

An Experimental Analysis of Perch Diameter and Substrate Preferences of *Anolis* Lizards from Natural Forest and Urban Habitats

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ABSTRACT.—Determining whether organisms have preferences for certain aspects of the habitat is important for understanding the process of habitat selection. *Anolis* lizards (anoles) have evolved to occupy distinct parts of the arboreal environment. Depending on the population or species, anoles perch on different aspects of the structural habitat varying in diameter, height, and type of substrate. We used laboratory and mesocosm trials to assess whether 2 species of *Anolis* lizards have preferences for the diameter and type of substrate they use for perching. Results reveal *A. cristatellus* and *A. sagrei* both prefer larger diameter perches. Lizards from natural forests and urban populations showed no difference in perch-diameter preference. In contrast, *A. sagrei* from an urban site overwhelmingly preferred to perch on wood substrates over polyvinyl chloride and metal ones. The larger diameter and wood substrates preferred by anoles in our trials should confer increased locomotor performance for these species based on previous studies. Rapid environmental change caused by humans can decouple the relationship between habitat preferences and fitness, so it is essential to test for changing preferences in organisms that experience urbanization and other forms of global change.

Structural habitat is a key axis of niche differentiation in *Anolis* lizards (anoles); the diameter, height, and type of perches used by anoles varies both within and among species (Rand, 1964; reviewed in Losos, 2009). In the *Anolis* adaptive radiation, species have diversified to occupy a broad range of vegetation, varying from narrow twigs to broad trunks, and from the ground to high in the canopy (Williams, 1983; Losos et al., 2003; Losos, 2009). Moreover, the repeated, convergently evolved *Anolis* ecomorphs (or habitat specialists) on the islands of the Greater Antilles are defined in part by their structural habitat use (e.g., twig or trunk-ground ecomorphs; Williams, 1983; Losos, 1990). Many studies of *Anolis* species support population-level differences in structural habitat use associated with changes in the presence or absence of competitors and predators (e.g., Jenssen, 1973; Schoener, 1975; Schoener et al., 2002, 2017) as well as changes in the availability of dimensions of the structural habitat itself (Johnson et al., 2006). For anoles, an important consequence of the structural habitat they occupy is its effect on their locomotor performance, often used as a proxy for fitness (Arnold, 1983; Irschick and Garland, 2001). For example, *Anolis carolinensis* jumps less effectively from more compliant (flexible) perches (Gilman et al., 2012), and most anole species run faster on broader diameter substrates (Losos and Sinervo, 1989). Furthermore, in natural habitats, some anole species tend to avoid structural habitats that impair their locomotor performance (Irschick and Losos, 1999; Gilman and Irschick, 2013).

In contrast to the natural habitats in which *Anolis* species originally evolved, several anole species currently live in environments highly modified by humans, such as urban areas. In response to living in cities, anoles have altered numerous aspects of their behavior, ecology, and morphology (e.g., Chejanovski et al., 2017; Lapiedra et al., 2017; Battles and Kolbe, 2018; Avilés-Rodríguez and Kolbe, 2019; Stroud et al.,

2019). For example, *A. cristatellus* populations in Puerto Rico have adapted to urban environments by evolving longer limbs and larger toepads (Winchell et al., 2016); these traits increase locomotor performance on the smooth, vertical substrates encountered more frequently in cities (Kolbe et al., 2016a; Winchell et al., 2018). Furthermore, *A. cristatellus* and *A. sagrei* living in urban areas in Miami display expanded structural habitat use, specifically perch diameter use, compared with lizards living in natural forests (Battles et al., 2018; Avilés-Rodríguez and Kolbe, 2019). Urban anoles select the larger diameter trees, poles, and walls more readily available in urban sites because of an underlying preference for broad-diameter perches (Battles et al., 2018). In this case, evaluating habitat preference was critical for understanding the mechanistic basis of the structural habitat niche expansion in urban areas.

