Urbanization affects body size and parasitism but not thermal preferences in *Anolis* lizards

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Abstract

Urbanization is accelerating worldwide and creates novel habitat conditions including increases in environmental temperature and changes in presence and abundance of predators, prey and parasites. For species that use urban habitats, these changes can have strong impacts on phenotypes. *Anolis* lizards commonly exploit urban habitats and, as ectotherms, are likely to experience pressures from these novel environments. Previous research shows that anoles may adapt to some aspects of urban habitats, but we lack an understanding of the breadth of traits that may shift in response to urbanization and how widespread these changes may be. To assess effects of urban habitat use on anole phenotypes, we measured morphology, thermal preference and parasitism in brown anoles (*Anolis sagrei*) and crested anoles (*Anolis cristatellus*) from urban and natural habitats within the Miami metropolitan area (FL, USA). In urban areas, individuals of both species were larger, but did not show any differences in preferred body temperatures. These results agree with other studies showing increased body size in anoles inhabiting urban areas, but the mechanisms underlying this pattern are unclear. Brown anoles experienced higher levels of parasite infection intensity in urban habitats, but crested anoles showed no differences between urban and natural sites. Increased infection intensity in urban brown anoles suggests that exploiting urban habitats may have costs and shows that urbanization can lead to species-specific changes in ecologically similar congeners. Understanding how urban habitats alter phenotypes of organisms that exploit these areas will be important in predicting costs of and adaptive responses to future urbanization.

Key words: *Anolis cristatellus*, *Anolis sagrei*, parasite, body temperature, invasive species

Introduction

Globally, urbanization is predicted to increase rapidly in the near future (Jiang and O'Neill 2017). Many species are capable of utilizing urban habitats, either by exploitation or adaptation. Using urban habitats can have benefits for organisms such as increased food or release from predators (Jessop et al. 2012; Rebolo-Ifrán, Tella, and Carrete 2017). However, living in urban habitats can also have costs, which may include use of artificial substrates, exposure to novel parasites, increases in predators and exposure to thermal limits (Shochat et al. 2006; Angilletta et al. 2007; Fischer et al. 2012; Loyd et al. 2013; Forman 2014; Kolbe, Battles, and Avilés-Rodríguez 2016). As a result of these costs and benefits, urban populations may have altered phenotypes, including differences in growth rate, body size, energy reserves and parasitism (Garden et al. 2007; Liker et al. 2008; Kolbe et al. 2016; Alberti, Correa, and Marzluff 2017; French et al. 2018). Quantifying

these impacts and associated novel pressures is a critical step in conserving at-risk species and understanding adaptive responses to changes associated with urban systems (Grimm et al. 2008; Hoffmann and Sgrò 2011; Donihue and Lambert 2015).

Thermal changes are one key signature of urban environments, which generally experience temperatures up to 5°C warmer than surrounding natural areas, a phenomenon termed the *urban heat island effect* (Grimm et al. 2008; Rizwan, Dennis, and Liu 2008; Angilletta 2009). These novel thermal conditions may influence activity levels, metabolic rate, behavior, performance and other organismal characteristics that can in turn affect fitness, especially in ectotherms (Angilletta 2009; Gunderson and Leal 2016). Indeed, organisms adapted to cooler, natural environments that utilize hotter urban habitats may suffer thermoregulatory costs (Battles and Kolbe 2018), and urban environments can favor organisms with higher thermal preferences and filter out those with lower thermal preferences (Piano et al. 2017). As a result, organisms exploiting urban habitats may adapt to these novel thermal conditions (Diamond et al. 2017). However, research documenting changes in thermal physiological traits driven by urbanization is uncommon in vertebrates.

Urban environments also feature novel species assemblages, which can result in new species interactions, including those involving parasites. Urbanization can cause changes in levels of blood, internal and ecto-parasites, including via novel host–parasite relationships (Delgado-V and French 2012; Goulson, Whitehorn, and Fowley 2012; Ortega et al. 2015). Impacts of parasitism on wildlife are diverse and can include upregulation of immune function, changes in behavior and reductions in body condition, signal quality, performance, survival and growth (Tompkins et al. 2011; Cook, Murphy, and Johnson 2013; Spence et al. 2017; Finnerty, Shine, and Brown 2018). However, the impacts of urbanization on parasitism, while likely diverse, require additional study (Bradley and Altizer 2007; Martin et al. 2010). The relationship between urbanization and parasite dynamics has received study in some taxa, especially birds (Delgado-V and French 2012), yet there is comparatively little known in reptiles (French et al. 2018), but see (Lazić et al. 2017).

