

Article

What Causes Differences in the Age-Class Structure between Suburban and Forest Populations of *Anolis homolechis*?

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Abstract: Although growing urbanization has direct negative consequences for local biodiversity, several native species have been observed maintaining populations in urban environments. Understanding which factors influence the ability of native species to persist in urban environments is crucial, both for the study of biological adaptation and of urban planning. The quantification of the proportion of juvenile individuals can be a good proxy for assessing the long-term persistence of urban populations. We present comparative data about spatial and temporal variations in the age-class structure in two suburban and two forest populations of the Cuban endemic lizard *Anolis homolechis*, obtained during a 20-month survey. We found a four-fold lower proportion of juveniles in the suburban habitat compared to the forest one. There was, however, no evidence for differential female fecundity between the two habitats, as assessed by the proportion of gravid females. Conversely, the rate of tail autotomy (an antipredator behavior) was significantly higher in the suburban juveniles compared to the forest ones, possibly reflecting a higher exposure to predators and, particularly, inter- and intraspecific cannibalism. However, tail loss at initial capture or habitat type had no effect on the probability of recapture of juveniles. We discuss the potential causes and consequences of a modified age-class structure in urbanized environments.



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1. Introduction

Growing urbanization is a worldwide phenomenon [1] that has direct negative consequences for local biodiversity [2,3]. Urbanization most often leads to the replacement of specialist species with generalist ones, resulting in biotic homogenization [4–9]. In addition, urbanization globally favors alien invasive species to the detriment of native ones [10–13]. However, several native species have been found to be able to maintain populations, or even flourish, in urban environments [14–18], including some of interest to conservation [19–21]. Understanding which factors favor or limit the ability of native species to persist in urban environments is of high importance, both for the study of biological adaptation and urban planning.

So far, research has largely focused on phenotypic differences between urban and rural populations or on phenotypic variation along a gradient of urbanization. A large number of studies, addressing various taxonomic groups, have shown that individuals from urban populations often differ markedly in terms of behavior, physiology, and morphology from their rural counterparts [22–26]. In addition, some studies have provided evidence that species cope with urbanization through behavioral adjustments [27,28] or thanks to preadapted inherent traits [29,30].

Less is known, in contrast, of the variation in demographic success and population dynamics among urban and non-urban populations of native species (see [31–33]). Although a precise quantification of demographic parameters in different populations may require an important research effort, the estimation of the age-class distribution, such as the proportion of juvenile individuals, provides a suitable and frequently used proxy, integrating reproduction and early juvenile survival in the population [34–36]. Such a parameter is of high importance in demographic and population viability studies [37,38], as well as for species conservation and management [39–41]. In particular, differences in age-class structure between populations can be indicative of differences in habitat quality [42] and population trends [43]. Urban and non-urban environments may differ in several dimensions, such as resource availability [44,45], predation risk [46,47], or ambient temperature [48,49], with potential effects on individual growth, age-specific rates of mortality, and fecundity, ultimately affecting age-class structure. Surprisingly, so far, variation in the age-class structure between urban and non-urban populations has received little attention [50,51].

Species of the genus *Anolis* provide a good biological model to investigate to what extent the age-class structure differs between urban and non-urban populations. This group has been extensively studied, particularly in the insular Caribbean, where species diversity was shown to result from adaptive radiation and adaptation to various ecosystems and microhabitats through morphological and behavioral differentiation [52]. In addition, several *Anolis* species have successfully adapted to urban and suburban areas [22,53]. Studies of urban anoles have addressed a wide range of topics, such as morphological differentiation [54,55], physiology [56,57], parasite load [58], habitat use [59,60], and behavior [61,62].

Here, we present new and original data about the spatial and temporal variation in the age-class structure among populations of the Cuban endemic *A. homolechis*. This medium-sized trunk anole is common and widespread in Cuba and can be found in natural habitats as well as anthropized ones [63]. Recently, Vidal et al. (2022), using a nested design, provided evidence for morphological differences between suburban and forest populations of *A. homolechis* [64]. In addition, the same study reported a significantly male-biased adult sex ratio in suburban populations, whereas the sex ratio was balanced in forest populations. We provide additional analyses on the variation in the proportion of juveniles among individuals captured at the same two suburban and same two forest sites. To document potential sources of variation in the age-class structure between suburban and forest sites, we also examined the variation in the proportion of gravid females and in the rate of tail autotomy in juveniles (as a proxy for predation risk in lizards [65–68]). As *A. homolechis* is a seasonal breeder [63], we expected both the proportion of juveniles and that of gravid females to vary between the dry (November–April) and the wet (May–October) season [69,70].