Many studies have quantified structural habitat use by anoles and other lizard species (e.g., Losos, 1990; Vanhooydonck and Van Damme, 1999; Goodman et al., 2008). These studies describe the actual distribution of heights, diameters, and types of vegetation that individual lizards of a population or species use for perching, among other activities. Fewer studies have combined assessment of habitat use with measures of habitat availability (but see Johnson et al., 2006; Kamath and Losos, 2017), typically by measuring habitat variables at randomly selected points at spatial and temporal scales relevant to lizards. The resulting ability to evaluate habitat selection (i.e., compare habitat use with availability) can provide a better understanding of the behavioral or environmental factors that result in differences in habitat use among sites (Jones, 2001). For example, differences in habitat use could result from either random use of available habitats that differ in their availability, or disproportionate use of certain aspects of the habitat regardless of their availability. This approach is critical for evaluating questions such as whether interactions with competitors or predators alter the habitat use of lizards, and why lizards differ in their habitat use in novel habitats. Lastly, it is often useful to assess what aspects of the habitat individuals prefer. This is typically done experimentally and free of biotic and abiotic variation unless such variation is manipulated as part of the study design. Habitat preferences are important for

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inferring the decision-making process that leads to habitat selection and interpreting potential fitness consequences of habitat selection (Jones, 2001). This is important because rapidly changing environments caused by human activities can alter the fitness consequences of evolved preferences, resulting in evolutionary traps (e.g., Robertson et al., 2013). Yet, preferences and their consistency among populations and across different types of habitats are rarely evaluated in studies of habitat use and selection. The numerous examples of rapid behavioral, ecological, and evolutionary shifts in human-modified environments (Hendry et al., 2007), including urban areas (Alberti et al., 2017), suggest we cannot assume habitat preferences are static.

In this study, we used laboratory and mesocosm experiments to evaluate the preference of *Anolis* lizards for 2 key aspects of their structural habitat niche: perch diameter and perch type. A previous study using *A. cristatellus* and *A. sagrei* from natural forest habitats in Miami found that both species preferred larger diameter perches, with *A. sagrei* appearing to have a stronger preference (Battles et al., 2018). However, we do not know whether these preferences vary among sites or are the result of living in different environments, such as natural forests versus urban areas. Here we extend previous findings by assessing preferences of lizards from both natural forest and urban sites. Additionally, anoles use artificial perches, such as poles and walls, when they are available in urban areas (Battles et al., 2018; Avilés-Rodríguez and Kolbe, 2019); these perches have important effects on locomotor performance (Kolbe et al., 2016a; Battles et al., 2019). Therefore, we wanted to know whether anoles have a preference for the type of perch they occupy. Based on previous findings (Wright, 2009; Langford et al., 2014; Battles et al., 2018), we predict that lizards from both natural forest and urban habitats will prefer the largest diameter perches. Additionally, based on their poor locomotor performance on artificial perches (Kolbe et al., 2016a; Battles et al., 2019), we predict that lizards will prefer natural wood over artificial substrates when perching. Moreover, because anoles in urban areas may have previously encountered artificial perches that are difficult for them to move on, we predict urban lizards will show a stronger preference for wood (and avoidance of artificial substrates) compared with lizards from natural forests. A similar pattern could arise if natural forest lizards, which are naïve to artificial substrates, have not evolved or learned to avoid them. Lastly, we predict anoles from urban sites will move from the initial starting point on the ground to a perch faster during perch-diameter preference trials compared with lizards from natural forests. This is because urban environments are more open than natural forests, and we predict urban anoles will seek the relative safety of perches more quickly (Lapiedra et al., 2017; Avilés-Rodríguez and Kolbe, 2019).

