can also directly cause shifts in body size distributions if they are limited to or prefer prey of certain size classes (Persson et al. 1996; Urban 2008). Whether biotic or abiotic factors are considered, they are most often evaluated in isolation, which makes determining their relative or habitat-specific effects on body size difficult (but see Peckarsky et al. 2001). Given that several abiotic and biotic factors likely influence body size, we need a study system that captures landscape-scale variation in multiple factors to determine their relative effects.

Urbanization produces considerable variation in many of the abiotic and biotic factors hypothesized to influence body size variation (Forman 2014). Temperatures are often higher in cities compared to less developed areas due to both increased canopy openness and impervious surface cover (i.e., the urban heat island effect; Yuan and Bauer 2007). Moreover, surface temperature variation within urban areas can be substantial and urban surface temperatures are driven primarily by heterogeneity in vegetative cover (Weng et al. 2004; Chen et al. 2006; Buyantuyev and Wu 2010). Arthropods that rely on such vegetation vary in their abundance and community structure among different urban land use types (McIntyre et al. 2001). Since arthropods form the basal food resource for many taxa, urban areas may contain fine-scale variation in food availability. Invasive species are also prevalent in urban habitats and the non-continuous nature of their spread often results in patchy distributions (With 2002). These discontinuous distributions can generate variation in both competition and predation regimes within a city (Shochat et al. 2010; Fischer et al. 2012). Such high variability across relatively small spatial scales makes urban areas ideal for testing whether and how these factors interact to influence body size.

Indeed, urbanization has been linked to altered body size in multiple taxa. For example, urban house sparrows attained smaller body sizes and decreased body condition compared to rural conspecifics (Liker et al. 2008; Meillère et al. 2015). In snakes, the impact of urbanization on body size appears to be species specific. When compared to individuals inhabiting rural areas, invasive brown tree snakes were found to be larger in urban areas (Savidge 1988). However, African rock pythons display the opposite pattern with urban individuals having smaller body size compared to those from rural environments (Luiselli et al. 2001). Moreover, no differences in body size were found between Massasauga rattlesnakes from urban and rural sites (Parent and Weatherhead 2000). Such inconsistences also extend to reptiles in general (as reviewed by French et al. 2018), and thus the mechanisms underlying morphological change in response to urbanization remain unclear.

Lizards of the genus *Anolis* (or anoles) are an appropriate system to test how urbanization-induced alterations of the environment may contribute to body size differences among populations. Several *Anolis* species, including the brown anole (*Anolis sagrei*) used in this study, are widespread in urban habitats and often occupy a gradient from natural forests to highly disturbed urban cores (Battles et al. 2013; Kolbe et al. 2016; Winchell et al. 2018). Moreover, urbanization has been shown to modify both anole morphology and behavior. Urban anoles have longer hind limbs, more lamellae and faster growth compared to forest conspecifics (Winchell et al. 2016; Hall and Warner 2017). Other studies have demonstrated differences in foraging behavior, risk-taking behavior, and body size between urban and forest anoles (Chejanovski et al. 2017; Lapiedra et al. 2017). Yet, while these and many other studies compare populations that occupy opposite ends of the urbanization gradient, they do not address trait variation among localities within an urban habitat. There may be substantial variation in both biotic and abiotic conditions among urban localities, which may produce selective pressures on body size that differ in magnitude and direction. Furthermore, changes in anole morphology, including body size, have been shown to result from both plastic responses to differing environmental conditions and genetic differences between populations (e.g., Bonneaud et al. 2016; Hall and Warner 2017). Therefore, by using anoles to study body size variation, we can also investigate the genetic mechanisms underlying body size differences among populations.

In this study, we simultaneously assess a suite of factors that are likely to exhibit high variation across an urbanized landscape and represent major hypotheses regarding body size variation in ectotherms and other animal groups: (1) temperature, (2) food availability, (3) conspecific abundance and (4) predator abundance. First, the metabolic rate of

ectotherms is highly sensitive to even minor temperature variation (Gillooly et al. 2001; Angilletta 2009). Increased temperatures in cities may then lead to elevated metabolic rates and enable faster growth assuming food is readily available (Dillon et al. 2010). When food is limited, such temperature-induced increases in metabolism may cause declines in physiological condition and result in the need for higher rates of food acquisition to meet higher energetic demands (e.g. Lienart et al. 2014). Second, while increased temperatures may exacerbate the negative consequences of food limitation, reductions in food availability generally inhibit growth in most animals, though this may vary depending on when food shortage occurs during ontogeny (Sebens 1987). Third, even if food is initially available, increases in population density can increase competition and result in resource limitation. Additionally, male–male competition can produce selection for larger sizes (Hunt et al. 2009), suggesting intraspecific competition as a mechanism of body size evolution independent of food availability. Lastly, predators have been shown to alter the body size of their prey. Shifts toward larger prey size occur when predators can only consume smaller prey (i.e., gape-limited predators) or when larger prey size confers greater ability to escape from predatory attacks (e.g. Janzen 1993; Mattingly and Butler 1994; Blomberg and Shine 2000; Allen 2008). Conversely, shifts toward smaller individuals can occur when larger prey are more conspicuous and thus suffer higher mortality through increased detectability by predators (Cote et al. 2008; Mascaro et al. 2003).