While much research on urban ecology of vertebrates has focused on mammalian and avian species, reptiles are good models for determining how urbanization impacts species because they can reach high local abundances and persist in extremely urbanized patches. Urban habitats affect reptiles via multiple pathways (Hamer and McDonnell 2009; French et al. 2018); for example, as ectotherms they are likely to respond strongly to altered thermal environments in cities (Ackley et al. 2015; Gunderson and Leal 2016). Furthermore, because urbanization has a strong impact on arthropod communities (Kotze et al. 2011), reptiles which rely on this food source are likely to experience changes in energy availability. In fact, reptiles in urban areas have shown changes in a suite of traits, including foraging and anti-predator behavior, diet, condition, abundance, physiology and survival (Jessop et al. 2012; Batabyal, Balakrishna, and Thaker 2017; Chejanovski et al. 2017; Lapiedra, Chejanovski, and Kolbe 2017; French et al. 2018). In some cases, reptiles may also be adapting to novel selective pressures imposed by urbanization (Winchell et al. 2016). Surveying phenotypic differences in urban populations is an important first step in understanding impacts of urbanization and sets the stage for discriminating between adaptation and plastic responses to urban landscapes (Donihue and Lambert 2015).

Anoles are an ideal system in which to study impacts of urbanization because they are abundant in urban areas, are a model group for ecological, physiological and evolutionary studies, and are known to be impacted by conditions altered during urbanization (Losos 2009). For instance, anoles suffer reduced performance on artificial substrates common in human-built habitats (Kolbe, Battles, and Avilés-Rodríguez 2016) and may experience costs when attempting to thermoregulate in hotter urban environments (Kolbe et al. 2016; Battles and Kolbe 2018). Anoles may also experience novel predators and higher predation in urban areas (Loyd et al. 2013; Lapiedra, Chejanovski, and Kolbe 2017). As a result, anoles are known to respond adaptively to urban environments via changes in hindlimb length, habitat selection and behavior, which may increase fitness in cities (Lapiedra, Chejanovski, and Kolbe 2017; Battles, Moniz, and Kolbe 2018; Winchell et al. 2018b, 2016). However, the extent of phenotypic shifts in anoles and whether they can be generalized across species and specific urban contexts is unclear.

In this study, we examined differences in three phenotypes—body size, thermal preference and parasitism—between populations of two species of anole lizards, the brown anole (*Anolis sagrei*) and the crested anole (*Anolis cristatellus*) inhabiting natural and urbanized areas in Florida, USA. Both species are introduced to southern Florida and use urban habitats in both their native and invasive ranges (Marnocha, Pollinger, and Smith 2011; Winchell et al. 2018a). We hypothesized that anoles in urban habitats would be both larger and have higher body condition indices (Chejanovski et al. 2017). As urban habitats are warmer than nearby natural areas, we predicted that anoles from urban populations would prefer higher body temperatures that would reduce potential thermoregulatory costs of using these habitats but have similar preferred thermal ranges compared to anoles from natural areas. As reptiles are known to exhibit behavioral fever, we hypothesized that parasitism and parasite infection intensity would be positively related to higher preferred body temperatures (Rakus, Ronsmans, and Vanderplasschen 2017). Lastly, we predicted that anoles in urban areas would have higher levels of internal parasite prevalence and infection intensity, an impact observed in other focal taxa and studies of hemoparasites in lizards (Perkins, Rothschild, and Waltari 2007; Lazić et al. 2017).

Methods

Field collection

In fall 2014, we captured brown ($n_{\male} = 30$, $n_{\female} = 64$) and crested anoles ($n_{\male} = 52$) via noose and hand from seven urban and natural sites (four sites per species; Supplementary Table S1) in the Miami metropolitan area and transported them to the University of Rhode Island. Natural sites were forested patches within the Miami urban matrix and featured generally closed canopies with an understory of palmetto, saplings and shrubs. Urban sites were characterized by high levels of human disturbance, impervious surfaces, managed vegetation and artificial substrates.

Husbandry

In the laboratory, lizards were housed in a climate-controlled room in individual cages furnished with terrarium liners, natural perches and plastic plants placed in containers with moist soil. Room temperature was maintained between 22 and 34°C with daily cycles from low (night) to high (day) temperatures. Room humidity ($53.1 \pm 0.5\%$) was maintained via humidifiers and twice daily misting of cages. Room lights were set on a 12 h L:12 h D cycle, and all cages were illuminated daily with ultraviolet light (Reptile UVB bulbs, Exo Terra, Mansfield, MA, USA).

Anoles were fed crickets dusted with vitamin and mineral powder (Rep-Cal Phosphorus-Free Calcium with Vit. D, Rep-Cal Research Labs, Los Gatos, CA, USA) three times weekly. Upon housing in the laboratory, snout-vent length (SVL) and mass of lizards were recorded. Lizard health was monitored daily.

