

Differences in Sex Ratio, Tail Autotomy, Body Size and Body Condition Between Suburban and Forest Populations of the Cuban Endemic Lizard *Anolis Homolechis*

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Abstract

Although growing evidence suggests that natural and sexual selection pressures may differ between natural and urban habitats, their consequences in terms of morphological differentiation, extent of sexual dimorphism and sex ratio remain poorly studied. *Anolis* lizards are an ideal model to study the phenotypic effects of urbanization, as they are well known for the existence of ecomorphs adapted to particular microhabitats. However, so far most studies of urban populations of anoles have considered invasive species and largely focused on males. Here, we compared morphological differentiation, sexual dimorphism and sex ratio between suburban and forest populations of the native *A. homolechis*, in Western Cuba, based on large sample size ($n > 800$) and a balanced nested design. Overall, both male and female individuals from suburban populations were larger and in better body condition than individuals from forest populations. In addition, evidence of caudal autotomy was more than twice more frequent in suburban populations compared to forest ones, with no sex effect. Habitat type and season of the year had additive effects on sex ratios, with a significant excess of males in suburban habitats and during the non-reproductive season. Accordingly, the extent of sexual dimorphism in size was more pronounced in suburban populations compared to forest ones. Our results suggest that the shape and direction of natural selection may differ between urban and natural populations of anoles.

Introduction

Urbanization is growing fast worldwide, with the perspective of two-thirds of the human population living in cities by 2050 (United Nations 2015). The rapid conversion of natural habitats to urban areas results in a drastic change in environmental conditions, such as the removal of primary vegetation and its replacement with artificial structures and managed vegetation (Forman 2014; McDonnell and Hahs 2015), that differ markedly from the more pristine ones to which most species have historically adapted. In addition, animal species living in the urban environment can be exposed to various threats, such as introduced generalist predators (Koenig et al. 2002), competition with invasive species (Shochat et al. 2010), warmer and drier conditions (Oke 1973; Arnfield 2003), or exposure to pollutants (Chatelain et al. 2021). All these factors contribute to the observed overall decline in biodiversity with increasing urbanization (McKinney 2002, 2008; McIntyre 2014; Newbold et al. 2015). However, some animal species are able to maintain themselves or even thrive in the cities, through exploiting remaining green patches (Alberti et al. 2017; Exantus et al. 2021), particular trophic resources (Chapa et al. 2020), or through local adaptation to the built environment (Campbell-Staton et al. 2020; Martin et al. 2021). Documenting the mechanisms by which species can persist in the urban environment is of obvious importance for conservation and land use management (McDonnell and Hahs 2015; Santini et al. 2019).

A first step in understanding the dynamics of urban colonization by wild animals is to examine potential differences in phenotypes between urban and natural populations of a species (e.g. Heppner and Ouyang 2021; Hutton and McGraw 2016; Lyons, Mastrodonato, Edwards and Schulte-Hostedde 2017; Mazza, Dammhahn, Lösche and Eccard 2020). This approach has been employed successfully to document behavioral and phenotypic shifts in response to urbanization in several lizard species (Lazić et al. 2013; French et al. 2018; Putman et al. 2019; Putman and Tippie 2020), and particularly in anoles (e.g. Winchell et al. 2016; Hall and Warner 2017; Lapiedra 2018; Prado-Irwin et al. 2019; Battles et al. 2019; Lailvaux 2020). The *Anolis* genus includes 436 species of small lizards from the Neotropical region, with a high level of endemism (Uetz et al. 2021). Such a large species diversity results from adaptive radiation and adaptation to various ecosystems and microhabitats, with noticeable morphological differentiation (Losos 2009). Overall, evidence shows that, for a subset of species, the morphology of urban anoles differs from non-urban ones, urban individuals being larger (Marnocha et al. 2011; Hall and Warner 2017; Thawley et al. 2019), having longer limbs relative to body size (Irschick et al. 2005; Marnocha et al. 2011; Winchell et al. 2016), and larger tail crests (Prado-Irwin et al. 2019).

However, most studies of anoles in the urban environment have considered invasive species, such as *Anolis carolinensis*, *A. cristatellus* or *A. sagrei*, which are expected to be more tolerant to habitat transformations than endemic ones (Francis and Chadwick 2012; Ducatez et al. 2018). Another limitation of previous studies in urban anoles is the tendency to focus on males, as a mean to reduce sampling effort and simplify data analysis (e.g. Chejanovski et al. 2017; Thawley et al. 2019; Tyler et al. 2016; Winchell et al. 2016; but see Hall and Warner 2017), taking for granted that variation in morphological traits is more important in males than in females (Losos 1990; Winchell et al. 2016). Actually, urban-rural phenotypic differences can vary between sexes, possibly because of different selective pressures (Battles et al. 2013; Hutton and McGraw 2016). The consequences of such differential selection in terms variation in sex-related survival and adult sex ratio across urban and natural environments, has

received so far little attention (but see Lailvaux 2020; Vanek and Glowacki 2019), although it may potentially affect sexual selection and, in turn, the size and morphology of individuals (Andersson 1994; Muralidhar and Johnson 2017).