To evaluate these hypotheses, we compare populations of brown anoles occurring across an urbanized landscape in south Florida (i.e., southwest Broward County) to determine the relative effects of the thermal environment, food availability, conspecific abundance, and predator abundance on body size variation. Overall, we predict that brown anole body size will increase with increases in each of these factors—temperature, food, competitors and predators. To further investigate the effect of predator abundance on body size, we also examine the relationship between brown anole body size and the attack behavior of an important predator, the curly-tailed lizard (*Leiocephalus carinatus*), using a tethered-intruder experimental design. These predators are known to be gape-limited (Schoener et al. 1982) and thus we expect larger brown anole lizards to experience lower approach rates (as a proxy for attack rates). Finally, we conduct a common garden laboratory experiment to test whether brown anole body size differences between sites with and without predators are genetically based.

Materials and methods

Body size variation across an urbanized landscape

Site selection

Our body size variation study was conducted from June–August 2016 across 38 sites located within the urban matrix of Broward County, Florida. We first generated random GPS points within cities in southwest Broward County using qGIS (QGIS Development Team, 2018). Any point < 1 km from a previously established site or deemed inaccessible (e.g. private property or water bodies) was excluded. We then surveyed the area within a 300-m radius of each point to delimit relatively continuous habitat and determine whether brown anoles were present. Sites mostly included urban parks and roadsides (see Fig. S1 in Supplementary Materials).

Land-cover measurements

We used line transects to measure percent cover of impervious surfaces at each site by placing five parallel transects along the site at random intervals between 10 and 20 m. Transect length varied depending on the site (e.g. roadside habitat transects ended at the road), but each was no more than 10 m (mean 9.3 m; range 3.5–10 m). Percent impervious surface cover was calculated by summing together the linear distances covered by impervious surfaces among the five line transects at each site, divided by the total distance of these transects multiplied by 100.

Arthropod food availability

To estimate arthropod availability, we used a sweep net to collect arthropods from vegetation at each site. We only collected arthropods from vegetation found < 50 m from where lizards were sampled (see Lizard Measurements below). To account for any potential daily variation in arthropod abundance, we swept vegetation during three time-periods: 09:00–10:00 (morning), 13:00–14:00 (afternoon), and 18:00–19:00 (evening). We swept grasses (most commonly *Stenotaphrum secundatum*) and bushes separately, with approximately 50 sweeps for each vegetation type during each time period. After collection, we immediately placed arthropods in a kill jar charged with acetone and kept them frozen until returned to the lab for sorting. In the lab, we removed small pieces of vegetation using a dissecting microscope and placed arthropods on a paper towel to remove any excess moisture. We then weighed these arthropods (i.e., wet mass excluding the paper towel and any moisture it had absorbed) to the nearest 0.0001 g using a digital balance. Biomass was grams per sweep for each vegetation type (grasses or bushes) within each time period. We found no effect of time period ($F_{2,221}=0.367$, $p=0.693$) or vegetation type ($F_{1,221}=3.426$, $p=0.066$) on arthropod biomass, and thus we calculated total biomass per site as the sum of all individual samples collected during the three time-periods from both vegetation types. Generally, the arthropod taxa we collected through sweep netting are well represented in the gut contents of brown anoles (Giery et al. 2013; Chejanovski 2018).

Conspecific and predator abundance

We conducted visual encounter surveys (VES) at each site to estimate relative abundance of brown anoles and curly-tailed lizards, the latter being well-documented predators of brown anoles (Schoener et al. 2002; Losos et al. 2004, 2006). Surveys consisted of walking the site at a constant pace and recording every individual lizard observed. We also measured the perch height of each brown anole observed using a laser distance meter. We performed these VES along the same route within each site during three time-periods: 08:00–09:00 (morning), 14:00–15:00 (afternoon), and 18:00–19:00 (evening) given previous work showing marked differences in daily activity times between brown anoles and curly-tailed lizards in similar habitats to this study (Lapiedra et al. 2017; also see Kolbe and Colbert 2008). These routes were left undisturbed for at least 30 min prior to each survey. Each survey was limited to a maximum of 10 min (discounting time taken to record observations), though some were shorter depending on the amount of habitat available and number of lizards observed. To standardize these measures, we calculated the number of lizards observed per minute for each survey. For brown anoles, males and females are

easily distinguished in the field and were thus counted separately. Relative abundance for both brown anoles and curly-tailed lizards at each site was the maximum number of individuals observed per minute among the three time-periods surveyed.

Lizard morphology and habitat measurements

In between VES, we captured 14–20 brown anoles of each sex as encountered at each site using a noose affixed to a telescopic fishing pole. We measured the internal body temperature of each lizard immediately upon capture using a thermocouple thermometer (Omega HH802U with Type K sensor) placed into the lizard's cloaca. Any lizard that moved from sun to shade or vice versa during capture was not used. Additionally, we only captured lizards between the hours of 09:30–18:00, the time of day when brown anoles are active and attain relatively stable body temperatures (Battles and Kolbe 2018). We then measured body size of each lizard as snout-vent length (SVL) to the nearest mm and mass to the nearest 0.01 g using a digital balance. We captured only sexually mature adult lizards for this study, corresponding to a minimum size of 42 mm SVL for males and 36 mm SVL for females (Lee et al. 1989). Lastly, we measured canopy openness of each site to assess potential differences in microclimate among sites. We took hemispherical photographs of the canopy from each lizard's original position (i.e., before capture) using a digital camera with a 180° fish-eye lens. From these photos, percent canopy openness was calculated for each image using Gap Light Analyzer (GLA) Version 2.0 (Frazer et al. 1999) and then averaged for each site.