Thermal preference trials

Thermal preferences were determined by placing lizards in a trial apparatus comprised of a series of eight visually and physically separated lanes, each of which contained a thermal gradient. At one end of each lane, an incandescent heat lamp was placed to allow for basking at high temperatures, whereas the opposite end of the gradient contained a small plastic container filled with ice. Temperatures at the warm end of the gradient averaged 46.6°C (SE: 0.30; range: 44–52°C) and averaged 15.4°C (SE: 0.28; range: 7–17°C) at the cool end. Temperatures in all gradients always included the range of preferred temperatures found for these species in previous studies and allowed for selection of temperatures up to the critical thermal maximum for each species.

All lizards used in trials ($n = 90$) were acclimated to standard care conditions for at least three days prior to testing. Lizards were placed individually in lanes for trials lasting 140 min. Internal body temperatures of lizards were measured by means of a thermocouple (K-type, 36-gauge, 0.13 mm-diameter) inserted into the cloaca and taped to the body, leaving lizards free to move throughout the thermal gradient to achieve preferred body temperatures. Thermocouples were connected to a controller that recorded temperature every ten seconds, allowing continuous monitoring of body temperature without disturbance by observers. If thermocouples became detached or lizards showed abnormal behavior, such as hiding, these trials were excluded from the analyses. In these cases, lizards were included in one additional trial. If a lizard did not successfully complete this second trial, it was excluded from thermal preference testing. Measurements from the first 35 min of each trial during which lizards were acclimating to the novel experimental environment were not included in analyses. Preferred body temperature was calculated as the mean of all temperatures after this acclimation period. The interquartile range of these temperature readings was used as a measure of range of preferred temperatures (Hertz, Huey, and Stevenson 1993).

Parasite identification

Lizards were euthanized using a two-stage protocol of intracoelomic injections of tricaine methanesulfonate [MS-222 (Conroy et al. 2009)]. Internal parasites were collected by dissecting lizards ($n = 103$) along the ventral midline. The digestive tract, liver, heart and lungs were removed separately and examined under a dissecting scope. Organs were opened and searched for parasites which were identified to morphotype and preserved in 95% ethanol. Each morphotype was identified to the lowest taxonomic group possible using morphological characters. For each morphotype, we attempted to generate diagnostic DNA sequence data to corroborate morphological identifications (see Supplementary data for details). After conducting DNA analyses, we determined that sampling did not allow for more detailed analyses for any specific taxonomic group, so parasites were grouped together for analyses of parasitism (presence or absence of parasites) and parasite infection intensity (number of parasites in individuals having at least one parasite).

Statistical analyses

We tested for effects of urbanization on body size using linear models. Starting models contained habitat type (urban or natural), site, sex or species and their interaction with habitat type. Body condition was calculated separately for each group (crested anole males, brown anole males and brown anole females) as residuals from ordinary least squares regressions of ln-transformed body mass on ln-transformed SVL (Warner, Johnson, and Nagy 2016). When used as a covariate in other analyses (below), SVL was scaled and centered separately for each group.

We tested for effects of urbanization on thermal preference characters using linear models. Starting models contained habitat type (urban or natural), site, sex or species and their interaction with habitat type. Covariates included scaled SVL and body condition. Mean preferred body temperature was squared, and range of preferred temperatures (interquartile range) was natural log-transformed to meet assumptions of normality. We tested for impacts of parasitism and infection intensity on mean preferred temperature and preferred temperature range on a reduced dataset ($n = 81$) for which we were able to measure both thermal physiology and parasitism. We added parasitism and infection intensity singly as predictors to the final models from thermal analyses and used F-tests to assess whether they affected thermal traits. Infection intensity (total number of parasites) was transformed by adding one and taking the natural log to meet assumptions of normality in model residuals.

We analyzed parasitism using generalized linear models with a binomial distribution. We analyzed parasite infection intensity of parasitized individuals using generalized linear models with a negative binomial distribution as implemented in function *glm.nb* in R (R Core Team 2018). Starting models contained habitat type (urban or natural), site, sex or species and their interaction with habitat type. Covariates included scaled SVL and body condition.

For each analysis, we first assessed whether the target variable (body size, thermal preference or parasitism) varied between sexes of *A. sagrei* either via an interactive effect with habitat type or as a main effect. If sex significantly predicted the target variable in either analysis, we analyzed the full dataset with *A. sagrei* males, *A. sagrei* females and *A. cristatellus* males treated separately as a group factor. If sex was not a significant predictor of the target variable, we pooled all *A. sagrei* individuals and tested for differences between species in our final analyses. For all analyses, we tested both site and all interactions with either F-tests or likelihood ratio tests as appropriate and removed terms if they did not meet significance thresholds. *Post hoc* tests were conducted in the *emmeans* package in R (Lenth 2018), and $\alpha = 0.05$ for all tests. Not all anoles had observations for each trait, so sample sizes varied for analyses of different traits, ranging from 81 to 146. We used the most complete dataset possible for each analysis.