In this context, we compared suburban and forest populations of the Cuban endemic *A. homolechis* in western Cuba. This little-studied "trunk-ground" anole species is typically found at the edges of forest margins but also occurs in the urban environment (Rodríguez Schettino 1999, Cádiz et al. 2013). Similar to *Anolis sagrei* (Losos 2009), a well studied suburban (Rodríguez Schettino 1999; Kanamori et al. 2021) and invasive species (Kolbe et al. 2004), *A. homolechis* shows typical "trunk-ground" anole characteristics such as stocky shape, medium size and long hind limbs (Cádiz et al. 2013). Nonetheless, to the best of our knowledge, there is no information comparing urban and forest populations of *A. homolechis*. Therefore, we assessed variation in sex ratio, body size, hindlimb length and the extent of sexual dimorphism between two suburban populations and two populations located in protected forested areas. In addition, we examined body condition and the rate of tail autotomy as they have been previously found to differ significantly between urban and non-urban populations of anoles (Tyler et al. 2016; Hall and Warner 2017; Chejanovski et al. 2017).

Methods

Study sites and sampling

Sampling in the urban environment took place along tree-lined streets in the suburban neighborhoods of Guanajay city (22.926323°N, 82.671959°W) and San José de Las Lajas city (22.957422°N, 82.126899°W). Guanajay is located about 58 km southwest of Havana (Fig. 1), and covers a total area of about 113 km², with a population of 22 930 habitants (CEPDE 2020). San José de Las Lajas is located 32 km southeast of Havana (Fig. 1), and covers a total area of about 591 km², with a population of 53 221 habitants (CEPDE 2020). Data on natural populations were collected in two protected areas. The Reserve of the Biosphere Sierra del Rosario (22.85752°N, 82.92957°W) is one of the best-conserved forest in the western Cuba, with about 250 km² of middle-sized mountains covered by evergreen tropical forest. The Natural Protected Landscape Escaleras de Jaruco (23.047286°N, 82.064062°W) covers about 25 km² of small hills of mesophilic, semi-deciduous forests. As *A. homolechis* naturally inhabits moderately shaded areas on edges of forests (Rodríguez Schettino 1999), we sampled anoles along pathways inside the forests.

We sampled all sites monthly, from February 2018 to August 2019. Lizards were captured by noosing, during sunny hours (9:00-17:00), when anoles are active and exposed. Once captured, each lizard was kept in a numbered mesh bag. Following each capture, a flag labeled with the same number than the bag was attached to the perch the lizard was standing upon, in order to allow subsequent release of the lizard at the exact same place. The same person (AV) measured each captured individual for snout-vent length (SVL) and right femur length from the groin to the knee as a proxy of hindlimb length with an electronic digital caliper (± 0.1 mm), and body mass (± 0.01 g) with a digital, high-precision Ascher balance. In addition, we registered the loss of the tail and the presence of scars of tail autotomy in regenerated tails. Tail autotomy is a self-defense mechanism developed by several groups of lizards, which consists in shedding a piece of the tail to distract a predator or a competitor or to elude its grasp (Arnold 1984; Tyler et al. 2016; Itescu et al. 2017). The breaking point is noticeable since the regenerated portion looks less colored and less flexible than the remaining portion (as the bone structure of the tail cannot be regenerated, the new tail is cartilaginous).

We sexed and aged each captured individual according to the size of their grey-white dewlap, fully developed in adult males, smaller in subadult males, and almost lacking in females (Williams and Rand 1977). Moreover, *A. homolechis* adult males are easily distinguished by the dark coloration of the body (Rodríguez Schettino 1999). Belly palpation allowed the determination of female reproductive status (gravid vs. non-gravid). We subsequently classified females as adults or immatures based on the minimal SVL we registered for a gravid female (see Results). We marked each captured individual before release with a unique combination of colored elastomer tags injected under the ventral skin of the limbs (Calsbeek and Irschick 2007), allowing identification of previously sampled individuals during capture sessions and, thus, avoiding pseudoreplication.

Statistical Analysis

Sex ratio and sexual size dimorphism

We performed a logistic regression to assess the effect of habitat type and site (nested within habitat) on the sex of captured individuals. As density varies across time in several anole species (Schoener and Schoener 1980) and therefore could affect sex

ratio (see Lailvaux 2020), season was included as a binomial variable (reproductive season vs. non-reproductive season) to take into account potential seasonal variation in sex ratio in relation to the reproductive cycle of the species. Following Rodríguez Schettino (1999), we considered that the reproductive season lasted from April to September, whereas the non-reproductive season lasted from October to March. We then tested whether the observed sex ratios (males/females) in each site, habitat and season differed from 0.5 (balanced sex ratio) using binomial tests. Differences in the degree of sexual dimorphism between habitats were tested using a Generalized Linear Model (GLM, non-parametric regression) with SVL as a function of sex, habitat, site (nested within habitat) and the interactions of sex with habitat and site.

Morphology and body condition

Because *A. homolechis*, similar to other trunk-ground anoles, shows marked sexual dimorphism in body size and growth (Rodríguez Schettino 1999; Butler et al. 2000), we analyzed body size and body condition for males and females separately. For each sex, we assessed the relationship between body size and habitat type through a GLM, with SVL as the response variable and habitat and site (nested within habitat) as predictors.

We further examined the degree of sexual dimorphism in the allometric relationship between hindlimb length and body length, using a GLM with $\log(\text{hindlimb length})$ as a function of $\log(\text{SVL})$, sex, habitat and site (nested within habitat), and all relevant double and triple interactions. The interaction of SVL with sex assessed the extent of sexual dimorphism on the allometric relationship. The triple interaction between SVL, sex and habitat measured the effect of habitat on the extent of sexual dimorphism in the hindlimb-body allometry.