MATERIALS AND METHODS

Study Species.—We sampled 2 nonnative *Anolis* lizard species from South Florida for this study. *Anolis cristatellus* is native to Puerto Rico and was introduced to South Miami and Key Biscayne in the 1970s (Kolbe et al., 2007). *Anolis sagrei* populations have been present in the Miami area for ≥ 60 yr, and were introduced primarily from Cuba (Kolbe et al., 2004). Both species are trunk-ground habitat specialists, which means they are typically found on the ground or perched up to 2 m high in vegetation, ranging from narrow twigs to broad tree trunks (Losos, 2009; Battles et al., 2018). They are common in natural forest remnants and urban areas in South Florida (Kolbe et al.,

2016b). In urban areas, both species perch on natural vegetation and artificial substrates, such as poles and walls (Battles et al., 2018). The larger *A. cristatellus* (males up to 75 mm snout-vent length [SVL]) commonly perches higher than the smaller *A. sagrei* (males up to 69 mm SVL). *Anolis cristatellus* always occurs sympatrically with *A. sagrei* in urban areas in South Florida, whereas *A. sagrei* occurs in many urban areas without *A. cristatellus* because of its much wider distribution (Kolbe et al., 2016b) and greater thermal tolerance (Battles and Kolbe, 2018). Most natural forest sites either have *A. cristatellus* or *A. sagrei*, but rarely both species.

Experimental Design.—To measure perch diameter preference in the laboratory, we collected 10 adult male *A. sagrei* from each of 2 natural and 2 urban sites outside the distribution of *A. cristatellus* in Broward County for a total of 40 lizards, measured their body size (SVL) and shipped them to the University of Rhode Island (Kingston, Rhode Island) in July 2017. Lizards were housed individually in the lab prior to trials. In a single 1.8 m \times 1.8 m \times 1.8 m mesh enclosure in the lab, we presented individual lizards with a choice of 6 perches consisting of 1.6-m-tall tree trunks, positioned vertically in 3 duplicated diameters of 2, 7, and 12 cm. These sizes span the range of vegetation diameters available and used by both species in urban and natural habitats in South Florida (Battles et al., 2018; Avilés-Rodríguez and Kolbe, 2019). After a 2-min acclimation period under an opaque cover, each lizard was given 15 min to explore the perches. We recorded trials to quantify the proportion of the total time spent on each perch, excluding time spent on the ground or on the walls of the mesh enclosure. We arranged the perches in the following order in a circle (i.e., 2, 7, 12, 2, 7, 12), and before each trial we randomized the location of the first perch in the circle to eliminate any location effects. The enclosure was lit overhead with fluorescent lights approximately 3 m above the floor, no lights or heat sources for basking were provided, and the room temperature was 28°C. During the initial round of trials, 10 lizards did not use any of the perches, either staying on the ground or climbing on the walls of the mesh enclosure. These 10 lizards were given a second trial, and all but one of them selected a perch for a total sample size of 39 lizards.

To measure substrate preference, we used the same 40 adult male *A. sagrei* from the perch-diameter preference trials in the laboratory and the same experimental procedures with the following modifications. All six perches were 12 cm in diameter based on the preference for large diameters detected in a previous study (Battles et al., 2018). The 3 duplicated substrates were wood (tree trunk), metal, and polyvinyl chloride (PVC) for a total of 6 perches. During the initial round of trials, 21 lizards did not use any of the perches. A second round of trials with these same individuals resulted in 12 additional lizards selecting perches for a total sample size of 31 lizards.

We expanded our experimental assessment of perch diameter preference by conducting trials in outdoor mesocosms in January 2017. We collected 20 male *A. cristatellus* and 20 male *A. sagrei* from urban sites in South Miami where both species occur, and 20 male *A. cristatellus* and 19 male *A. sagrei* from natural forest sites (Matheson Hammock Park and A.D. Barnes Park, respectively) for a total of 79 lizards. Lizards were housed individually prior to trials. We used 4 fiberglass tanks measuring 1.8 m in diameter and 1.2 m tall as mesocosms; these tanks were housed outside under a canopy at Florida International University's Biscayne Bay Campus in North Miami, Florida. Mesocosms were shaded during trials, and daytime air temperatures were typical of winter conditions in