2. Materials and Methods

2.1. Study Sites and Data Collection

Monthly sampling took place at two suburban sites and two forest sites over a 20-month period, from January 2018 to August 2019. The suburban sites were at the limit of Guanajay City and San José de Las Lajas City, both with similar urban development. The natural sites were located in relatively well-preserved forests of the Reserve of the Biosphere Sierra del Rosario and the Natural Protected Landscape Escaleras de Jaruco (see [64,71] for details). The main potential predators of *A. homolechis* observed in the suburban sites were cats, dogs, domestic chickens, wild birds, and reptiles (including other *Anolis* species), whereas in the forest sites, they mainly corresponded to birds, reptiles (including other *Anolis* species), and large arthropods.

During each sampling session, we captured individuals following an established path of about 500 m along tree-lined streets and forest pathways. Captured individuals were sexed, aged, measured for body size (snout-vent length, SVL), and the incidence of tail autotomy was registered as described in [64]. As female *A. homolechis* typically lay a single-egg clutch [72], we considered the proportion of gravid females in each population

as a measure of mean female fecundity. We determined female reproductive status (gravid vs. non-gravid) in the field through belly palpation. We subsequently classified females as adults or juveniles based on the minimal SVL we recorded for a gravid female. Juveniles were recognized by the presence of postanal scales [73] when visible and distinguished from adult and subadult males by the lack of a development of the dewlap [74]. Following Calsbeek and Irschick (2007), we injected elastomeric implants (Visible Implant Elastomers, Northwest Marine Technology, Inc., Anacortes, WA, USA) under the ventral skin of the limbs of captured individuals [75], combining various colors with the four limbs, to allow for subsequent individual recognition on recapture [52]. Colored marks were not conspicuous, thus minimizing the risk of increased predation or interference with normal behavior during interspecific interactions. After capture and processing, we released the lizards at the exact location where they had been captured.

2.2. Statistical Analysis

As we could not mark some juveniles because of their very small size, we used data on the age-class of individuals at the time of first capture to assess the variation in the proportion of juveniles. To that end, we performed a logistic regression with age-class (juveniles/adult; subadult males were classed as adults) as the response variable and habitat (suburban/forest), site (nested within habitat), season (wet/dry), the interactions between season and habitat, and the interactions between season and site (nested within habitat) as factors.

In order to assess factors affecting the probability of females being gravid or not, we build a general linear mixed model (GLMM) for binomial data, with females' identity as a random factor (as some females were recaptured more than once) and habitat, site (nested within habitat), and season as explanatory variables. Because body size may influence the percentage of gravid females in lizard populations [76,77], we added the covariable SVL to the model. Second- and third-order interactions were also included in the model.

We tested the effect of habitat, site (nested within habitat), and season on juveniles' tail autotomy rate (presence/absence of evidence of tail breakage at the first capture) using a logistic regression model. SVL was included in the model as a proxy for the age of individuals, as older individuals should have experienced more predation attempts [78,79].

Finally, to assess the effect of urbanization on juvenile apparent survival, we used a logistic regression with the probability of whether or not a juvenile was recaptured as a response variable and habitat and site (nested within habitat) as explanatory variables. We excluded juveniles that were too small to be marked and those captured for the first time during the last sampling session from the analysis. We added tail autotomy rate and SVL to the model as explanatory variables, both at the first capture, as tail autotomy is supposed to affect survival [80] and SVL has a positive effect on recapture probability [81]. Second- and third-order interactions were also included in the model.

Linearity was confirmed for all models by inspecting diagnostic graphs of residuals and fitted values. All models were simplified using a backward elimination of non-significant variables, and the results from the simplified models are presented. When the simplest model was the null one, the values for all tested explanatory variables in the additive model are provided. Confidence intervals for means were computed through bootstrapping (10,000 simulations). All analyses were conducted using the R programming language, version 4.0. [82]. The results of the tests were considered significant at the 0.05 level.