We used the scaled mass index of body condition (SMI; Peig and Green 2009) as a measure of body condition. This index provides a measure of the mass of each individual scaled to a unique value of body size, as if all individuals were of the same size. It computes a scaling exponent for the allometric relationship between mass and size (slope of the linear regression of log-mass on log-size) by the standardized major axis method (SMA), which is an accurate method to adjust variables measured with different scales (Peig and Green 2009). Here, we scaled the individual's size to the mean SVL. We analyzed the effect of urbanization on body condition, through a GLM using SMI as dependent variable and habitat and site nested within habitat as factors. Since gravid females were expected to be heavier than non-gravid ones, we added the apparent reproductive status (non-gravid vs. gravid) as a factor to the model fitted for females. Females for which the reproductive status could not be determined were excluded from the analysis.

Tail autotomy

To test the influence of urbanization on the occurrence of tail autotomy, we used a logistic regression model with the presence/absence of evidence of tail breakage as response variable and habitat, site (nested within habitat), sex, and SVL as explanatory variables. SVL was included as a proxy the age of individuals, as older individuals should have experienced more predation attempts (Lovely et al. 2010; Tyler et al. 2016).

Linearity was confirmed for all models by inspecting diagnostic graphs of residuals and fitted values. All models GLM and logistic models were simplified using a backward elimination of non-significant variables and results from simplified models are presented. Confidence intervals for means was computed through bootstrapping (10 000 simulations). All analyses were conducted using the R programming language, version 4.0.0 (Team R Core 2020).

Results

Overall, we captured 811 adult lizards at the four study sites, of which 471 were males (58.08%) and 340 were females (41.92%) (Table 1). Both habitat type and season had significant and additive effects on variation in sex ratio (season: Likelihood-ratio $\chi^2_{1,808} = 13.15$, $P < 0.001$; habitat: Likelihood-ratio $\chi^2_{1,808} = 7.34$, $P = 0.007$). The sex ratio was significantly male-biased in the two suburban sites, with an overall male proportion of 64.56% (Table 1). In contrast, there was no deviation from a balanced sex ratio in the two forest sites. The overall sex ratio was balanced during the reproductive season (52.77 % of males, binomial test: $P = 0.221$), whereas it was significantly male-biased during the non-reproductive season (67.77 % of males, binomial test: $P < 0.001$).

Habitat ($F_{1,467} = 69.69$, $P < 0.001$) and site (nested within habitat: $F_{2,467} = 30.96$, $P < 0.001$) had a significant effect on SVL in males. On average, SVL in suburban males was 6.55% longer than that of forest males (Fig. 2a). A similar pattern was observed in females with a significant effect of habitat ($F_{1,336} = 40.33$, $P < 0.001$) and site (nested within habitat: $F_{2,336} = 14.38$, $P < 0.001$) on SVL. On average, body size of suburban females was 5.30% longer than that of forest ones (Fig. 2b).

Considering the extent of sexual dimorphism in body size, the additive effects of sex ($F_{1,803} = 1588.39$, $P < 0.001$), habitat ($F_{1,803} = 233.56$, $P < 0.001$), and site (nested within habitat: $F_{2,803} = 41.96$, $P < 0.001$) explained the majority of variation in SVL. However, the sex-site (nested within habitat) interaction was significant ($F_{2,803} = 6.40$, $P = 0.002$), as well as the sex-habitat interaction ($F_{1,803} = 4.60$, $P = 0.032$), the second one corresponding to a slightly more pronounced sexual dimorphism in the suburban environment.

Hindlimb length (log-transformed) was significantly influenced by SVL (log-transformed; $F_{1,806} = 5760.03$, $P < 0.001$), sex ($F_{1,806} = 338.14$, $P < 0.001$), the interaction between SVL and sex ($F_{1,806} = 12.81$, $P < 0.001$), and habitat ($F_{1,806} = 4.585$, $P = 0.033$). After correcting for SVL, overall males had longer hindlimbs than females (differences in slope estimators for size allometry = 0.158, standard error = 0.044), and suburban individuals had hindlimbs 7.84 % longer than forest ones. None of the interactions with habitat or site (nested within habitat) was significant, indicating that the extent of sexual dimorphism in the allometric relationship between hindlimb and body size did not differ between habitats or sites.

Male body condition (SMI) was significantly influenced by habitat ($F_{1,467} = 24.08$, $P < 0.001$) and site (nested within habitat: $F_{1,467} = 13.60$, $P < 0.001$). Males from the suburban habitat were on average 4.99% heavier than that of males from forest areas (Fig. 3a). Minimal observed SVL for a gravid female was 35.4 mm. Based on this, 308 females with SVL > 35.4 mm were considered as adults and included in the analysis of female body condition. Of them, 215 were gravid (69.80%) and 93 non-gravid (13.19%). On average, suburban females were 4.38% heavier than forest ones (Fig. 3b, c). Female body condition was significantly influenced by habitat ($F_{1,303} = 12.77$, $P < 0.001$), site (nested within habitat: $F_{2,303} = 18.67$, $P < 0.001$), and reproductive status ($F_{1,303} = 28.90$, $P < 0.001$).