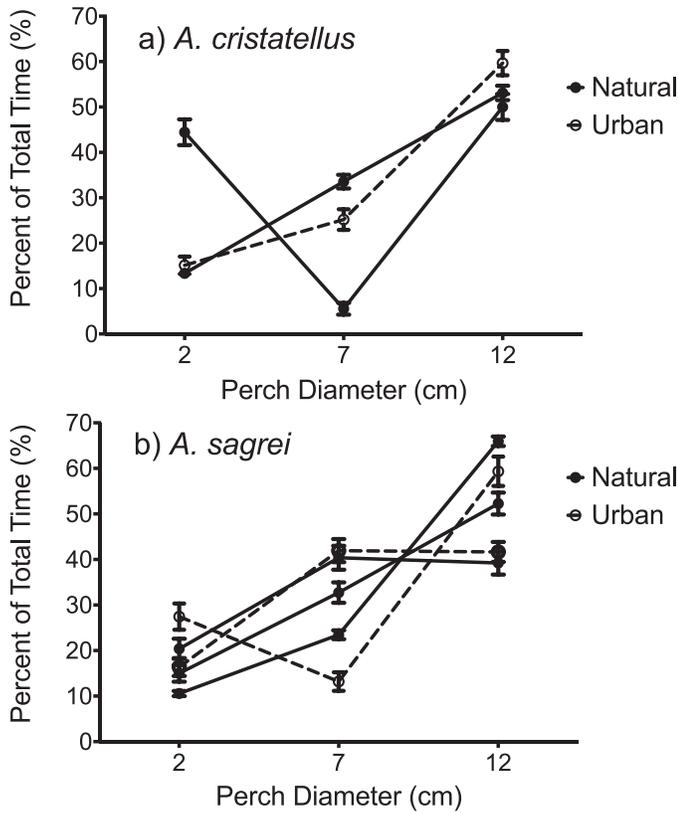


FIG. 1. Mean (\pm SE) for the percent of total time lizards spent on the small (2-cm), medium (7-cm), and large (12-cm) -diameter perches during perch-diameter-preference trials. Results are derived from previous laboratory trials (Battles et al., 2018) as well as newly reported laboratory and mesocosm trails for (a) *A. cristatellus* and (b) *A. sagrei* (see Tables 1–4). Separate trials for lizards from natural forest (solid circles) and urban (open circles) habitats are connected by solid and dashed lines, respectively.

South Florida, averaging 24.4°C with an average high of 29.1°C and average low of 19.7°C for the days we conducted trials. Lizards were randomly assigned to 1 of the 4 mesocosms using a stratified design (i.e., each species–habitat type group was equally represented in each mesocosm). We presented individual lizards with a choice of 3 perches consisting of 1 m tall, vertically positioned tree trunks in diameters of 2, 7, and 12 cm. After a 2-min acclimation period under an opaque cover on the ground, we remotely raised the cover and allowed each lizard to explore the perches for 25 min. We photographed each trial with 2 Canon Powershot ELPH 160 cameras mounted on opposite sides of the mesocosms to capture the location of lizards. We used the Canon Hack Development Kit (<https://chdk.fandom.com/wiki/CHDK>) to enable time-lapse features and set cameras to take photos every 20 sec. To more easily track a lizard in photos, we marked each individual with a white dot on their back. We used photos to determine the proportion of the total time spent on each perch, and the time to move from the ground to the first perch. Ten lizards did not use any of the perches during trials, so the final sample size was 69 lizards.

Statistical Analyses.—We assessed perch diameter and substrate preferences from the laboratory and mesocosm trials using multinomial mixed models, which account for the nonindependence of response values by including lizard ID as a random effect. Models evaluating perch diameter preference compared the proportions of time spent on small, medium, and large

TABLE 1. Sample sizes and mean percentage of total time spent on small (2-cm), medium (7-cm), and large (12-cm) -diameter perches during preference trials, separated by species and habitat from which the lizards were collected. Results are from previously published laboratory trials for perch diameter preference (Battles et al., 2018). Bold percentages in the large-diameter column indicates statistically significant differences compared with the small perch (see text for details).