Statistical analyses

We performed a principal component analysis to assess variation in abiotic and biotic variables in relation to each other and across our study sites. The first three principal components had eigenvalues greater than one and accounted for over 70% of the variation in our data. These three principal components generally corresponded to variables that describe the thermal environment (body temperature: range 27.8–37.9 °C, mean 33.0 °C $\pm$ 0.12 °C; impervious surface cover: range 0–51%, mean 15% $\pm$ 2%; canopy openness: range 11–36%, mean 18% $\pm$ 1%; PC1), food availability (range 0.001–0.048 g/sweep, mean 0.010 $\pm$ 0.002 g/sweep; PC2), and conspecific (range 0.015–0.123 lizards/min, mean 0.060 $\pm$ 0.004 lizards/min) and predator abundance (range 0–0.017 lizards/min, mean 0.003 $\pm$ 0.001 lizards/min; PC3). See the Supplementary Materials for visualization of PC axes 1–3 (Fig. S2) and values for PC loadings (Table S1).

We used linear mixed-effect models with site as a random effect to determine the abiotic and biotic factors that contribute to body size variation among sites. We utilized the R packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) to construct these models and generate p values via Satterthwaite's degrees of freedom method. In accordance with our principal component analysis, we included body temperature with time of day as a covariate, impervious surface cover and canopy openness as measures of the thermal environment, as well as food availability, conspecific abundance and predator abundance as fixed effects in the model. We used the total abundance of both male and female brown anoles as our measure of conspecific abundance in our analysis given that the abundances of males and females were moderately correlated (r = 0.53, 95% CI = (0.26, 0.73), df = 36, t = 3.77, p < 0.001). Because brown anoles are sexually dimorphic with regard to body size, we modeled the body size of each sex separately.

Due to the right-skewed distribution of our body size measurements, we ln-transformed SVL measurements to improve normality. Results for transformed and non-transformed data were quantitatively similar (see Tables S2 and S3 in the Supplementary Materials for a comparison of model results for non-transformed and square-transformed data). We report the results from the analysis with ln-transformed data to facilitate comparison to the results from the common garden study. Previous studies have shown that brown anoles increase their perch heights in response to the experimental introduction of curly-tailed lizards (Schoener et al. 2002, 2017; Losos et al. 2004, 2006). Therefore, we tested for a positive correlation (Pearson's product-moment correlation) between curly-tailed lizard abundance and brown anole perch heights among sites. We used only brown anole perch heights obtained from the afternoon VES as this is when curly-tailed lizards are most active and thus when brown anoles are most likely to shift their perch heights in response to curly-tailed lizards (Kolbe and Colbert 2008; Lapiedra et al. 2017). Furthermore, perch height has been observed to differ between the sexes for *A. sagrei* and other anoles (Butler and Losos 2002), and therefore we analyzed males and females separately. We calculated correlations among all sites (n = 38) and a reduced set of sites including only those with curly-tailed lizard predators present (n = 19). All analyses in this and the following studies were performed using R statistical software (R Core Team 2018).

Tethered-intruder experiment

Experimental design

We performed a field experiment in May 2017 to test whether larger brown anole body size results in lower attack rates by predatory curly-tailed lizards. We utilized a tethered-intruder experimental design (Reedy et al. 2017; Wu et al. 2018) in which we presented male brown anoles (N = 49) of varying size to free ranging curly-tailed lizards and measured the latency (in seconds) of curly-tailed lizards to approach each anole. Since we could not allow curly-tailed lizards to actually attack each tethered brown anole for ethical reasons, we used approaches as a proxy for predatory attacks. Trials took place in areas of high curly-tailed lizard abundance located within the same general area as the body size variation study described above (i.e., southwest Broward County).

We only used male brown anoles for this experiment to avoid any potential differences in anti-predator behavior between the sexes. However, the body size range used (SVL = 41–65 mm) includes sizes typical of both male and female adult brown anoles. We tethered each male brown anole to a telescopic fishing pole via a 10-cm long piece of dental floss and held it in a 5-gallon bucket prior to being presented to a curly-tailed lizard. We used each anole on the same day of capture and for only a single trial.

We identified focal adult curly-tailed lizards from a distance of at least 3 m. Once a focal curly-tailed lizard was observed, we expanded the telescopic fishing pole with tethered anole so that the distance between the observer and the anole was 3 m. We then placed the anole ~ 1 m from the curly-tailed lizard and the pole was laid flat on the ground. Trials began when the anole reached the ground and were terminated when either the curly-tailed lizard approached to within 20 cm of the anole or 3 min had elapsed. We only conducted trials between the hours of 10:00–16:00 when curly-tailed lizards are most active (Lapiedra et al. 2017). Following each trial, we captured focal curly-tailed lizards to measure (mass and SVL) and temporarily marked them to prevent repeated trials with the same individual.