Tail autotomy was observed in 262 lizards. There was a positive relationship between the probability of autotomy and SVL (Likelihood-ratio $\chi^2_{1,806} = 6.44$, $P = 0.011$, slope = 0.029), as well as a significant effect of habitat (Likelihood-ratio $\chi^2_{1,806} = 5.44$, $P = 0.020$) and site (nested within habitat: $\chi^2_{2,806} = 6.93$, $P = 0.031$). Indeed, 52.67% (138 of 364) of suburban individuals showed signs of tail autotomy compared to only 22.59% (124 of 447) among individuals captured in forests (Fig 5). Sex did not influence the frequency of autotomy (Likelihood-ratio $\chi^2_{1,805} = 0.975$, $P = 0.323$). There was no evidence for an influence of tail loss on body condition ($F_{1,777} = 0.60$, $P = 0.438$).

Discussion

Variation in body size and body condition

Overall, the observed mean SVL values for each sex in both suburban and forest populations of *A. homolechis* compares with what has been previously reported for this highly sexually dimorphic species (Rodríguez Schettino 1999; Butler et al. 2000). We however observed a significant habitat-related difference in SVL for both sexes, with suburban individuals being on average larger than forest ones, confirming a general trend in lizards (Putman and Tippie 2020). In the particular case of anoles, a similar pattern has been previously reported in *A. sagrei* (Marnocha et al. 2011; Lapiedra et al. 2017; Battles et al. 2018; Thawley et al. 2019). In contrast, Battles et al. (2013) found no difference between urban and rural individuals of *A. carolinensis*. On the other hand, there is only mixed evidence for an effect of urbanization on the morphology *A. cristatellus*. Some studies reported a larger size in urban individuals compared to rural ones (Hall and Warner 2017; Chejanovski et al. 2017; Thawley et al. 2019), whereas others did not detect any difference (Winchell et al. 2016, 2018a; Battles et al. 2019). However, such discrepancies might due to differences in the definition of the "urban" environment between studies (Putman and Tippie 2020). Interestingly, Putman and Tippie (2020) suggested that the observed larger size of urban anoles might be related to the invasive status of the studied populations. The present study, however, shows that the phenomenon is not limited to invasive anole species as *A. homolechis* is a native species in Cuba.

We also found some evidence for a positive effect of urbanization on the relative size of hindlimb (Putman and Tippie 2020). This character is supposed to be highly plastic in anoles, in relation to its importance in locomotion and habitat use (Losos and Sinervo 1989; Kolbe and Losos 2005; Vanhooydonck et al. 2006). Indeed, several studies found that urban individuals develop proportionally

longer limbs than conspecifics from natural populations (Irschick et al. 2005; Marnocha et al. 2011; Winchell et al. 2016), improving their locomotion on broad surfaces such as manufactured structures and garden vegetation (Kolbe et al. 2016; Winchell et al. 2018).

Body condition of both males and females was significantly higher in suburban sites than in forest ones. Body condition could then have a positive effect on the survival of suburban individuals (Lyons et al. 2017; Morrison, Davidson and Wilson 2007; Schmutz and Ely 1999; but see Cox and Calsbeek 2015), allowing them to reach a larger size than those of forest. Further evidence on the effect of urbanization on the body condition of anoles is necessary, as previous studies have been inconclusive on this point, with positive (Hall and Warner 2017), negative (Battles et al. 2013; Thawley et al. 2019) or mixed evidence (Chejanovski et al. 2017; Winchell et al. 2019). However, these studies used different methods of estimation of body condition, what can be a source of inconsistency between studies. We therefore recommend that future studies estimate body condition based on the central principle of scaling (Peig and Green 2010).

Several non-mutually exclusive causes can be responsible for the observed larger body size and higher body condition of both males and females in suburban populations (Putman and Tippie 2020). First, it might be the consequence of improved trophic conditions in the suburban environment (Balakrishna et al. 2016; Putman and Tippie 2020; but see Battles et al. 2013). For instance, the abundance of insects might be higher in the suburban environment, because of the accumulation of garbage (Gross 2015), providing a food supplement for reptiles (Iglesias et al. 2012; Putman & Tippie, 2020; but see Battles et al. 2013). In addition, ants, a favorite prey of anoles (Rodríguez-Schettino 2010; Narváez et al. 2020), might be more abundant in the urbanized environment (Uno et al. 2010), compared to natural ecosystems. In turn, improved body condition could positively influence the survival of suburban individuals (Lyons et al. 2017; Morrison et al. 2007; Schmutz and Ely 1999; but see Cox and Calsbeek 2015), allowing them to live longer and, thus, reach a larger size than forest ones. Increased body size in suburban populations could also result from interspecific interactions, including both competition and predation. Interspecific competition (Pacala and Roughgarden 1982; Leal and Losos 1998; Dufour et al. 2018; Stroud et al. 2019) and intraguild predation (Gerber and Echternacht 2000; Reedy et al. 2012; Herrmann et al. 2018) are relatively common in anoles. We indeed recorded the presence of the *A. sagrei* in both habitat types, and regularly observed antagonistic encounters with *A. homolechis* individuals of both sexes. Interestingly, previous studies have shown that individuals of suburban populations of *A. sagrei* have larger body size than conspecifics from rural sites (Marnocha et al. 2011; Chejanovski et al. 2017; Battles et al. 2018; Thawley et al. 2019), such that a larger body size may also be favored in *A. homolechis* when competing with its natural rival. The same phenomenon may result from predation pressure, if larger individuals are more likely to escape from predation attempts (Putman and Tippie 2020). Accordingly, Chejanovski and Kolbe (2019) found that the abundance of the predatory lizard *Leiocephalus carinatus* was the main predictor of *A. sagrei* body size for both males and females among urban habitats. Although, we did not quantify the abundance of predators in our study, we did notice a higher abundance of exotic predators, especially cats (see Bateman and Fleming 2011; Loyd et al. 2013) at suburban sites, as well as an important concentration of avian predators (Icteridae; see Anderson and Burgin 2008; Lopes et al. 2005; Wunderle 1981)