3. Results

We captured 168 juveniles and 1048 adults (16.03% of juveniles), distributed between suburban (22 juveniles and 449 adults) and forest habitats (146 juveniles and 599 adults), and wet (86 juveniles and 586 adults) and dry seasons (82 juveniles and 462 adults) (see Appendix A for sample size per site). Habitat (likelihood ratio $\chi^2_{1,1214} = 68.39$, $p < 0.001$) and season ($\chi^2_{1,1214} = 7.96$, $p = 0.005$) were retained in the simplest model as significant

effects on the proportion of juveniles captured, but not site (nested within habitat). The differences corresponded to a four-fold decrease in the proportion of juveniles in suburban habitats (4.67%) compared to forest habitats (19.59%) and about a 18% increase in the dry season (15.07%) compared to the wet season (12.79%; Figure 1). Removing the 11 smallest and unmarked juveniles from the data set did not affect the model selection and results.

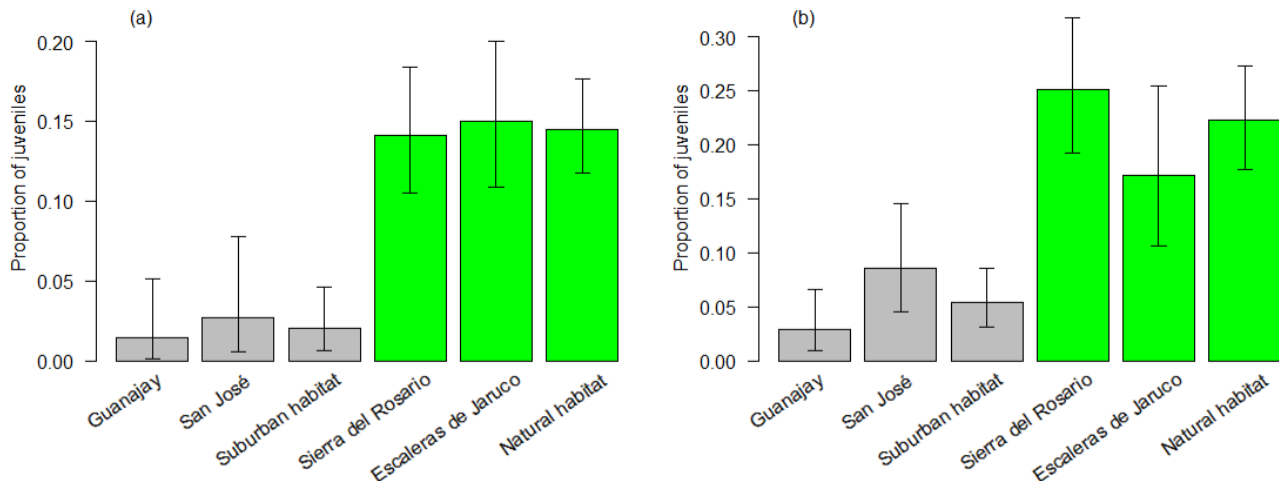


Figure 1. Proportions of juvenile *Anolis homolechis* captured in each sampled site and habitat type (gray: suburban habitat, green: forest habitat) during (a) the wet season (May–October) and (b) the dry season (November–April), from January 2018 to August 2019. Whiskers show confidence intervals (95%) for each proportion.

Table 1 shows the reproductive status of 307 different females, of which 50 individuals were captured on more than one occasion (2–5 recaptures). The simplest model retained season (GLMM: likelihood ratio $\chi^2_{1,363} = 42.12$, $p < 0.001$) and SVL ($\chi^2_{1,363} = 26.02$, $p < 0.001$) as significant effects, but not habitat and site (nested within habitat), thus indicating that urbanization and site characteristics did not affect females' gravidity. The probability of females being gravid increased during the wet season (wet vs. dry season: slope = 1.84, confidence interval, CI_{slope} 0.91 to 2.77) and with female body size (SVL: slope = 0.24, CI_{slope} 0.08 to 0.40).