Statistical analysis

We performed a survival analysis to test for differences in the latency of curly-tailed lizards to approach differently sized brown anoles. We used the semi-parametric Cox proportional hazards model available in the R package "survival" (Therneau and Lumley 2015), which is ideal for handling right-censored data such as these. We included the body size of brown anoles and curly-tailed lizards, both as continuous variables, as well as their interaction as factors in the model. The interaction term was not significant and was removed from the model. We then compared the model including brown anole and curly-tailed lizard body size as factors to the model with brown anole body size alone using a Chi square difference test. When not significantly different, we chose the model with the fewest parameters as the best model.

Common garden experiment

Experimental design and husbandry

We utilized a common garden experimental design to determine whether body size differences among urban sites with and without curly-tailed lizards are genetically based. We collected a total of 60 females from habitats containing high curly-tailed lizard abundance and habitats containing no curly-tailed lizards, each replicated three times (i.e., three sites per habitat with 10 females per site). The body size distributions of females in the common garden experiment matched the site-specific size distributions determined from the body size variation study described previously. We measured mass and SVL of each female before transporting them to the University of Rhode Island. Each female was housed individually in a $33 \times 19 \times 20$ cm (length $\times$ width $\times$ height) terrarium provided with cage carpet, a single perch, artificial plants, and a plastic container filled with moist, ground coconut husk for egg laying. We provided full spectrum lighting that was set on a 14:10 h light:dark cycle, and each cage was misted daily to provide drinking water. Temperatures in the room ranged from 31 °C during the day to 24 °C at night. We fed females five appropriately sized crickets every third day and we searched containers for eggs just prior to feeding. We collected eggs continuously from June 3, 2017 until August 14, 2017. Females used stored sperm from matings in the wild prior to capture (Calsbeek et al. 2007).

We measured the mass (0.0001 g), length and width (0.1 mm) of each egg before half-burying them in glass containers filled with moistened vermiculate (1:1 water:vermiculite by weight), which we then sealed with plastic wrap to prevent evaporation and incubated at 28 °C until hatching. We used the presence/absence of post-anal scales and dorsal patterning to sex each hatchling and measured SVL to the nearest 0.5 mm and mass to the nearest 0.01 g within 24 h of hatching. We hatched 150 brown anoles for the predator treatment (73 males and 77 females) and 165 brown anoles for the non-predator treatment (64 males and 101 females) with an overall mean of 5.42 ($\pm$1.73) hatchlings/dam. Hatchlings were housed in a $28 \times 17 \times 17$ cm terrarium with cage carpet, two perches, artificial plants and a small container filled with moistened coconut husk to maintain humidity. We housed hatchlings in pairs that were from the same habitat (i.e., with or without predators) and within 1 week of age to minimize any dominance effects within cages. Mortality over the course of the experiment required that we re-pair single hatchlings using these criteria. Lighting, misting and feeding schedules for hatchlings were the same as those for adult

females. We randomized cage positions every 2 weeks to eliminate potential positional effects. Hatchlings below 6 weeks of age were fed five 0.5-week old crickets every third day. We then provided five one-week old crickets for hatchlings between six and 14 weeks of age. Lastly, we increased the amount of one-week old crickets from five to eight for hatchlings over 14 weeks of age. We measured the mass and SVL of each hatchling prior to feeding every 2 weeks for up to 18 weeks. It should be noted that our termination of the common garden experiment at 18 weeks of age was due to logistical constraints and therefore this end point was not intended to represent any specific developmental stage (e.g. age at maturity) of our hatchlings. Nonetheless, the early stages during hatchling development may represent the time period when these hatchlings are most vulnerable to predation (i.e., when they are small).

Statistical analysis

We ln-transformed body size for analysis using linear mixed-effect models with habitat type, age, egg mass, egg order, and maternal SVL as fixed effects. We also included the interaction between habitat type and age to test for differences in growth rate between habitats. Survival rates of hatchlings did not differ between habitats for either males (ß=0.12, exp(ß)=1.13, SE(ß): 0.21, z=0.57, p=0.57) or females (ß=−0.03, exp(ß)=0.97, SE(ß)=0.20, z=−0.17, p=0.87) and thus all individuals (i.e., both survivors and non-survivors) were included in the analysis. We used a nested random effect structure (random intercept) with hatchling ID (to account for repeated measures) nested within maternal ID, which was nested within site. Due to the sexual dimorphism observed in this species, we modeled male and female body size separately.

