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Article

Do Suburban Populations of Lizards Behave Differently from Forest Ones? An Analysis of Perch Height, Time Budget, and Display Rate in the Cuban Endemic *Anolis homolechis*

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Abstract: Urbanization transforms natural ecosystems into novel habitats, which can result in negative consequences for biodiversity. Therefore, it is important to understand the mechanisms of maintenance of native species in urbanized environments, including behavior—which can act as a fast response to rapid environmental changes. We compared some behavioral traits between two suburban and two forest populations of *Anolis homolechis*. Direct observations of 779 individuals revealed that perch height was positively influenced by body size, but not by sex. Suburban individuals perched higher than forest ones, and even more so in the afternoon compared to the morning; a behavior that was not observed in forests populations. These differences might be due to a change from foraging activities in the morning to vigilance, display, and/or thermoregulation in the afternoon, promoted by suburban habitat conditions (e.g., higher predator abundance, open habitat structure, and urban heat). Video recordings of 81 focal individuals showed that males were more active than females (i.e., spending less time in stationary behavior and having a higher display rate), with no significant effect of habitat type. As some of our results diverge from previous studies on invasive anoles, we recommend extending comparative studies of urban and non-urban populations to other native *Anolis*.

Keywords: anoles; habitat effect; lizards; perch height; sex-habitat interaction; suburban populations; urbanization



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1. Introduction

Human population growth has resulted in the rapid expansion and development of urban areas [1–3], to the detriment of natural ones [4]. Urbanization transforms natural ecosystems into novel habitats whose main characteristics are fragmented and/or concentrated distribution of resources (e.g., food, shelter, and vegetation), abundance of humans and exotic species, concentration of pollutants, and a dryer and warmer climate [5–7]. This most often results in a significant decrease in biodiversity, with simplified assemblages of plant and animal species, and a dominance of generalist and/or invasive species over specialist and/or native ones [3,8–11]. In this context, understanding the mechanisms by which native species can maintain themselves in urbanized environments [12–14] is of particular relevance to conservation actions and urban planning, as well as the study of biological adaptation [15–18].

There is now ample evidence that behavioral traits play a major role in the successful adaptation of various animal species to urban conditions [19–21]. Behavioral alterations may allow a fast response to rapid environmental changes, such as urbanization [22,23],

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and various behavioral differences have been seen between urban and non-urban populations of different species [24]. For instance, shorter flight-initiation distances in reaction to approaching humans have been observed in urban populations of birds [25,26], mammals [27], and reptiles [28–31]. In addition, several experiments using a common garden design have revealed rapid evolution of personality traits, such as boldness, exploration, or neophobia in urban populations of reptiles [32] and birds [33,34]. Urban populations may also differ from non-urban ones in terms of sexual behavior [35] as characteristics of urban habitats, such as noise pollution in birds [36], open spaces in lizards [31,37], or reduced risk of predation in frogs [38], can affect the expression of sexual display. Most studies examining behavioral adaptability to the urban environment have been conducted at the species level, without consideration for potential sex-related differences (but see [39]). Another limitation is that most studies in urban ecology have been carried out in the United States, Europe, and Australia [40]. In comparison, little is known about the influence of urbanization on animal behavior in tropical regions, especially in hotspots of biodiversity, such as the Insular Caribbean, a region composed of small territories with growing urban populations [41].

Anolis lizards are excellent biological models to test predictions about behavioral adaptation to the urban environment. Anolis is a genus of small lizards from the neotropical region with more than 400 species and a high endemism in the Insular Caribbean [42]. Anoles constitute a favorite model in functional, evolutionary, and behavioral ecology [43–45]. Most Anolis species are diurnal ambush predators, hunting visually from perches, that mainly feed on invertebrates [46]. They can use various substrates for perching, such as tree trunks, branches, twigs, leaves, rocks, walls, or artificial supports [47–49]. Some studies have reported that anole males perch higher than females [48,50–52], whereas others failed to find any difference in perch height between sexes [53,54]. However, most studies on perch height did not include body size as a covariate and, since males are larger than females in many anole species, results regarding sex effect on perch height might be confounded by body size. Perch height in anoles can also be influenced by other factors, such as nutritional state, food availability, predation risk [53,55], molting status [54], or individual color pattern [56].