Results

Body size

Anoles from urban habitats were consistently larger than those from natural habitats ($\beta_{Urban} = 1.469$, $F = 4.600$, $P = 0.034$), and site was not a significant predictor of body size ($F = 2.116$, $P = 0.067$). *Post hoc* comparisons of urban and natural populations showed that, within each group (male crested anoles, male brown anoles and females brown anoles), anoles from urban populations were larger (all $P < 0.05$) (Fig. 1). Initial analysis of data from *A. sagrei* indicated that sex had an interactive effect
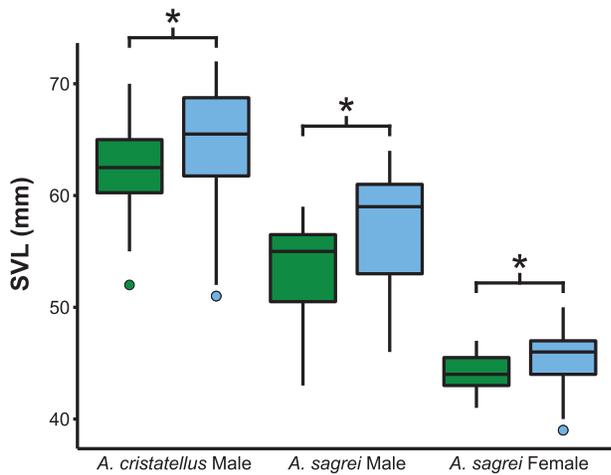
Figure 1: For each group, male crested anoles, male brown anoles and female brown anoles, lizards from urban (blue) habitats were larger than those from natural (green) habitats. Asterisks denote comparisons with significant differences.
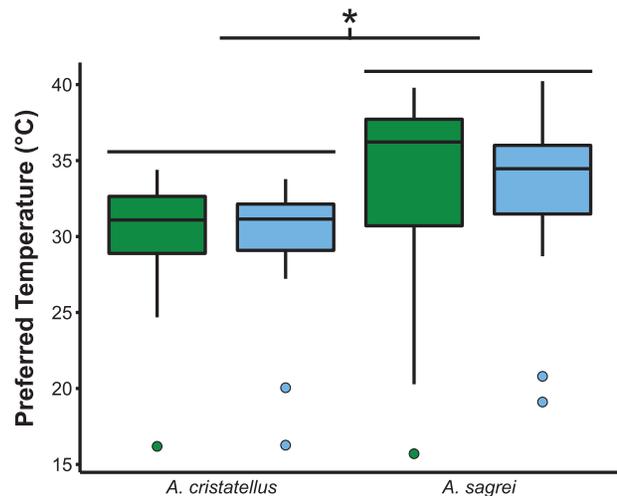

Figure 2: Preferred body temperature did not vary between urban (blue) and natural (green) habitats but was significantly higher in brown anoles than in crested anoles. Asterisk denotes significant difference in *post hoc* testing.

with urban habitat on body size ($\beta_{\beta*\text{Urban}} = -3.003$, $F = 4.169$, $P = 0.044$), so male and female *A. sagrei* were not pooled. Groups were significantly different from each other in body size ($F = 294.90$, $P < 0.001$), and *post hoc* comparisons showed that all groups differed significantly in body size from each other (all $P < 0.05$) (Fig. 1). Body condition of anoles did not differ between urban and natural habitats ($\beta_{\text{Urban}} = 0.192$, $F = 1.353$, $P = 0.247$), nor did body condition differ by sex ($\beta_{\beta} = -0.101$, $F = 0.002$, $P = 0.962$), species ($\beta_{sagrei} = 0.003$, $F < 0.001$, $P = 0.986$) or site ($F = 2.192$, $P = 0.059$).

Thermal preference

Anoles from urban populations did not prefer higher body temperatures in the laboratory ($\beta_{urban} = -15.94$, $F = 0.061$, $P = 0.806$), and preferred body temperature did not differ with site ($F = 0.590$, $P = 0.708$), SVL ($\beta = 8.40$, $F = 0.065$, $P = 0.799$) or body condition ($\beta = -30.71$, $F = 0.970$, $P = 0.328$) (Fig. 2). Brown anoles preferred higher body temperatures (mean $= 33.2°$C) than crested anoles (mean $= 29.9°$C) ($\beta_{sagrei} = 234.22$, $F = 14.21$, $P = 0.0003$). Preferred temperature range did not differ between urban and natural populations ($\beta_{urban} = 0.149$, $F = 0.527$, $P = 0.470$; Battles and Kolbe 2018). Preferred temperature range did not vary by sex ($\beta_{\beta} = -0.042$, $F = 0.010$, $P = 0.921$) or species ($\beta_{sagrei} = 0.286$, $F = 2.094$, $P = 0.152$) or with site ($F = 0.841$, $P = 0.525$), SVL ($\beta = 0.123$, $F = 1.380$, $P = 0.243$) or body condition ($\beta = 0.006$, $F = 0.004$, $P = 0.951$). Parasitism had no effect on preferred body temperature ($\beta_{\text{Parasites}} = -72.25$, $F = 0.0977$, $P = 0.326$) or preferred temperature range ($\beta_{\text{Parasites}} = -0.449$, $F = 3.573$, $P = 0.063$), though parasitized lizards tended to have narrower ranges of preferred body temperatures. Parasite infection intensity had no effect on preferred body temperature ($\beta = -4.064$, $F = 0.014$, $P = 0.906$) or range of preferred temperatures ($\beta = 0.013$, $F = 0.131$, $P = 0.909$).