Results

Predator abundance was the only significant predictor of anole body size for both males and females among the 38 urban sites (Table 1). Specifically, body size increased with increasing predator abundance (Fig. 1). For males, body temperature (33.04 °C±0.07 °C; N=600) was also significantly related to body size such that larger individuals had higher temperatures, but there was no relationship between female body temperature (32.96 °C±0.07 °C; N=599) and body size (Table 1). We observed a significant negative correlation between body size variation (i.e., the coefficient of variation for SVL) of male brown anoles and predator abundance (r=−0.33, 95% CI=(−0.59, −0.01), df=36, t=−2.09, p=0.04), but this relationship was not significant for females (r=−0.10, 95% CI=(−0.41, 0.23), df=36, t=−0.62, p=0.54). The correlation between brown anole perch heights (in the afternoon) and predator abundance was not significant across all 38 sites for males (r=0.07, 95% CI=(−0.26, 0.38), df=35, t=0.39, p=0.70) or females (r=0.14, 95% CI=(−0.19, 0.44), df=35, t=−2.09, p=0.42). These correlation coefficients increased when considering only those sites with non-zero predator abundance, but they were still non-significant (males: r=0.32, 95% CI=(−0.18, 0.68), df=16, t=1.34, p=0.20; females: r=0.39, 95% CI=(−0.08, 0.72), df=16, t=1.74, p=0.10).

In the tethered intruder survival analysis, brown anole SVL was the only significant predictor of latency to approach (ß=−0.05, exp(ß): 0.95, SE(ß): 0.03, z=−1.96, p=0.05). Large and medium-sized brown anoles were approached less often (48% and 42% of the time, respectively) compared to smaller individuals (86%). Additionally, curly-tailed

Table 1 Results of the linear mixed effect models for male and female body size (i.e., SVL)

| Variable	Value	Std. error	DF	T-statistic	p
Males					
Intercept	3.843	0.073	348.600	52.303	0
Body temperature	0.006	0.002	571.900	2.636	0.009
Time of day	0.001	0.002	585.800	0.280	0.779
Canopy openness	0.001	0.001	31.570	0.100	0.921
Impervious surface cover	− 0.045	0.053	31.880	− 0.835	0.410
Anolis sagrei abundance	− 0.001	0.005	32.030	− 0.179	0.859
Leiocephalus carinatus abundance	0.063	0.028	31.150	2.282	0.029
Food availability	0.384	0.681	30.690	0.564	0.577
Females					
Intercept	3.835	0.051	335.400	75.142	0
Body temperature	− 0.001	0.001	581.500	− 0.584	0.559
Time of day	− 0.001	0.001	577.900	− 1.082	0.280
Canopy openness	− 0.001	0.001	31.410	− 1.403	0.170
Impervious surface cover	− 0.005	0.040	32.810	− 0.122	0.904
Anolis sagrei abundance	0.002	0.003	31.980	0.715	0.480
Leiocephalus carinatus abundance	0.043	0.020	31.470	2.133	0.041
Food availability	0.867	0.504	31.310	1.720	0.095

Site was included as a random effect. SVL was ln-transformed before fitting each model to improve normality of the residuals

lizards approached smaller lizards at shorter latencies compared to anoles from the medium and large size classes (Fig. 2).

For the common garden experiment, we found significant effects of age (males: value = 0.019, SE = 0.001, DF = 547.300, t = 38.825, p < 0.001; females: value = 0.020, SE = 0.001, DF = 762.400, t = 48.152, p < 0.001) and egg mass (males: value = 0.622, SE = 0.158, DF = 101.100, t = 3.938, p < 0.001; females: value = 0.707, SE = 0.129, DF = 94.750, t = 5.504, p < 0.001) on both male and female hatchling body sizes. Body size increased with age and egg mass. For males, we also found a significant interaction between site and age (value = − 0.002, SE = 0.001, DF = 543.500, t = − 3.432, p < 0.001) indicating faster growth rates for brown anoles from sites with predators compared to sites without predators. In contrast, no differences in female growth rate were observed between sites with and without curly-tailed lizard predators (Fig. 3).