Comparisons between urban and non-urban populations of anole species have provided evidence for differences in morphology [57–61], reproductive traits [57], and population structure [60,62]. Differences between urban and non-urban populations of anoles have also been reported for territorial and sexual behavior [31,37,63,64], locomotor performance [37,65], foraging behavior [66], and substrate choice [67,68]. Overall, individuals in urbanized areas appear to be more active, more tolerant to humans, and able to take advantage of the wider variety of perches available in urban habitats (but see [66]). In particular, Borden et al. (2022) provided evidence that urbanization drives an increase in perch height in *A. carolinensis* [69]. Most studies of the effect of urbanization on anoles have compared a single urban site and a single non-urban site at a time, or were based on relatively low sample sizes. Furthermore, most behavioral studies on urban anoles focused on populations of three species known to be highly invasive; *A. carolinensis*, *A. sagrei*, and *A. cristatellus*. Successful invasive species may have a higher potential for behavioral flexibility, facilitating adaptation to the urban environment. To what extent native *Anolis* species have similar abilities remains underrepresented in the literature (but see [70]).

A good model to study the effect of urbanization on the behavior of native anole species is the Cuban endemic *A. homolechis*. A previous study provided evidence for phenotypic differences between suburban and forest populations [60], with increased body size and body condition, and a higher rate of tail loss in suburban populations. Suburban populations of *A. homolechis* also showed a more pronounced sexual dimorphism in body size, possibly associated with more intense male-male competition resulting from the male-biased sex ratio observed in suburban populations [60]. Here, we tested some specific predictions about behavioral differences between suburban and forest populations of *A. homolechis*, focusing on perch height, time budget, and rate of display. Similar to other

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anoles [71], *A. homolechis* uses various displays, including "head-bobs" (up-and-down movements of the head), "push-ups" (up-and-down movements of the body and tail caused by leg flexion), and dewlap extension (pulsing of the throat fan), that can be used in a variety of contexts, such as territorial defense, mate attraction, or predator deterrence [72]. As perch height has been previously shown to increase with temperature in anoles [52] and as air temperature tends to be higher in cities than in surrounding natural areas worldwide [73], we predicted higher perch heights in suburban vs. forest populations. Based on previous evidence [31,37], we expected display behavior and intensity to differ between urban and non-urban populations of anoles.

2. Materials and Methods

2.1. Species and Study Sites

Anolis homolechis naturally inhabits forest environments, but it is also common in the suburban environment, mainly in wooded areas, such as parks, gardens, and streets decorated with trees [51]. Males are recognized by their brown to dark brown coloration and a well-developed gray-white dewlap in adults, which is smaller in subadult males. In contrast, females are smaller, have a lighter coloration, and the dewlap is almost absent [74]. Males limit access to their partners by defending their territory against other intruding males [51,75]. Mating and reproduction occurs following rainfall, from April to September [76,77]. In this study, we considered females as adults when their snout-vent length (SVL) was greater than 35.4 mm, which was the minimum recorded size for gravid females at the sampled sites [60].

Direct observations were made from January 2018 to August 2019, and video recording took place from June 2018 to August 2019. Observations were made on adult individuals from two suburban sites and two forest sites in western Cuba (Figure 1). Suburban sites were at the limit of Guanajay City (22.926323° N, 82.671959° W; datum WGS84) and San José de Las Lajas City (22.957422° N, 82.126899° W; datum WGS84), both with similar urban development. The natural sites were located in relatively well-preserved forests of the Reserve of the Biosphere Sierra del Rosario (22.85752° N, 82.92957° W; datum WGS84) and the Natural Protected Landscape Escaleras de Jaruco (23.047286° N, 82.064062° W; datum WGS84) (see [60] for site description).