Tail autotomy rate

The frequency of tail autotomy was more than double in suburban sites than in forest ones (52.67% vs. 22.59%), with no difference between males and females. Other studies have also reported higher frequency of tail autotomy (Bateman and Fleming 2011; Tyler et al. 2016) or injuries (Winchell et al. 2019) in urban populations of anoles, compared to rural ones. Bateman and Fleming (2011) reported a higher frequency of tail loss in adult males *A. sagrei* compared to females and subadult males and concluded that territorial adult males were more exposed to predators. There was no such evidence in the present study, as the rate of tail loss did not differ between the two sexes, irrespective of habitat type, similarly to what was reported by (Pafilis et al. 2017) for 12 continental and island species of lacertid lizards.

The causes and consequences of higher frequency of tail loss in the suburban habitat are unclear. On the one hand, it might be the consequence of an overall higher predation pressure in the suburban environment. On the other hand, although vertebrate predator numbers tend to increase with urbanization, predation rates actually tend to decline (Fischer et al. 2012), possibly because urban vertebrate predators have an easy access to alternative food sources. The high rate of tail autotomy in urban environments may actually reflect a lower performance of urban predators such as domestic cats when attempting to prey upon anoles compared to feral cats in the rural environment (Bateman and Fleming 2011), and successful predator escape by suburban anoles. Whether tail loss and the regeneration of a new tail incur a fitness cost is not quite clear either, as we did not find any associated decrease in

body condition in either males or females, similar to what has been observed in other reptile species (Sousa et al. 2016; Balakrishna et al. 2021).

Variation in sex ratio

Sex ratios can vary extensively among species and populations of anoles (Muralidhar and Johnson 2017), from strongly female-biased (Kustra et al. 2019) to strongly male-biased (Bishop and Echternacht 2003). Here, we found evidence for additive effects of habitat type and season of the year on sex ratios, with male preponderance in the suburban habitat and during the non-reproductive season. Rodríguez Schettino (1999) reported an overall male proportion of 0.68 for more than a hundred populations of *A. homolechis* across the Cuban archipelago, but provided no detailed information on methodology, relative proportions of urban and rural populations or season of the year during which the populations were sampled.

As anoles have male heterogametic sex determination (Gamble et al. 2014), observed variation in adult sex ratio might be due to a sex bias in capture (Eaton et al. 2002), biased sex ratio at birth (Cox and Calsbeek 2010), sex-dependent mortality and/or dispersal (Muralidhar and Johnson 2017) or sex-related habitat selection (Schoener and Schoener 1980). Anoles are mostly polygynous species and, accordingly, show a marked sexual dimorphism, with males being more conspicuous than females (Losos 2009). Moreover, while males of the "trunk-ground" ecomorph tend to perch higher, females occupy lower portions of the perch and may therefore be less visible (Rodríguez Schettino 1999). One could then expect females to be more difficult to detect and capture. However, because suburban habitats were more open, there is no reason to suppose that females were harder to detect there than inside forests, where we captured as many females as males. One possibility is that parental body condition influences sex ratio at birth (Cox and Calsbeek 2010). Indeed, the existence of a mechanisms allowing the control of progeny sex ratio by females depending on male quality (Calsbeek and Bonneaud 2008; Cox and Calsbeek 2010) has been suggested in *A. sagrei*. Furthermore, Cox and Calsbeek (2010) provided evidence that increased paternal body condition resulted in male-biased progeny in the same species. Although the existence of such a mechanism in *A. homolechis* has not been confirmed, the higher body condition observed in both males and females in the suburban habitat could contribute to explain the associated male-biased sex ratio. However, additional data would be necessary to quantify sex ratio at birth and sex-related juvenile survival in suburban and forest populations of *A. homolechis* to validate this hypothesis. Alternatively, the observed male-biased sex ratio could be the consequence of habitat-related differential adult mortality between the two sexes, particularly if cost of reproduction is higher for females in the suburban habitat, such that female mortality exceeds that of males at the end of the breeding season there (Bishop and Echternacht 2003). Estimates of sex-related survival using capture-mark-recapture data would be required to test this hypothesis (e.g. Siliceo-Cantero et al 2019). Finally, variation in sex ratio may reflect different strategies of habitat selection by the two sexes. In *A. sagrei*, Schoener and Schoener (1980) observed that the sex ratio tended to be male-biased at low population density, and argued that females tend to concentrate in sites with high resource availability, where they can more easily defend small territories. Calsbeek (2009) confirmed that, although both sexes are essentially philopatric, female *A. sagrei* tend to disperse to areas of better quality and with a higher density of females. Female aggregation in sites with high perch availability may thus explain the observed deficit of females in suburban sites, as population density and perch sites were markedly lower there compared to forests, similar to what has been reported in other studies (Germaine and Wakeling 2001; McMillan and Irschick 2010).