Table 1. Variation in the percentage of gravid individuals (%G) among female *Anolis homolechis* captured in suburban and forest sites during the wet (May–October) and dry (November–April) seasons from January 2018 to August 2019 (N = sample size; n = number of different individuals).

	Wet Season			Dry Season			Total		
	N	n	%G	N	n	%G	N	n	%G
<i>Suburban sites</i>									
Guanajay	50	42	90.0	23	19	52.2	73	61	78.1
San José de las Lajas	37	34	91.9	27	25	44.4	64	59	71.9
Total	87	76	90.8	50	44	48.0	137	120	75.2
<i>Forest sites</i>									
Sierra del Rosario	90	73	77.8	36	31	38.9	126	104	66.7
Escaleras de Jaruco	82	82	86.6	20	18	10.0	102	83	71.6
Total	172	155	82.0	56	49	28.6	228	187	68.9

We observed tail autotomy in 31 juveniles. The probability of tail loss was significantly affected by habitat (likelihood ratio $\chi^2_{1,166} = 8.69$, $p = 0.003$) and SVL ($\chi^2_{1,166} = 4.67$, $p = 0.03$), whereas site (nested within habitat) and season were not retained in the simplest model. Overall, 36.36% (8 of 22) of the suburban juveniles experienced tail autotomy compared

to 15.75% (23 of 146) in the forest juveniles (Figure 2). Contrary to our expectation, tail autotomy decreased with increasing size in juveniles (SVL: slope = -0.10 , CI_{slope} -0.20 to -0.01).

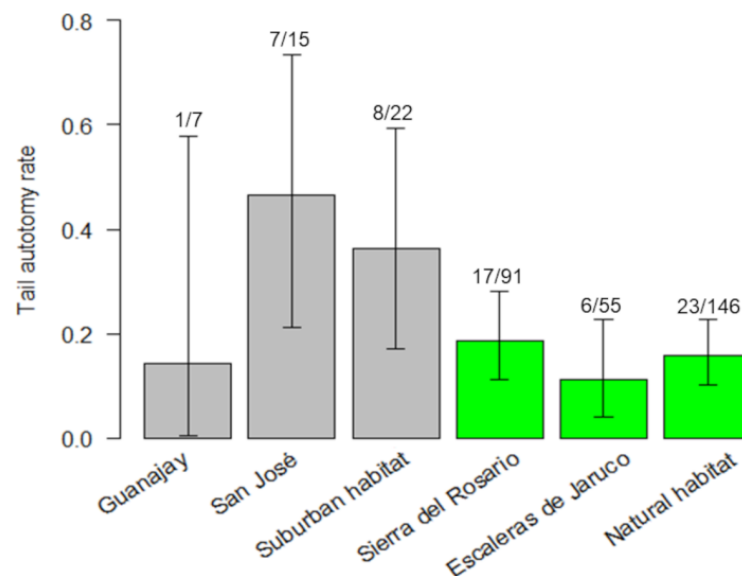


Figure 2. Proportions of juvenile *Anolis homolechis* with evidence of tail autotomy for each sampled site and habitat type (gray: suburban habitat, green: forest habitat). Whiskers show confidence intervals (95%) for each proportion. Values above bars show the number of individuals with autotomized tails over the total number of juveniles.

We recaptured 24 juveniles out of 142 marked before the last sampling session. None of the tested explanatory variables had an effect on the probability of recapture (likelihood ratio test, habitat: $\chi^2_{1,140} = 0.01$, $p = 0.90$; site (nested within habitat): $\chi^2_{2,140} = 0.56$, $p = 0.75$; tail autotomy: $\chi^2_{1,140} = 0.21$, $p = 0.65$; SVL: $\chi^2_{1,140} = 0.11$, $p = 0.74$).

4. Discussion

This is, to the best of our knowledge, the first study to document the variation in the proportion of juveniles between urbanized and natural populations of anoles. We observed a significantly and consistent lower proportion of juveniles in the suburban populations of *A. homolechis* compared to the forest ones. Using a nested design allowed us to quantitatively assess the effect of urbanization, independently of chance events or differences that may exist between sites, with no relation to their degree of urbanization [83]. We are therefore confident that the marked difference between the two habitats is ecologically meaningful.