2.2. Data Collection

We captured individuals of both sexes between 9:00 and 17:00, corresponding to the period of full activity of the species. On each capture, we recorded perch height and time of the day. On first capture, we marked all captured individuals with a unique combination of colored elastomers, implanted under the skin into the ventral area of the limbs [78], as part of a long-term capture-marking-recapture study [79]. We also temporarily identified 184 captured individuals (adult males and females, in equal proportions) with a numbered tag pasted with an hypoallergic substance on the dorsal posterior area [80] (Figure 2). The first mark allowed individual recognition of lizards upon physical recapture. The second mark allowed individual identification at distance (up to 4 m with binoculars) during behavioral observations. After being marked, individuals were released to the exact place where they had been captured (see [60] for details). One to two days after capture and marking, we returned to the sites to make behavioral observations on the temporarily marked individuals, from 9:30 to 17:00. Videos were made focusing on one individual at a time [81] for up to 20 min, placing the camera (Panasonic Lumix DMC-FZ300) at 2–4 m from the lizard, according to field conditions. Whenever possible, we made more than one video per individual, with an interval of at least 30 min between them. Based on the literature [71,72], we primarily considered six different behavior categories during the analysis of video recordings: stationary (surveying the immediate surroundings and/or basking without perch changing movements), foraging (pursuing and eating prey), display, movement, resting, and close interactions (any encounter with a conspecific or individual from another anole species at a distance of four times the body length of the focal individual

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or less). We recorded the percentage of time spent in each behavior category for each recording. On several occasions, individuals briefly went out of the scope of the camera because of sudden and fast movement. In such cases, we subtracted the time the lizard was out of view from the total recording time. We retained videos with a duration of at least 5 min and pooled data from videos made on a same individual. Each video recording was analyzed twice at an interval of a few days to increase reliability. All recordings and video analysis were made by the same person (AV).



Figure 1. Locations of sampled sites (yellow points) during the capture-mark-recapture study of suburban and forest populations of *Anolis homolechis* (**left**), and representative photos of the habitat at each location (**right**).

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Figure 2. Adult male *Anolis homolechis* marked with a numbered temporarily tag.

2.3. Statistical Analysis

2.3.1. Perch Height

We used data on perch height recorded on initial captures and, for a subset of individuals, on subsequent recaptures. We assessed the effect of habitat and site (nested within habitat) on perch height by using Generalized Linear Mixed Models (GLMM). We included individual identity as a random factor to correct for pseudo-replication arising from repeated measures on a same individual, and to assess individual's consistency (repeatability) in perch height. As perch height can be influenced by time of the day (AM vs. PM) and sex [45], we added them to the model as explanatory variables, as well as SVL as a measure of body size. The model was completed with the addition of second-order interactions between explanatory variables. We relied on backward elimination of non-significant variables to obtain the simplest model, which was used to present results on perch height analysis.

2.3.2. Time Budget and Display Rate

We first analyzed time budgets by calculating the percentage of time allocated to each behavior (total time the individual spent performing this behavior divided by the total observation time). As anoles spent more than 90% of their time in a single behavior (see Section 3.2. Time Budget), we finally limited our analysis to the percentage of time allocated to this unique behavioral category as an overall index of time budget. We used arcsine square root transformation of time budget to normalize the data. Then, we assessed the effect of urbanization on time budget using Generalized Linear Models (GLM, non-parametric regression), with time budget as a function of habitat type in a third-order interaction with sex and season (reproductive season vs. non-reproductive season). In order to control for the effect of sites within each habitat type, we added the factor site (nested within habitat) to the model, also in a third-order interaction with sex and season. From this complete model, we derived the set of all possible models and selected the best-fitted model on the basis of the Akaike Information Criterion corrected for small sample size (AICc). Models with a difference in the AICc score (Δ AICc) < 2 were considered informative [82].

We defined display rate as the number of times a display was initiated by an individual divided by the total time during which its activity was recorded. We normalized data on display rate using the arcsine square root transformation and followed the same analysis as used for time budget.

Model linearity was confirmed by inspecting diagnostic graphs of residuals and fitted values. Confidence intervals for means were computed through bootstrapping

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(10,000 simulations). Significance was set at a 95% confidence level. All analyses were conducted with R Statistical Software 4.2.0 [83].