Parasites

Analysis of body cavity and gut parasites ($n = 742$) via DNA sequencing allowed identification of morphospecies representing 81% of all parasites sampled. Parasites included representatives from six orders within three phyla (Nematoda, Arthropoda and Platyhelminthes; Supplementary Table S3 and Fig. S1);

the overwhelming majority of identified parasites (94%) were nematodes. Common nematodes included the atractid *Rondonia rondoni* and species in the genus *Physaloptera*. Both brown and crested anoles were found with lungs infected by pentastomids in the genus *Raillietiella*. These represent major groups known to parasitize lizards and, in several cases, are known previously from *A. sagrei* (Goldberg and Bursey 2000; Bursey, Goldberg, and Telford 2007; Reedy et al. 2016).

Urbanization had no effect on parasite prevalence ($\beta_{\text{Urban}} = 0.219$, $\chi^2 = 0.195$, $P = 0.659$). Initial analysis of data from brown anoles indicated that sex had an interactive effect with urban habitat on parasite prevalence ($\beta_{\beta*\text{Urban}} = 19.299$, $\chi^2 = 48.58$, $P = 0.028$), but *post hoc* comparisons revealed no significant differences between males or females at urban and natural sites (all $P > 0.577$). Analysis of the full dataset indicated that groups differed significantly in parasite prevalence ($\chi^2 = 20.121$, $P < 0.001$), and *post hoc* analyses showed that both male and female brown anoles had higher parasite prevalence than male crested anoles (all $P < 0.018$), but the brown anole sexes did not differ from each other ($P = 0.446$) (Fig. 3). Lizard body size ($\beta = -0.103$, $\chi^2 = 0.166$, $P = 0.684$), body condition ($\beta = 0.086$, $\chi^2 = 0.120$, $P = 0.729$) and site ($\chi^2 = 7.339$, $P = 0.119$) had no effect on parasite prevalence.

Urbanization affected parasite infection intensity in species differently ($\beta_{\text{Urban}*sagrei} = 0.967$, $\chi^2 = 1.010$, $P = 0.037$). *Post hoc* analyses showed that infection intensity was similar in crested anoles in both urban and natural areas and brown anoles from natural habitats (all comparisons $P > 0.516$) but was significantly higher in brown anoles in urban areas (all comparisons $P < 0.003$) (Fig. 4). Infection intensity tended to increase with SVL ($\beta = 0.181$, $\chi^2 = 2.953$, $P = 0.086$) though this trend was not significant, and infection intensity was also not related to body condition ($\beta = 0.176$, $\chi^2 = 2.739$, $P = 0.098$), sex in *A. sagrei* ($\beta_{\beta} = 0.034$, $\chi^2 = 1.010$, $P = 0.295$) or site ($\chi^2 = 6.7338$, $P = 0.150$).