We observed only a slight, albeit significant, seasonal variation in the proportion of juveniles, with, surprisingly, higher values in the dry season compared to the wet season. Unfortunately, little information is available on the temporal variation in the proportion of juveniles in other *Anolis* species, such that comparisons with previous studies are very limited. Opposite to our results, Andrews and Wright (1994) reported a higher abundance of juveniles during the wet season than during the dry season in the neotropical and relatively short-lived *A. limifrons* [84]. However, patterns of rainfall in our study area (northwestern Cuba) are characterized by heavier rainfall during the dry season over the last 40 years compared to other parts of the country [85], such that the contrast between the dry and wet season might be less pronounced there. Future studies are, however, necessary to better document the seasonal variation in age-class structure among populations of *Anolis* species, particularly in relation with climate change.

The observed difference in age-class structure between the suburban and forest populations is open to alternative explanations. On the one hand, it may result from a reduced adult survivorship in forest populations compared to suburban ones. However, the results

from a capture–mark–recapture study conducted at the same sites failed to show any significant effect of habitat on adult survival rate [81]. On the other hand, the differences in age-class structure may reflect habitat-related differences in female fecundity and/or in juvenile mortality. Whereas we did not detect any significant effect of habitat type on the proportion of gravid females, there was a marked seasonal effect on female fecundity, with a much higher proportion of gravid females during the wet season compared to the dry season, as observed in other anoles species [86–88]. Nevertheless, this did not translate into a higher proportion of juveniles during the wet season. This may be due to the longer incubation time with relatively cooler temperatures during the wet season or to the fact that newly hatched juveniles are more difficult to detect in the field. In addition, juvenile quality, and hence survival, improves late in the wet season (see [89]), possibly contributing to the higher proportion of juveniles in the following months corresponding to the dry season.

The difference in age-class structure between the two habitats might then be caused by higher predation risk in the suburban sites. Suburban habitats, with reduced vegetation cover and more impervious surfaces than natural areas [90–92], are less complex than natural habitats and may therefore offer fewer refuges for prey, making juveniles particularly exposed to predation risk. Accordingly, the proportion of juvenile *A. homolechis* showing tail autotomy in the suburban habitat was more than twice that in the forest habitat. However, interpreting the significance of tail loss in relation to predation pressure and survival is not straightforward. Balakrishna et al. (2021) observed that although urban males of the tropical lizard *Psammophilus dorsalis* had greater tail loss than rural males, predation risk (assessed from incidences of attacks on artificial models of lizards) did not differ between the two habitats [68]. On the other hand, Koenig et al. (2002) found that domestic cats killed mainly juvenile lizards, especially following parturition, in suburban populations of bluetongue lizards, *Tiliqua scincoides* [93]. Bateman and Fleming (2011) argued, however, that tail autotomy in the brown anole *A. sagrei* would not necessarily reflect predation rate but rather the ability of individuals to escape predation attempts by more or less efficient predators [94]. The study was based on observations of the rate of tail loss between sites with pet cats (fed by pet owners and supposedly less efficient), sites with feral cats (supposedly more efficient), and sites with no cats. Accordingly, we did not record the presence of feral or domestic cats at our forest study sites, whereas they were relatively abundant at the two suburban sites. However, unlike central Florida where the study by Bateman and Fleming (2011) took place [94], domestic cats in Cuba are rarely fed by pet owners and do actively hunt for prey. Moreover, the rates of tail autotomy in the juvenile *A. homolechis* observed in the present study were well above that reported by Bateman and Fleming (2011) for *A. sagrei*, in which tail loss was observed in only 1% of juveniles [94]. In addition, contrary to our expectations, the rate of tail loss was negatively related to the body size of juveniles, possibly indicative of attacks by predators of a much smaller size than cats, such as large arthropods [95–97], snakes, or other lizard species [98]. Capizzi et al. (2008) observed an increasing proportion of lizards in the diet of two Mediterranean snakes along a gradient of habitat alteration [99], and, recently, Rodríguez-Cabrera and Hernández Gómez (2021) provided evidence for predation by urban snakes upon anoles in Cuba [100]. However, the frequency of encounters with snakes and large arthropods during our field study was higher in the forest habitat than in the suburban one.