3. Results

3.1. Perch Height

We recorded 974 perch heights from a total of 779 different individuals, consisting of 452 males (suburban: 230; forest: 222) and 327 females (suburban: 128; forest: 199). We observed 470 individuals (268 males and 202 females) in the morning and 309 (184 males and 125 females) in the afternoon (see Appendix A for sample size at each site). Perch height was significantly influenced by SVL (GLMM: $F_{1,779} = 62.16$, p < 0.001), habitat $(F_{1.779} = 10.94, p < 0.001)$, site (nested within habitat: $F_{2.779} = 13.27, p = 0.001)$, and the interaction of habitat with time of the day ($F_{1,779} = 4.16$, p = 0.04), but not by time of the day ($F_{1.779} = 2.79$, p = 0.09). Perch height was not repeatable at the individual level as only a low amount of variance was explained by individual identity (GLMM random factor variance: 0.019, standard deviation: 0.138). Sex was not retained in the most parsimonious model, indicating that perch height did not differ between sexes, after correcting for the effect of body size. Lizards with larger body size (SVL) perched higher than smaller ones (slope = 0.021, confidence interval, CI_{slope} 0.012 to 0.030; Figure 3). On average, suburban individuals perched at about 1 m above the ground compared to 0.8 m for forest individuals (Figure 4). Perch height increased by 20.9% from the morning to the afternoon in suburban individuals, whereas individuals from forest populations maintained a similar perch height throughout the day (Figure 5).

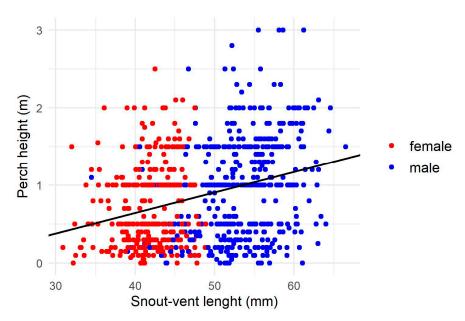


Figure 3. Relationship between snout-vent length and perch height in *Anolis homolechis*. The solid black line indicates linear regression.

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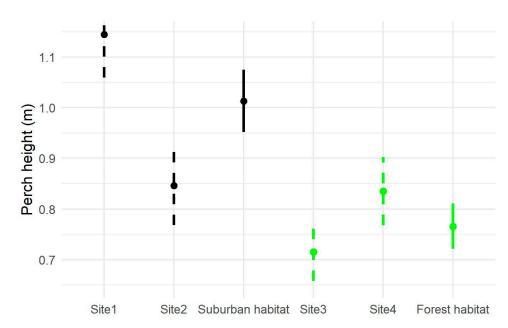


Figure 4. Perch height in suburban (black) and forest (green) populations of *Anolis homolechis*. Sampled sites are referred to as Site 1: Guanajay, Site 2: San José de Las Lajas, Site 3: Sierra del Rosario, and Site 4: Escaleras de Jaruco. Vertical bars indicate 95% confidence intervals.

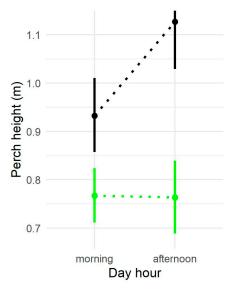


Figure 5. Relationship between perch height and time of the day (morning vs. afternoon) in suburban (black) and forest (green) populations of *Anolis homolechis*. Vertical bars indicate 95% confidence intervals.

3.2. Time Budget

We obtained two video recordings for 44 different individuals, and a single one for 37 additional ones. Recorded individuals consisted of 46 males (suburban: 20; forest: 26) and 35 females (suburban: 16; forest: 19). Fifty three videos were made during the breeding season (males: 32; females: 21) and 28 during the non-reproductive period (males: 14; females: 14) (see Appendix B for sample size in each site). All individuals were observed in stationary behavior, 76 were seen displaying, 73 were seen moving away from their perch, 12 were involved in close interactions, and 10 were seen foraging.