Species	Habitat	N	Small	Medium	Large
<i>A. cristatellus</i>	Natural	16	13%	34%	53%
<i>A. sagrei</i>	Natural	19	11%	23%	66%

perches, and the model for substrate preference compared time spent on the wood, metal, and PVC substrates. Analyses were conducted in Program R (R Core Team, 2014) using the MCMCglmm package (Hadfield, 2010), which runs Markov chain Monte Carlo iterations to generate posterior distributions of the response levels. For example, the mean distributions for time spent on medium and small perches are each compared with time spent on the large perch. We tested for a correlation between body size (i.e., SVL) and the proportion of time perching on the large-diameter and wood substrates in the laboratory trials using Pearson correlations. We also tested for a difference in the time to move to the first perch between natural forest and urban populations of each species in the mesocosm trials using 2-tailed *t*-tests.

RESULTS

Laboratory perch-diameter-preference trials were consistent with a previous study (Battles et al., 2018), in that *A. sagrei* from a natural forest site preferred broader diameter perches (Fig. 1; Tables 1, 2), spending 52% of their time on the large-diameter perches. These lizards preferred the large perches to small ($P = 0.008$) but not medium ($P = 0.15$) perches. When evaluating the perch diameter preference of *A. sagrei* from an urban site, lizards spent 42% of their time on both the large and medium perches (Table 2). Lizards used these perches more than the small perch, but differences with the small perch were marginally nonsignificant ($P = 0.06$). These same lizards were used in perch substrate preference trials (Fig. 2, Table 3). Natural forest *A. sagrei* spent most of their time on wood (57%) and metal (41%) perches with no preference between the two substrates ($P = 0.27$) and preferred both over PVC ($P < 0.0001$). *Anolis sagrei* from an urban site overwhelmingly preferred the wood substrates, spending 93% of their time on wood compared with 7% on PVC and 0% on metal ($P < 0.0001$). During the substrate preference trials, 12 lizards used or attempted to use the metal perches and 7 of these lizards slipped or fell from this perch

TABLE 2. Sample sizes and mean percentage of total time spent on small (2-cm), medium (7-cm) and large (12-cm) -diameter perches during preference trials, separated by species and habitat from which the lizards were collected. Results are data from this study for laboratory trials for perch diameter preference. Bold percentages in the large-diameter column indicates statistically significant differences compared with the small perch (see text for details).

Species	Habitat	n	Small	Medium	Large
<i>A. sagrei</i>	Natural	20	15%	33%	52%
<i>A. sagrei</i>	Urban	19	16%	42%	42%

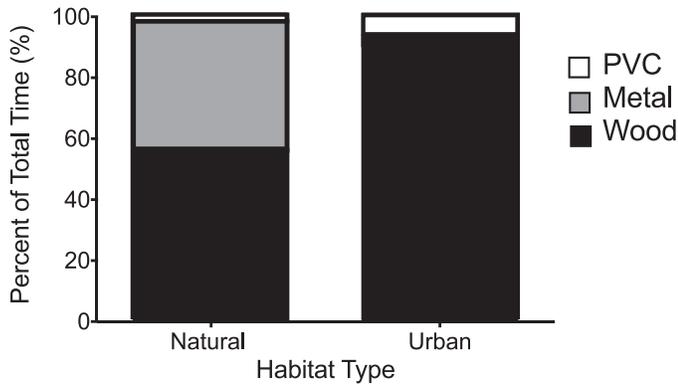


FIG. 2. Bars show the percent of total time *A. sagrei* spent on polyvinyl chloride (PVC), metal, and wood perches (all 12-cm diameter) during substrate preference trials, separated by lizards from natural forest and urban habitats.

type. Of the 3 lizards that used the PVC perches, 1 slipped. In contrast, no lizards slipped or fell when using the wood perches.

As opposed to laboratory trials for perch diameter preference where *A. sagrei* from natural forests preferred large-diameter perches, lizards from this habitat type showed no preference amongst the three sizes of perch in mesocosm trials (Fig. 1, Table 4). These lizards did not prefer the large perch over either the medium ($P = 0.89$) or small ($P = 0.23$) perch. In contrast, urban *A. sagrei* in mesocosm trials preferred the large-diameter perch 59% of the time, which was significantly more than the 13% and 27% of time spent on medium ($P = 0.004$) and small ($P = 0.036$) perches, respectively. We found no correlation between SVL and proportion of time on the large perch ($r = -0.074$, $P = 0.659$, $n = 39$) or between SVL and proportion of time on wood ($r = 0.217$, $P = 0.241$, $n = 31$) for the laboratory trials.