Discussion

In this study, we utilized the variation in multiple abiotic and biotic factors among urban localities to test simultaneously their relative effects on body size variation of urban brown anoles. Across 38 sites, brown anole body size in both males and females was positively related to predator abundance. To further assess the role of curly-tailed lizard predation on brown anole body size, we also demonstrated that larger anole body size confers reduced approach rates by this important predator, suggesting that being larger might offer
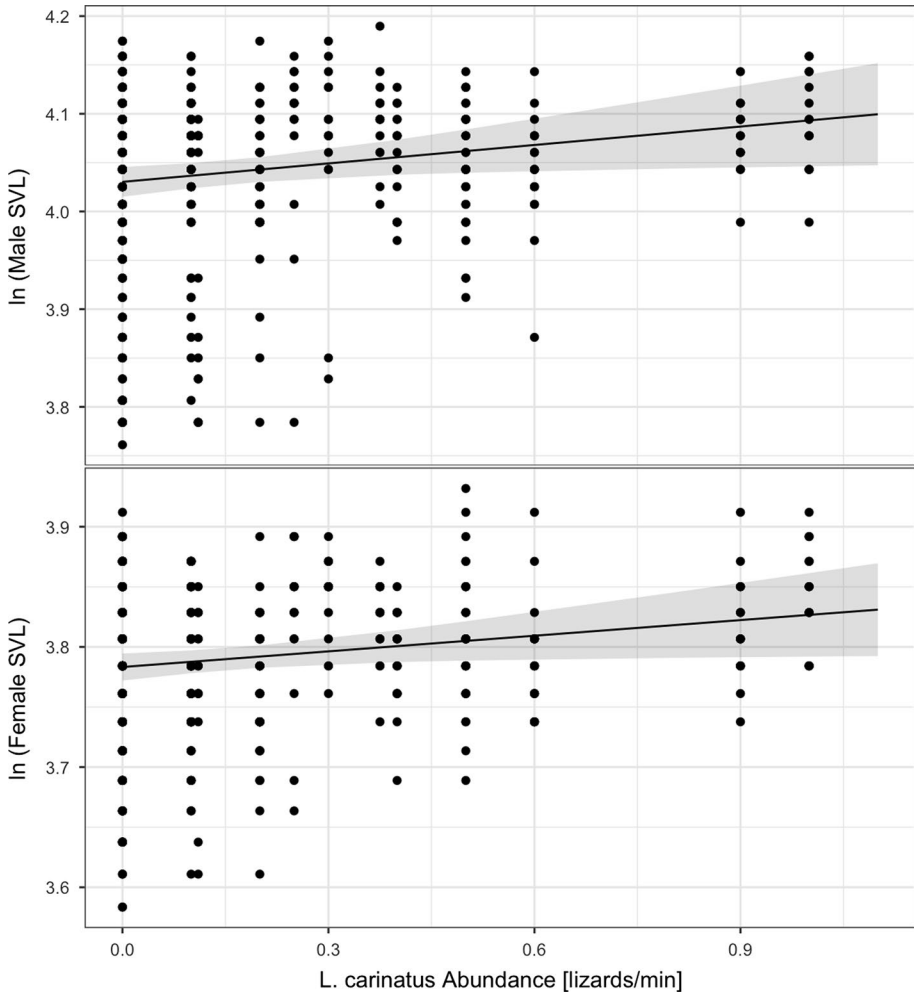
Fig. 1 Relationships between body size (i.e., ln-SVL measured in mm) and *L. carinatus* abundance (lizards/min) for male (top) and female (bottom) brown anoles. Lines and 95% confidence intervals (shaded) indicate the marginal effect of curly-tailed lizard abundance on brown anole SVL while holding all other variables at their mean values. Each point represents the average SVL of a single site, but individual ln-SVL values were used in the model

a survival advantage when confronted with this predator. Lastly, male body size differences between sites with and without predators were, at least in part, determined by genetic differences in growth rate. Overall, these results suggest that curly-tailed lizard predators may be important agents of evolution by natural selection on brown anole body size in urban environments.

Both ecological and evolutionary mechanisms have been previously proposed as drivers of body size variation of anoles. First, a recent study in the Bahamas found that in the field, male body size of brown anoles was explained by the availability of arthropod biomass (Bonneaud et al. 2016). In their study, male hatchlings reared in the lab under high
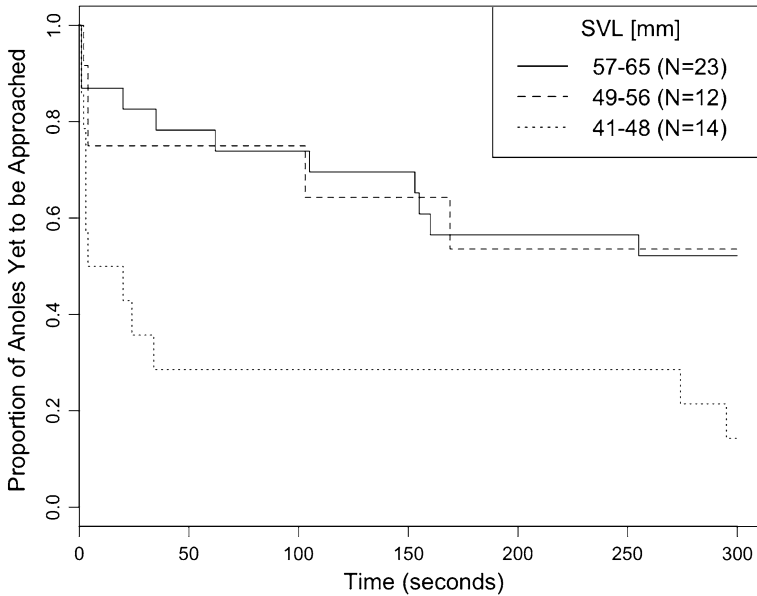
Fig. 2 Survival analysis comparing latency of *L. carinatus* individuals to approach male brown anoles of varying body size (i.e., SVL). To better visualize this relationship, brown anole SVLs were binned into large, medium and small sizes, which were determined by evenly splitting the overall body size range of brown anoles used in this study. Note that brown anole SVL was a continuous variable in the survival analysis

food availabilities had faster growth and attained larger maximum body sizes compared to males raised under a low food treatment (Bonneaud et al. 2016). While genetic differences between populations were not assessed in this study, these results provide support for a plastic response to food availability in determining brown anole body size. Second, changes in male brown anole body size have been attributed to variation in population density, with larger size favored in populations with higher density (Calsbeek and Cox 2010).