Sexual dimorphism

We observed a significant, although slight, increase in sexual size dimorphism in suburban populations compared to forest ones. In contrast, we found no evidence for an effect of habitat type on sexual dimorphism in the allometric relationship between hindlimb length and body size. Increased sexual size dimorphism in the suburban habitat might be the consequence of more intense male-male competition resulting from the observed male-biased sex ratio (Darwin 1871; Andersson 1994). Indeed, a larger size is supposed to benefit male anoles through increased intrasexual competitive ability (Andersson 1994), accruing from increased bite force (Wittorski et al. 2016), especially among species with pronounced sexual size dimorphism such as *A. homolechis* (Lailvaux and Irschick 2007; see also Duryea, Bergeron and Ryan 2016). However, Muralidhar and Johnson (2017) found no relationship between the extent of sexual size dimorphism and sex ratio across a sample of 14 *Anolis* species in 21 localities. Alternatively, differences in sexual size dimorphism between suburban and forest populations may result from different potential for rapid growth between the two habitat types, associated with sex-specific plasticity (Cox and Calsbeek 2009). Under this scenario, male *A. homolechis* would benefit more than females from increased food availability at suburban sites, in terms of growing faster and reaching larger sizes (Bonneaud et al. 2016). It has been suggested that faster growth in male anoles could be triggered by

increased levels of circulating testosterone (Cox et al. 2009). There is, to the best of our knowledge, no available data comparing testosterone levels between urban and rural anoles. However, Amdekar et al. (2018) found that urban rock agamas, *Psammophilus dorsalis*, have actually lower testosterone levels compared to rural ones. Additional data on growth patterns and physiology of male and female *A. homolechis* in suburban and forest habitats might thus prove useful in interpreting observed patterns of habitat-related variation in sexual size dimorphism.

Conclusion

Based on relatively large sample size ($n > 800$) and a balanced nested design, the present study adds to the knowledge of the exploitation of the urbanized environment by *Anolis* lizards (French et al. 2018; Putman and Tippie 2020), particularly though considering both males and females. The observed pattern of differentiation between suburban and forest populations confirms previous findings in other species, while opening new perspectives on the influence of urbanization on population sex ratio and sexual dimorphism (Muralidhar and Johnson 2017). An important step for future research on urban anoles is to quantify differences in resource availability, resource use and foraging success by male and female anoles between urbanized and natural habitats (Battles et al. 2013; Balakrishna et al. 2016; Narváez et al. 2020), and to test for fitness consequences of habitat-related phenotypic differences using capture-mark-recapture methodology (Bock et al. 2010; Moreno-Arias and Urbina-Cardona 2013; Siliceo-Cantero et al. 2019).

Declarations

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Conflicts of interest/Competing interests

The authors declare not having any conflict of interest.

Availability of data and material

The datasets used are available from the corresponding author upon reasonable request.

Code availability

The codes generated are available from the corresponding author upon reasonable request.

Authors' contributions

Conception and design of the study: F.C, A.V., C.A.M., M.I.M.; data collection: A.V., M.I.M.; analysis and interpretation of data: A.V., F.C.; drafting the article or revising it for important intellectual content: A.V., F.C., C.A.M. All authors approved the final version of the manuscript.

Ethics approval

Access to restricted areas of Sierra del Rosario, as well as the capture and handling of animals were carried out with the agreement of the Director of the Sierra del Rosario Biosphere Reserve Fidel Hernández Figueroa and the Environmental License 2019/01 of the Oficina de Regulación y Seguridad Ambiental, Ministerio de Ciencia, Tecnología y Medio Ambiente of Cuba.

Consent to participate

Not applicable

Not applicable

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Table

Table 1. Variation in the sex ratio of *Anolis homolechis* among sampled sites.

	Reproductive season				Non-reproductive season				Total			
	Males	Females	Sex ratio	P*	Males	Females	Sex ratio	P*	Males	Females	Sex ratio	P*
<i>Suburban Sites</i>												
Guanajay	48	42	0.53	0.598	73	21	0.78	<0.001	121	63	0.66	<0.001
San José de Las Lajas	67	43	0.61	0.028	47	23	0.67	0.006	114	66	0.63	<0.001
<i>Forest Sites</i>												
Sierra del Rosario	90	92	0.49	0.941	44	28	0.61	0.076	134	120	0.53	0.415
Escaleras de Jaruco	71	70	0.50	1	31	21	0.60	0.212	102	91	0.58	0.472
*Binomial test for equal proportion of sexes												

Figures



Figure 1

Map of sampled sites for the capture of *Anolis homolechis*, with the Cuban capital Havana City as reference.