On average, individuals allocated 90.53% of their time budget to stationary behavior. Displays accounted for 6.15% of the total time budget. Feeding behavior and close interactions accounted for less than 0.01% of the time budget, such that we did not consider them

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in subsequent analyses. We could not quantify movements precisely because of individuals moving too often out the scope of the camera. As there were significant and negative correlation between percentage time spent in stationary behavior and percentage time spent in display (Pearson correlation coefficient, r = -0.47, df = 79, p < 0.001), we focused on stationary behavior (performed by all individuals) for subsequent analyses. The model that best suited the data based on the AICc score included a sex-season interaction effect on percent time spent in stationary behavior (normalized). During the non-reproductive season, both sexes allocated most of their time to stationary behavior (Figure 6). In contrast, during reproduction, males significantly decreased the percentage of time spent in stationary behavior (-12.36%), while no such difference was observed in females (Figure 6). No effect of habitat was retained in the best model, suggesting that time budget did not differ between suburban and forest populations.

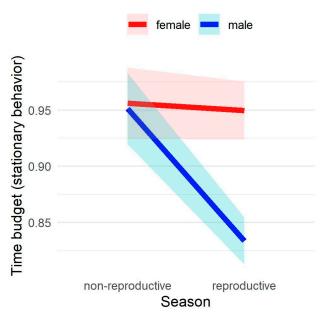


Figure 6. Relationship between season (reproductive vs. non-reproductive) and the proportion of time (time budget) spent performing stationary behavior by males and females of *Anolis homolechis*. Colored ribbons represent 95% confidence intervals.

3.3. Display Rate

The recorded individuals showed an average rate of 0.12 displays/min (i.e., 7.2 displays/hour). The best model based on the AICc score retained the interaction between sex and season, and the additive effects of habitat and site (nested within habitat) as explanatory variables. The second best model (Δ AICc < 2) included the interaction between sex and habitat. Males displayed significantly more than females, and significantly increased their display rate (+34.69%) during the reproductive season (Figure 7). Suburban males showed a slight, albeit significant, decrease in display rate compared to forest males (Figure 8a), but this difference was mainly due to a significant reduction in display rate in males from the Guanajay suburban site. Females' display rate did not differ between habitats, nor between sites (nested within habitat) (Figure 8b).

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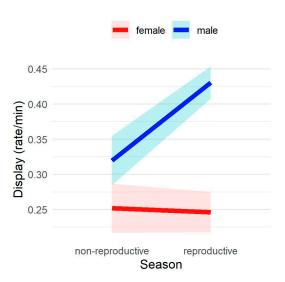


Figure 7. Relationship between display rate (arcsine square root transformed) and season (reproductive vs. non-reproductive) in males and females of *Anolis homolechis*. Colored ribbons represent 95% confidence intervals.

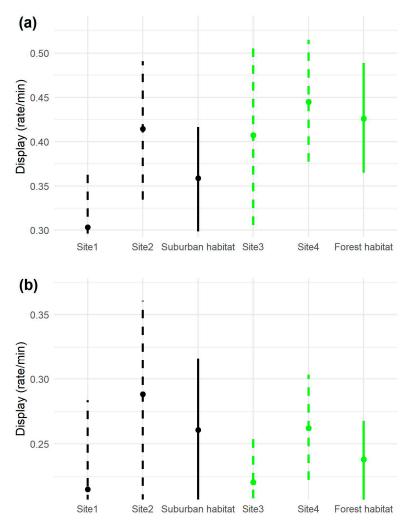


Figure 8. Display rate (arcsine square root transformed) in (a) males and (b) females of *Anolis homolechis* from suburban (black) and forest (green) population. Sampled sites are referred to as Site 1: Guanajay, Site 2: San José de Las Lajas, Site 3: Sierra del Rosario, and Site 4: Escaleras de Jaruco. Vertical bars indicate confidence intervals at 95%.

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4. Discussion

Our study addressed the behavioral variation between and among suburban and forest populations of a common, albeit understudied, Cuban anole. The use of a nested design, with two replicates per habitat type, allowed us to find evidence of significant behavioral differences between suburban and forest populations of *A. homolechis* for both perch height and display rate, but not for time budget. As predicted, anoles from suburban populations perched higher than anoles from forest ones, whereas there was only a slight difference in display rate between habitats. Contrary to some previous findings, sex had no effect on perch heigh after body size was accounted for. Variation in behavior was also explained for by several other variables, such as sex, body size, and season, alone or in interaction with habitat type.