For food availability, we found no relationship between arthropod biomass and body size for either male or female brown anoles in south Florida. Though the methodologies to sample arthropods were generally similar between our study and that performed by Bonneaud et al. (2016), the latter study used a combination of sweep netting and pitfall traps. The use of only sweep netting in our study may have led to incomplete sampling of arthropod prey, which may account for the conflicting results between studies. Another possibility is that the relationship between food availability and body size could theoretically be obscured if arthropod abundances exceed that which would promote maximum anole growth. Therefore, the discrepancy between studies could be explained by food saturation in urban habitats. Arthropod biomass in our urban sites was on average over 12 times greater than the Bahamian site with the highest biomass in the Bonneaud et al. (2016) study. Moreover, other studies have also found that some groups of arthropods can reach exceedingly high abundances in urban areas (Shochat et al. 2004; Bang and Faeth 2011; Philpott et al. 2014). For competition, we did not observe any relationship between body size and conspecific abundance suggesting that, at least in our system, predator-induced selection may be relatively more important compared to that generated by intraspecific competition.
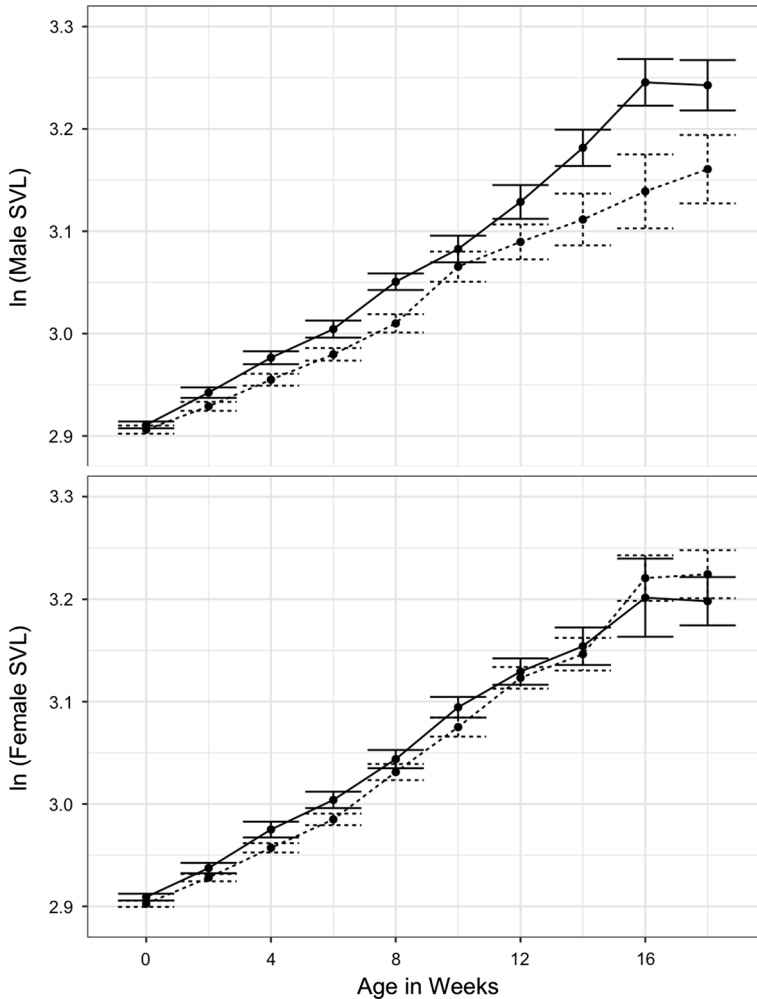
Fig. 3 Growth rate (mean ± SE of SVL over time) for male (top) and female (bottom) brown anole hatchlings whose mothers were from habitats with (solid line) and without (dashed line) predators

However, our ability to detect the potential effects of competition and the thermal environment may be limited in this urban system. For example, the high food availability in our urban localities is likely to decrease the intensity of intraspecific competition among urban lizards. When this is coupled with relatively lower anole abundances (though not significantly so) in areas of high predator abundance, it is unsurprising that competition was found to have little effect on brown anole body size compared to other factors. As for the thermal environment, behavioral thermoregulation may constrain the range of ambient temperatures experienced by urban brown anoles. This is supported by a recent study showing that brown anoles in Miami, FL are able to maintain field body temperatures within their preferred thermal range (i.e., 30.2–35.7 °C), despite operative temperatures (i.e., a proxy for lizard body temperature without behavioral thermoregulation) that far exceeded these limits (Battles and Kolbe 2018). While we did not measure operative temperatures

at our field sites, the brown anole body temperatures measured in this study generally fall within their preferred range. Specifically, we observed that body temperatures ranged between 27.8 and 37.3 °C for males and between 27.9 and 37.9 °C for females. Therefore, behavioral thermoregulation may shield urban brown anoles from potentially extreme temperatures and their associated selective pressures. Yet, temperatures experienced during development, when thermoregulatory behavior is limited, may be more important than adult body temperatures in influencing lizard morphology. Such developmental plasticity has been shown in many ectothermic vertebrates (e.g., lizards: Shine and Harlow 1996; turtles: Rhen and Lang 1995, snakes: Shine et al. 1997), and Goodman (2008) found latent effects of incubation temperature on the growth rate of *Anolis carolinensis*. However, similar work found little effect of incubation temperature on hatchling morphology in *A. sagrei* (Warner et al. 2011), as well as in the congener *Anolis cristatellus* (Hall and Warner 2018), but latent effects were not evaluated. In light of these caveats, we caution against dismissing the potential effect of these environmental variables (i.e., competition and the thermal environment), while still emphasizing the greater role of predators in determining brown anole body size in the urban environments we studied.