Discussion

In this study, urbanization was linked to increases in body size across species and sex, suggesting a consistent effect on morphology. Additionally, we found species-specific responses to urbanization, with crested anoles showing no impact of
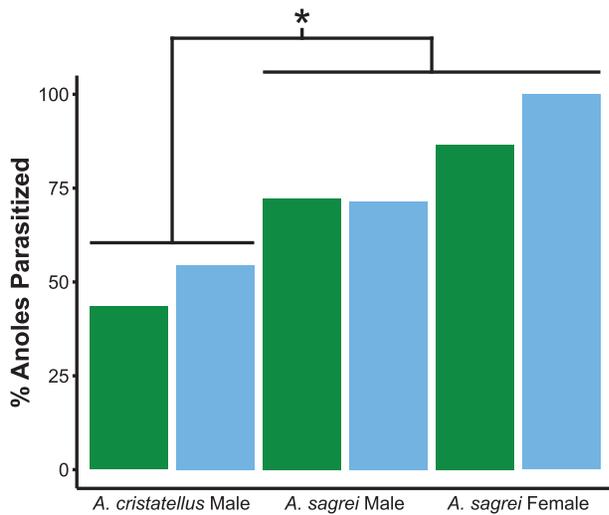
Figure 3: Anoles from urban habitats (blue) have similar levels of parasitism to anoles from natural habitats (green). Male and female brown anoles (*A. sagrei*) have significantly higher parasite prevalence than male crested anoles (*A. cristatellus*). Asterisk denotes groups significantly different in *post hoc* tests.
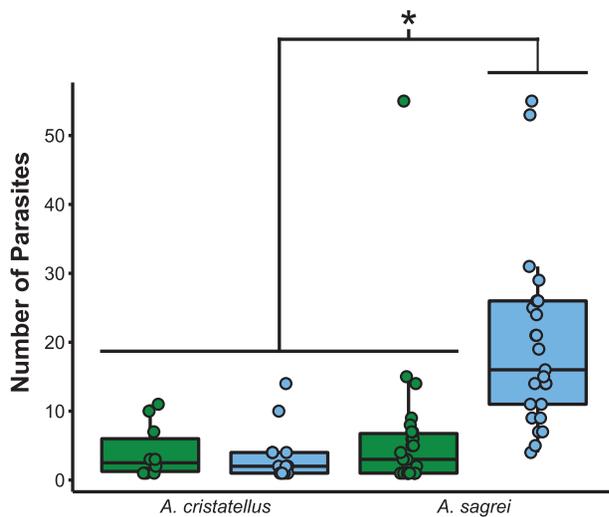

Figure 4: Crested anoles from both urban (blue) and natural (green) habitats have similar levels of infection intensity (number of parasites) to brown anoles in natural habitats, but brown anoles in urban habitats show significantly higher levels of infection intensity. Asterisk denotes groups significantly different in *post hoc* tests.

urbanization on parasite infection intensity, but brown anoles showing increased intensity of infection in urban habitats. For other phenotypes studied, including body condition, thermal preference and parasite prevalence, no impact of urbanization was found. This work shows that urbanization can have strong impacts on fundamental aspects of species' ecology, affecting traits including body size and parasite load. While some of these effects of urbanization may be consistent across species, other effects may vary with the specific species or population studied.

Our results showing increases in body size in urban areas in both male *A. sagrei* and *A. cristatellus* confirm those found in other studies of these species. Other researchers have found increased size in urban populations of male *A. sagrei* in other areas of Florida where this species is invasive (Chejanovski

et al. 2017) and the Bahamas where it is native (Marnocha, Pollinger, and Smith 2011). Similarly, some studies have found increased body size in male *A. cristatellus* in urban areas of their native range in Puerto Rico (Chejanovski et al. 2017) and female crested anoles in Florida, where the species is invasive, though this effect varied with season (Hall and Warner 2017). However, Winchell et al. (2016) found no differences in body size between male *A. cristatellus* from urban and natural habitats in Puerto Rico. Female anoles are often less studied than males due to being more time-consuming to capture, and our research is the first to document this pattern of increased body size in urban areas in female *A. sagrei*. Increases in body size with urbanization have been found in other ectotherms, including other lizard species (French, Fokidis, and Moore 2008) and amphibians (Iglesias-Carrasco, Martín, and Cabido 2017), but results from other taxa including endotherms are mixed (e.g. Meillère et al. 2015).

While this study shows no impact of urbanization on body condition in anoles, effects of urbanization on body condition in other anole systems have been mixed, with some studies showing positive effects in some species (Aviles-Rodriguez 2015; Chejanovski et al. 2017; Hall and Warner 2017), but others showing negative or no effects or variation with sex and season (Battles et al. 2013; Chejanovski et al. 2017; Hall and Warner 2017). Results from other lizard species are also mixed (Knapp and Perez-Heydrich 2012; Balakrishna, Batabyal, and Thaker 2016; Lazić et al. 2017) as are those from other vertebrates (Meillère et al. 2015; Iglesias-Carrasco, Martín, and Cabido 2017). Taken in context, these results suggest that impacts of urbanization on body condition in anoles are not consistently strong and likely vary with the ecological, environmental, or seasonal context.

Several potential factors may drive impacts of urbanization on morphology. For instance, food subsidies associated with urban environments may drive increased size and condition in some lizards (Jessop et al. 2012). In *A. sagrei*, higher levels of food availability may drive increases in body size of males, but not females (Bonneaud et al. 2016). However, we did not quantify food availability at sites used in this study, and it is unclear whether this factor may impact body size at our study sites. The presence of invasive predators, such as the curly tailed lizard (*Leiocephalus carinatus*), may drive changes in body size in some urban anole populations (Chejanovski et al. 2017), but this species is not present at the sites used in this study. Other work in this system has shown that growth rates of hatchling crested anoles from urban environments are higher than those from natural areas, suggesting that differences in body size may be due to heritable variation or other intrinsic factors (Hall and Warner 2017), though factors enabling higher growth are currently unknown. Given the observations of larger body size in urban anoles in multiple species and contexts, including this work, more research into the factors driving this phenotypic change is warranted.