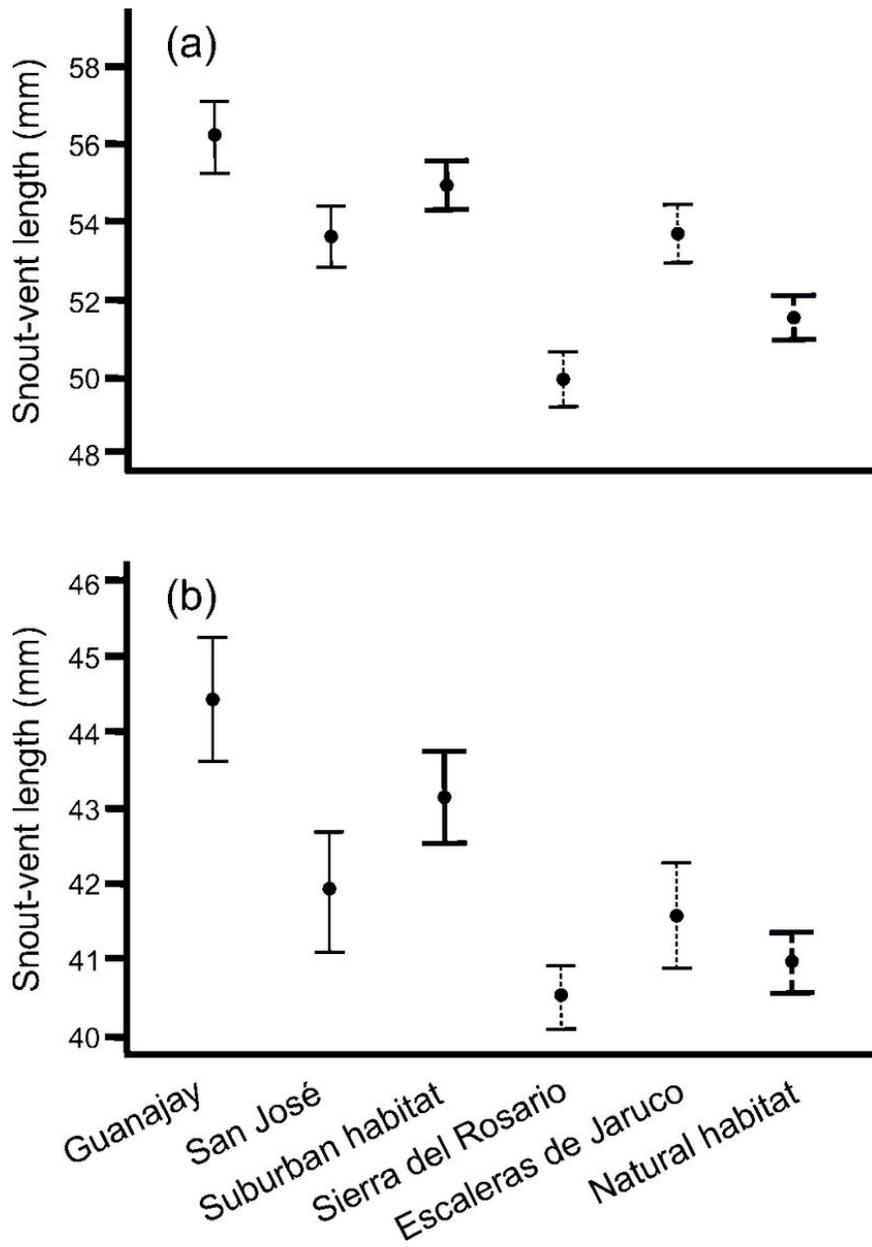


Figure 2

Snout-vent length in each sampled site and habitat by sex, in *Anolis homolechis*: a) males, b) females. Mean values are represented with points and confidence intervals (95%) with whiskers vertical bars for suburban sites (solid lines) and forest sites (dashed lines). Pooled values for each habitat type are in bold.