Predators have previously been shown to alter body size distributions and selection on body size in brown anoles. The experimental introduction of curly-tailed lizards to naturally occurring populations of brown anoles in the Bahamas revealed selection for larger body size in females, but not males (Losos et al. 2004). In a different study in the same island system, curly-tailed lizard introductions resulted in narrower brown anole body size distributions such that smaller lizards were less common on islands with predators (Schoener et al. 2002). We also found reductions in brown anole body size variation in habitats where predators occurred, which were at least partially driven by a reduction in the number of smaller individuals in each population. Unlike the Bahamian study, our results suggest that predatory curly-tailed lizards similarly influence both male and female body size. While it is uncertain why predator-induced selection was found only for female body size in the Bahamas, this island study provides evidence that predatory curly-tailed lizards can indeed generate natural selection on anole body size.

Though we did not measure selection in our study, we present multiple lines of evidence that suggest size-selective predation may be a source of natural selection influencing brown anole body size in urban habitats. Several criteria are needed to support evolution by natural selection. First, body size variation must exist for selection to act. We observed the greatest variation in body size (i.e., coefficient of variation for SVL) in sites without predators, and brown anole body size variation decreased with increasing predator abundance. This reduction in body size variation is consistent with the expectation from directional selection favoring larger body size (Endler 1986). Second, body size must be linked to differences in survival. Our tethered intruder experiment suggests that curly-tailed lizards approach, and presumably attack, smaller anoles more rapidly and more often than larger ones, which may lead to larger lizards having a higher probability of survival during predatory confrontations compared to smaller lizards. Additionally, hind-limb length is positively related to body size and sprint speed in many squamate lizards, including *A. sagrei*, meaning that larger lizards are also faster (Losos 1990; Van Damme and Vanhooydonck 2001). Thus, even smaller brown anoles (e.g. females) can benefit from being relatively large compared to other individuals through an increased ability to escape from predators. Lastly, some component of body size must be heritable for selection to translate into evolution in the next generation. Our common garden experiment supports that genetic differences in male growth rate contribute to the observed differences in body size between sites with and without predators. This is

further supported by other studies demonstrating relatively high heritability estimates ($h^2 = 0.55$) for body size in brown anoles (Calsbeek and Smith 2007; also see Calsbeek and Bonneaud 2008). Therefore, we have shown that the relationship between body size variation and predator abundance is consistent with expectations under predator-induced selection, larger brown anoles may have a survival benefit when confronted with predatory curly-tailed lizards, and body size is genetically based. Yet, to verify that predators are in fact producing selection on brown anole body size, we suggest that future work should use mark-recapture studies to estimate selection gradients on the body size for brown anoles in urban areas.

While increases in body size may include substantial fitness benefits, it is important to also consider the potential costs. For example, the resting metabolic rate of many reptiles scales with body size, which increases the amount of food needed by larger individuals for maintenance (Andrews and Pough 1985). Such increases in metabolism likely require higher foraging rates and may lead to greater risk-taking behaviors to fuel higher metabolic demands. However, even if urban environments contain sufficient food, the presence of predatory curly-tailed lizards can reduce food availability through reductions in anole ground use, a proxy for foraging activity (Lapiedra et al. 2017). The higher growth rate of males from habitats with predators can also entail costs, specifically in immune function. Trade-offs between growth and immune function have been demonstrated in a variety of taxa (e.g. chickens: van der Most et al. 2011; insects: Rantala and Roff 2005) including lizards (Uller et al. 2006). Furthermore, the costs of impaired immune function may be exacerbated in urban environments as some studies have linked urbanization to increased parasitism in lizards (Lazić et al. 2017; Thawley et al. 2019) while others have found this not to be the case (Amdekar et al. 2018).

Urban habitats have been increasingly regarded as hotspots for evolutionary change (Johnson and Munshi-South 2017). Over the past decade, evidence for genetically based changes between urban and non-urban populations has been growing (e.g. Partecke and Gwinner 2007; Cheptou et al. 2008; Whitehead et al. 2010). Yet, most of these studies fail to explicitly address the fitness consequences of these changes as well as the specific drivers underlying them (Donihue and Lambert 2015). Nonetheless, the altered abiotic and biotic conditions in cities are generally hypothesized to create novel selection pressures that result in phenotypic divergence between urban and natural populations (e.g. Garroway and Sheldon 2013; Winchell et al. 2016; Brans et al. 2017). These selective pressures are likely to differ even among neighboring localities and reduced dispersal of individuals among these localities could promote local adaptation. In our study, curly-tailed lizards were patchily distributed and we speculate that urbanization-induced habitat fragmentation is likely facilitating body size evolution by reducing the potential for genetic mixing between brown anoles from habitats with and without predators. Therefore, to better predict the potential for adaptive evolution in urban habitats, it is important to identify the specific factors responsible for phenotypic changes and the geographic scale at which these factors vary.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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