Our measurements of mean preferred body temperatures in *A. cristatellus* concur with those from the literature for the species in both their native (Heatwole et al. 1969; Huey and Webster 1976; Hertz, Huey, and Stevenson 1993) and invasive ranges (Fitch, Henderson, and Guarisco 1989), and match body temperatures this species achieves in the field in its native and invasive ranges (Lister 1976; Huey 1983; Hertz 1992; Hertz, Huey, and Stevenson 1993; Kolbe et al. 2016). Preferred body temperatures of *A. sagrei* measured in this study match previous measurements of body temperatures in the laboratory (Corn 1971) as well as from the field in its native (Ruibal 1961; Lister 1976) and

invasive ranges (Losos, Marks, and Schoener 1993; Kolbe et al. 2016, Lister 1976). These results suggest that for both species some aspects of the thermal niche of the native range are conserved in their invasive range in south Florida. Additionally, this work demonstrates that the higher field body temperatures of *A. sagrei* compared to *A. cristatellus* are reflective of an underlying preference for these body temperatures, and shows that field body temperatures from the same system accord with preferred temperatures determined in the laboratory (Kolbe et al. 2016).

Field body temperatures of anoles in other systems are higher at urban sites, which have higher mean air temperatures than natural habitats due to lower canopy cover and higher proportions of impervious surfaces (Winchell et al. 2016). This pattern holds at urban sites used by anoles in the Miami area, which are characterized by similarly low canopy cover and high levels of impervious surfaces (Kolbe et al. 2016). While we were unable to collect thermal data from our study sites during the period when anoles were captured for this study, previous studies which include these sites have demonstrated that operative temperatures and body temperatures of anoles are higher at urban sites than natural sites in this system (Kolbe et al. 2016; Battles and Kolbe 2018). However, while we hypothesized that urban anoles would show higher preferred body temperatures as they are likely exposed to warmer temperatures at our urban study sites (Winchell et al. 2016; Battles and Kolbe 2018), we found no differences in preferred body temperature between urban and natural habitats for either species. In a similar vein, preferred temperature ranges were also not different between urban and natural habitats for either species. This result was somewhat surprising as previous studies have shown that crested anoles in urban environments in their native range have higher body temperatures, even when controlling for higher air temperatures in urban areas, suggesting that urban anoles might prefer higher body temperatures (Winchell et al. 2016).

The lack of adaptive change in thermal traits which we observed could be due to several mechanisms. The preferred body temperatures of lizards could have acclimated away from field values while kept in the laboratory. This seems unlikely as the few data that exist show that preferred body temperatures in anoles do not seem to acclimate in the laboratory (Licht 1968), though preferred temperature may acclimate to environmental conditions during development (Goodman and Walguarnery 2007). Regardless, all anoles were housed under identical thermal conditions and still maintained species-specific preferred body temperatures during the study. Alternatively, these species could lack the requisite amount of thermal plasticity to respond to elevated urban temperatures. However, other work in crested anoles has shown that at least some south Florida populations have demonstrated plasticity in their thermal tolerances (i.e. low-temperature tolerance; Kolbe et al. 2012). Similarly, brown anole populations in their invasive range across Florida show latitudinal variation in low-temperature tolerance (Kolbe et al. 2014), suggesting that both these species have some capacity to respond adaptively to novel thermal conditions present in their invasive range. However, selection on thermal tolerances is expected to be stronger than on preferred temperatures, as activity and survival can be limited by nonoptimized thermal tolerances, while the cost of nonoptimized preferred temperatures would be lower. Finally, urban lizards may experience elevated field body temperatures despite preferring lower temperatures. Lizards often show maximal performance at or near their preferred body temperatures (Huey and Kingsolver

1993), and previous researchers have suggested that urban anoles experiencing higher body temperatures might perform better at these elevated temperatures (Winchell et al. 2016). However, if lizards are forced to maintain nonpreferred, elevated body temperatures, they may experience reduced performance and lowered fitness, a potential cost of utilizing urban habitats. Given that climate-change driven increases in environmental temperature may cause widespread extinctions in lizards (Sinervo et al. 2010), continued research into how lizards exploit urban habitats despite elevated temperatures should be valuable.

In addition, we rejected our hypotheses that parasite prevalence and infection intensity would drive increases in preferred body temperature. A variety of ectothermic vertebrates undergo behavioral fever, whereby they thermoregulate at temperatures greater than their preferred body temperatures, presumably to support an enhanced immune function in response to exposure to pathogens (Rakus, Ronsmans, and Vanderplasschen 2017). While behavioral fever has been observed in many lizards, previous studies in anoles have failed to document behavioral fever in response to pyrogenic bacteria (Muchlinksi, Estany, and Don 1995), a bacterial pyrogen (Merchant et al. 2008) or parasites, including mite larvae (Conover et al. 2015) and malaria (Schall and Staats 2002). Our results add to the evidence for a lack of behavioral fever in anoles in a variety of contexts and suggest that parasites may not impose thermoregulatory costs on anoles.