4.1. Variation in Perch Height

The absence of difference between sexes in perch height is in apparent contrast with previous observations in *A. homolechis* [51] and some other *Anolis* species [47,84–86]. Vertical segregation between male and female anoles might be explained by various phenomena, such as reduced food competition between sexes [86–88] or males benefiting from high perch height to defend their territory from intruders and to enhance display visibility [52]. Another explanation could be that it might simply result from the confounding effect of sexual dimorphism in body size (but see [52]). Indeed, we found a significant and positive relationship between perch height and body size (SVL), independent of the sex of individuals. Body size is related to toepad width and claw size, both of which are of importance for climbing efficiency in anoles [89]. Vertical segregation by size might also be accentuated by inter-individual competition for perches, with larger individuals being dominant over smaller ones. Future studies could then investigate to what extent the magnitude of vertical segregation by sex among anole species is confounded by the importance of sexual dimorphism or actually reflect different strategies between the two sexes.

In our study, suburban individuals, which were larger than forest ones on average [60], also used higher perches, as initially predicted based on thermal differences between the two habitats. Alternatively, this result could be explained by the benefits associated with higher perches in terms of improved visibility of the surroundings in open suburban areas, compared to closed spaces, such as forests [37]. Comparing with previous studies, alteration in perch height of suburban *A. homolechis* contrasts with observations in urban populations of both *A. sagrei* and *A. cristatellus*, which did not differ from their non-urban counterparts in perch height [37,61,90], following the general pattern for lizards [91]. Further studies of differences in perch height between urban and non-urban populations should take into account a measure of habitat openness and visibility, potentially through an experimental approach.

Interestingly, suburban individuals perched higher in the afternoon compared to the morning, a behavior that was not observed in forest populations. Given that perch height is related to activity in which a lizard is engaged [47], one possibility is that individuals from urban populations engage in different activities between the morning and the afternoon. Unfortunately, the number of video recordings was too low to check for an effect of time of the day on behavior. An alternative hypothesis is that the risk of predation was greater in the afternoon than in the morning at suburban sites, such that climbing higher would actually be an anti-predatory response. For example, urban populations of A. sagrei modify their daily activity in presence of the predator Leiocephallus carinatus, whose activity is limited to midday [28], although no correlation was found between perch height in A. sagrei and the abundance of *L. carinatus* [92]. Our working hypothesis involved the typically hotter urban climate [6], a feature that may affect some anole species [93]. While in forests temperature variation between morning and afternoon remains moderate due to vegetation cover, in suburban sites the scarce vegetation on the ground, coupled with substrate that absorbs heat, could lead to extreme temperatures in the afternoon, causing anoles to climb onto elevated perches. Although results are compatible with our initial hypothesis,

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the extent to which perch height of anoles varies according to time of the day in urban environments deserves further consideration.

Our data showed that, overall, individuals were not consistent in perch height between captures. Experiments on *A. sagrei* revealed some individual consistency in ground avoidance rapidly evolving in response of predation [94]. The study also found that perch height increased in environments where predators were present in contrast with predator-free environments. We did not observe a similar pattern in suburban and forest *A. homolechis*. Given the empirical evidence for variation in individual behavioral consistency in anoles in relation to the degree of urbanization [28], future capture-recapture of anoles studies may address variation in personality between urban and non-urban populations [95], for instance, through measuring display and aggressive behavior at the time of capture.

4.2. Time Budget and Display Rate

We found no marked effect of urbanization on time budget, as suburban individuals had similar proportions of time spent stationary to forest individuals, supporting the general pattern for lizards of similar levels of activity between urban and natural habitats [91]. This agrees with what has been previously reported for other anole species, with individuals remaining stationary most of the time, basking and scanning the environment for prey, while remaining vigilant to predators, or competitors [45]. Similar to *A. homolechis*, several anole species also allocate about 90% of their time budget to this behavior, allocating little time for other activities [47,71,84]. Staying quiet most of the time might be a compensatory strategy for low input energy, compared to birds and mammals [96–98].