The lower proportion of juveniles in the suburban environment could actually be related to more intense cannibalism in the suburban environment. Both inter- and intraspecific cannibalism on juveniles have been evidenced in several anole species [101–103], including *A. homolechis* (A. Vidal, personal observation). For instance, juveniles of native anole species tend to be disproportionately rare in areas where the invasive *A. sagrei* is abundant [101]. Interestingly, we noted a higher abundance of *A. sagrei* in the suburban sites compared with the forest ones during our study. As prey diversity might be lower for reptiles in urbanized environments [104], cannibalism may constitute an alternative foraging strategy for adult anoles at our suburban study sites. Indeed, resource availability

often determines the intensity of cannibalism, with potential consequences on the age-class structure, particularly in the case of size-dependent cannibalism [105]. In addition, cannibalism might be an adaptive strategy in populations invading new environments [106] (see also [107]). Further investigations into the variation in levels of inter- and intraspecific cannibalism between urban and non-urban populations of *Anolis* species are needed to test this hypothesis.

More to the point, irrespective of its origin, tail autotomy can incur fitness costs to lizards, such as increased vulnerability to predators, possibly due to reduced locomotor performance [108,109]. This was not directly confirmed in the present study, as we failed to find any influence of tail loss or habitat on the probability of recapturing marked juveniles. This negative result should, however, be taken with caution, as we were unable to mark the smallest juveniles (which could be more vulnerable to predation attempts, as suggested by the negative relationship between tail loss and body size of juveniles) and because the probability of recapture is affected by both survival and permanent emigration outside of the study area. Juveniles with autotomized tails may thus have a lower probability of survival such that juveniles with intact tails (because they have fled from predators or because they have not encountered predators) have a higher survival probability and, thus, and can grow to larger sizes. A more detailed study of juvenile survival in *A. homolechis* relying on capture–mark–recapture analysis with weekly or shorter intervals between capture sessions would be more appropriate to test for the effect of tail loss and habitat on juvenile survival.

Independently of predation, other factors may contribute to explaining the lower proportion of juveniles in the suburban environment. For instance, urbanized environments often have reduced canopy cover and more heat-absorbing surfaces, resulting in higher mean ambient and ground temperatures and higher maximum temperatures in urban areas compared to natural ones, including tropical areas [110], with potential effects on reproductive success. Indeed, Tiatragul et al. (2019) showed that suburban nest sites of anoles were warmer and drier with greater thermal variance than forest ones [111]. Recent evidence in *A. sagrei* [112] suggests that the so-called “urban heat island effect” [48] may increase egg mortality and alter embryonic development in urban anoles, although its ultimate effect on the age-class structure has not been addressed yet. Similarly, pathogen transmission among reptiles previously occupying natural habitats could be enhanced by urbanization [22,113]. For instance, wall lizards, *Podarcis muralis*, show higher parasite loads in urban areas compared to in rural areas [114]. Although evidence from a wide range of host taxa suggests that juveniles are almost always more susceptible to pathogens than adults [115], the consequences of pathogen transmission on the age-structure of urban populations of vertebrates has received little attention.

The generality of the contrasted age-class structure between urban and non-urban populations of anoles, as well as its causes and consequences, deserves further consideration. Differences in age-class structure may have numerous implications, particularly in terms of population dynamics and stability [38]. In that respect, comparing the proportion of juveniles between urban and non-urban populations of *Anolis* species and other lizard species may contribute to a better understanding of the ability of native species to persist in urbanized areas.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Age-class and the percentage of juveniles (%J) of *Anolis homolechis* captured in suburban and forest sites during dry (November–April) and wet season (May–October) from January 2018 to August 2019.

	Wet Season			Dry Season			Total		
	Juveniles	Adults	%J	Juveniles	Adults	%J	Juveniles	Adults	%J
<i>Suburban sites</i>									
Guanajay	2	97	2.02	5	137	3.52	7	234	2.90
San José de las Lajas	3	96	3.03	12	119	9.16	15	215	6.52
<i>Forest sites</i>									
Sierra del Rosario	43	217	16.53	48	128	27.27	91	345	20.87
Escaleras de Jaruco	38	176	17.76	17	78	17.89	55	254	17.80

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