We rejected our hypothesis that parasite prevalence is higher in anoles living in urban habitats. However, we partially confirmed our hypothesis that parasite infection intensity is higher in anoles in urbanized areas, finding that brown anoles in urban habitats had higher parasite loads than those in natural habitats and crested anoles in both habitat types. Within the urban matrix of Miami, *A. cristatellus* favors sites with higher canopy cover and cooler temperatures (Kolbe et al. 2016), while *A. sagrei* occupies more strongly urbanized areas, potentially exposing them to greater impacts of urbanization, including parasitism. These results show divergent responses of parasitism to urbanization in two congeners that are ecologically very similar (Kolbe et al. 2016), suggesting that the impacts of urbanization on parasitism and other aspects of an organism's life history are likely to be species and context specific. More broadly, the relationships between anthropogenic disturbance, including urbanization, and parasitism in other lizard species are not consistent (Amo, López, and Martín 2006, 2007; French, Fokidis, and Moore 2008), and mirror the diversity of responses seen across many taxa (e.g. Fokidis, Greiner, and Deviche 2008; Goulson, Whitehorn, and Fowley 2012; Volokhov et al. 2017).

Observed changes in parasitism in urban environments may depend on many factors including effects of urbanization on other organismal systems, such as the stress and immune responses (Bradley and Altizer 2007; Fokidis, Greiner, and Deviche 2008; French, Fokidis, and Moore 2008). The available research on effects of urbanization on parasitism in anoles is scant. However, research using brown anole populations across peninsular Florida shows that presence of fresh water and urbanization are associated with increased infection by malarial parasites (Perkins, Rothschild, and Waltari 2007). Considered in conjunction with our results, this work suggests that the factors mediating effects of urban habitat use on parasitism in this species may be generalized across diverse parasite taxa. Previous research into parasites of Caribbean anoles has shown that higher parasitism and parasitemia occurs in habitats or islands with more humid environmental conditions (Dobson et al. 1992; Schall 1992). Irrigation may provide water subsidies that elevate

moisture levels in urban habitats year-round (Shochat et al. 2006; Ackley et al. 2015), providing a potential mechanism for the higher rates of parasitism we observed in urban habitats. Additionally, altered prey communities in urban areas could lead to increased or decreased energy reserves or provide different host communities for parasites that infect anoles (Bradley and Altizer 2007). Changes in congeneric diversity could affect transmission dynamics of disease and parasites via inter- or intra-specific competition (Goulson, Whitehorn, and Fowley 2012), which is generally mediated by body size in anoles (Losos 2009), but more research is needed to determine which mechanisms may be driving the observed patterns.

While the effects of urbanization on parasitism in anoles are not well-known, the costs of parasitism are diverse. Parasitism can reduce body condition and signal quality (based on dewlap color) (Cook 2013). Malarial infections alter blood cell composition, reduce hemoglobin levels and may even mediate interspecific competition in some species (Schall 1992; Schall and Staats 2002). In *A. sagrei*, reproductive activity and parasitism trade off, suggesting that higher parasitism may be a cost of increased reproduction (Reedy et al. 2016). Given these potential costs, future research into the relationship between urbanization and parasitism is relevant to understanding how many species exploit urban habitats. Studies which address how stress, immune function and urbanization interact to affect parasitism would be useful as well as those considering how altered community structure, including presence and density of conspecifics, prey and vectors, in urban habitats may affect parasite dynamics.

In conclusion, urbanization has concrete impacts on anoles, including increases in body size and parasite load, although these effects can vary even between species that occupy similar niches. However, despite exposure to higher urban temperatures for at least 40 years, these anole populations do not show any elevation in preferred body temperature that might adapt them to these urban environments. Future work should examine mechanisms underlying changes in body size and parasitism as well as their fitness consequences. In anoles, larger body size is often correlated with enhanced competitive ability (Tokarz 1985) and higher reproductive output (Wright et al. 2013), both of which are linked to higher fitness. However, it is unclear how anoles achieve higher body sizes in urban areas in spite of potentially increased costs due to parasitism. More broadly, future work should consider whether phenotypic differences observed between urban and natural populations represent instances of evolutionary divergence (Donihue and Lambert 2015; Alberti, Correa, and Marzluff 2017). Plastic and evolutionary responses to urban conditions are likely to become increasingly prevalent as urbanization accelerates.

Supplementary data

Supplementary data are available at *JUECOL* online.

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