Another agreement with the general pattern observed in polygamous species with high sexual dimorphism is the intersexual difference in both time budget and display rate. Throughout the year, A. homolechis males displayed more frequently than females, but during the breeding season, males spent even more time displaying, whereas females showed no such trend. Increased display of males during the reproductive season is most probably the consequence of intense male-male competition for access to females. Conversely, females may remain stationary during the reproductive season for foraging benefits, in order to improve body condition and fertility [47,71,99,100]. Regarding variation between habitats, suburban males displayed at a significantly lower frequency than forest males. This result was unexpected as the increase in sexual size dimorphism observed in suburban populations of A. homolechis was suggestive of more intense male-male competition [60]. In addition, previous studies found increased display rates in urban populations of A. sagrei and A. carolinensis [31,37], possibly as an effect of increased distance between individuals in open urban areas, requiring more intense signaling to ensure efficient communication. However, the observed difference between habitat types in the present study was slight and mainly due to one suburban site (Guanajay), whereas in the other (San José de Las Lajas), the male rate was similar to that observed at the two forest sites. One possibility is that predation risk was particularly high in Guanajay as several studies have shown that lizards reduce display activity in risky environments, whereas display frequency increases in environments with a lower abundance of predators [99,101,102]. Since Vidal et al. (2022) found no difference in levels of tail loss (an index of predation pressure) between the two suburban populations [60], the latter explanation lacks support. Additional behavioral observations, coupled with experimentations, are needed to ascertain to what extent display behavior differs between suburban and forest populations of *A. homolechis*.

5. Conclusions

Our study provides new and original information on the effect of urbanization on the behavior of a native, endemic lizard, despite having some limitations associated with sample size and the typical reduced activity of anoles. We found that some aspects of the behavior of *A. homolechis* differs between suburban and forest populations. Future studies should investigate the origin of such differences. In particular, we suggest assessing behavioral plasticity vs. consistency in perch height among individuals from different

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populations along a gradient of urbanization. Such a study should be coupled with a more detailed investigation of the behavior of anoles from urban and non-urban environments, possibly using common garden experiments [32,103]. As some of our results diverge, to some extent, from previous studies conducted on invasive anole species, we recommend extending comparative studies of urban and non-urban populations to other *Anolis* species [43]. Particular attention should be given to perch height, a behavior that links together habitat structure, biological interactions, and morphological capacities, well studied in the *Anolis* group [45]. More generally, studies on native species, rather than invasive ones, might be important in improving our understanding of the ability of natural populations to face the consequences of increasing urbanization.

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Appendix A

Number of observed males and females in suburban and forest populations of *Anolis homolechis* during morning and afternoon hours from January 2018 to August 2019 for perch height.

| | | Morning | | | Afternoon | | | Total | | |
|-----------------------|-------|---------|-------|-------|-----------|-------|-------|---------|-------|--|
| | Males | Females | Total | Males | Females | Total | Males | Females | Total | |
| Suburban sites | | | | | | | | | | |
| Guanajay | 66 | 30 | 96 | 52 | 32 | 84 | 118 | 62 | 180 | |
| San José de las Lajas | 73 | 45 | 116 | 39 | 21 | 60 | 112 | 66 | 178 | |
| Forest sites | | | | | | | | | | |
| Sierra del Rosario | 72 | 72 | 144 | 53 | 42 | 95 | 125 | 114 | 239 | |
| Escaleras de Jaruco | 57 | 55 | 112 | 40 | 30 | 70 | 95 | 85 | 182 | |

Appendix B

Number of recorded males and females in suburban and forest populations of *Anolis homolechis* during reproductive and non-reproductive season from June 2018 to August 2019.

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| | Reproductive Season | | | Non-Reproductive Season | | | Total | | |
|-----------------------|---------------------|---------|-------|-------------------------|---------|-------|-------|---------|-------|
| | Males | Females | Total | Males | Females | Total | Males | Females | Total |
| Suburban sites | | | | | | | | | |
| Guanajay | 9 | 6 | 15 | 1 | 0 | 1 | 10 | 6 | 16 |
| San José de las Lajas | 6 | 5 | 11 | 4 | 5 | 9 | 10 | 10 | 20 |
| Forest sites | | | | | | | | | |
| Sierra del Rosario | 9 | 3 | 12 | 4 | 8 | 12 | 13 | 11 | 24 |
| Escaleras de Jaruco | 8 | 7 | 15 | 5 | 1 | 6 | 13 | 8 | 21 |

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