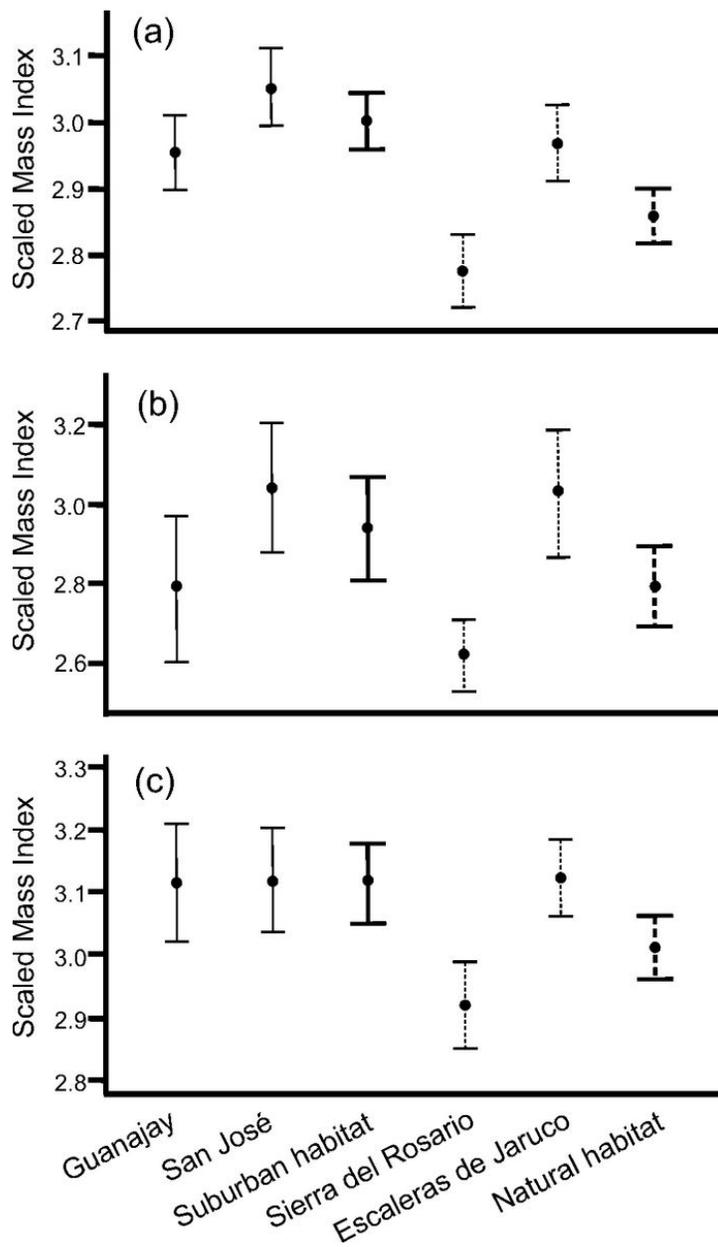


Figure 3

Scaled mass index in each sampled site and habitat by sex and female reproductive state, in *Anolis homolechis*: a) males, b) females, c) gravid females. Mean values are represented with points and confidence intervals (95%) with whiskers vertical bars for suburban sites (solid lines) and forest sites (dashed lines). Pooled values for each habitat type are in bold.

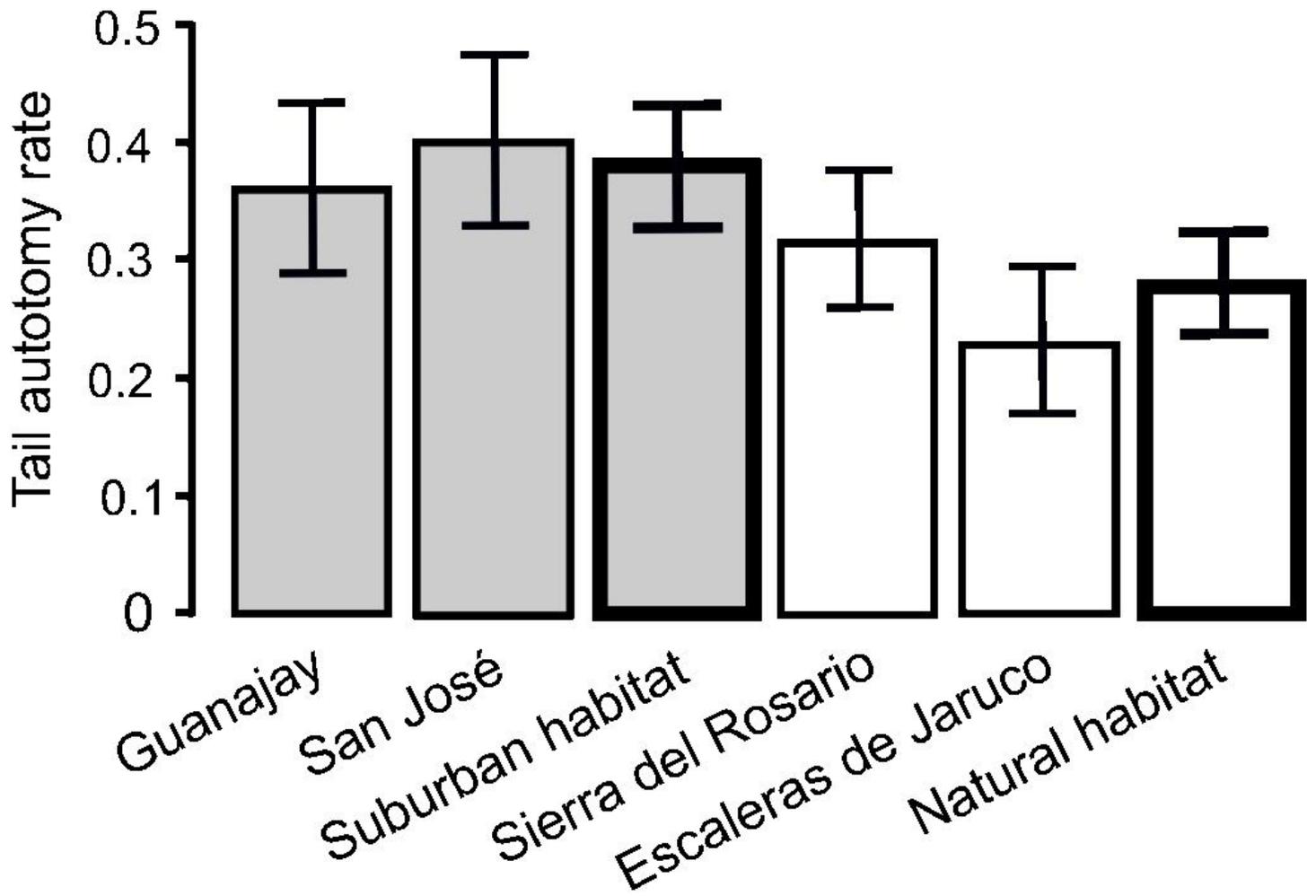


Figure 4

Proportion of individuals with evidences of tail autotomy (tail lost or regenerated) in each sampled site and habitat type (suburban in gray and forest in white), in *Anolis homolechis*. Whiskers show confidence intervals (95%) for each proportion. Pooled values for each habitat type are in bold.