Results for *A. cristatellus* perch-diameter-preference trials in mesocosms showed natural forest populations preferred both large (50%) and small (44%) diameter perches with no significant difference between these diameters ($P = 0.74$), and used medium (6%) perches significantly less often ($P = 0.004$; Fig. 1, Table 4). In contrast, urban *A. cristatellus* preferred large perches compared with medium ($P = 0.022$) and small ($P = 0.002$) perches, using them 60% of the time (Table 4).

In mesocosm trials, *A. cristatellus* from the urban area were >2 times faster (mean \pm SD = 2.6 ± 2.6 min) when moving from the ground to their first perch compared with conspecifics from a natural forest site (mean \pm SD = 5.9 ± 4.0 min; $t = 2.99$, $df = 34$, $P = 0.005$). In contrast, *A. sagrei* from these two habitats did not differ in their time to the first perch (urban: mean \pm SD = 5.1 ± 3.0 min; natural forest: mean \pm SD = 5.7 ± 4.7 min; $t = 0.41$, $df = 32$, $P = 0.69$).

TABLE 3. Sample sizes and mean percentage of total time spent on 12-cm-diameter perches of polyvinyl chloride (PVC), metal, and wood during preference trials, separated by species and habitat from which the lizards were collected. Results are data from this study for laboratory trials for substrate preference. Bold percentages in the wood substrate columns indicate statistically significant differences compared with the PVC substrate (see text for details).

Species	Habitat	<i>n</i>	PVC	Metal	Wood
<i>A. sagrei</i>	Natural	17	2%	41%	57%
<i>A. sagrei</i>	Urban	14	7%	0%	93%

TABLE 4. Sample sizes and mean percentage of total time spent on small (2-cm), medium (7-cm), and large (12-cm) -diameter perches during preference trials, separated by species and habitat from which the lizards were collected. Results are data from this study for mesocosm trials for perch diameter preference. Bold percentages in the large-diameter column indicates statistically significant differences compared with the small perch (see text for details).

Species	Habitat	<i>n</i>	Small	Medium	Large
<i>A. cristatellus</i>	Natural	18	44%	6%	50%
<i>A. cristatellus</i>	Urban	18	15%	25%	60%
<i>A. sagrei</i>	Natural	18	20%	40%	39%
<i>A. sagrei</i>	Urban	15	27%	13%	59%

DISCUSSION

Overall, experimental assessment of perch diameter preference revealed males of these two *Anolis* species preferred large-diameter perches over small ones with some variability among trials (Fig. 1). *Anolis cristatellus* used large perches between 50–60% of the time and small ones 13–44% of the time, whereas *A. sagrei* used large perches 39–66% of the time and small ones 11–27% of the time (Tables 1–4). *Anolis sagrei* seemed to have a somewhat more consistent use of perch diameters among trials, and possibly a stronger preference for use of large-diameter and avoidance of small diameter perches compared with *A. cristatellus* (Battles et al., 2018; Fig. 1). The preference of *A. sagrei* for large perches was similar to a previous laboratory study where 66% of lizards from a natural forest sites used the large perch (Battles et al., 2018; Table 1); however, it differed from the laboratory trials presented in this study where natural forest *A. sagrei* showed no preference for perch size (Table 2). The pattern for urban *A. cristatellus* was more similar to a previous laboratory study using *A. cristatellus* from a natural forest site (Battles et al., 2018; Table 1) than it was to the natural forest population used in these mesocosm trials.

We found no support for consistent differences between lizards from natural forests and urban habitats in their preference for perch diameters for either species. However, we did detect differences in the time to move from the ground to the perch during trials; urban *A. cristatellus* did so twice as fast as natural forest *A. cristatellus* and *A. sagrei* from both habitats. In terms of substrate preference, there was a marked difference between lizards from different habitats. Although both sets of lizards used wood perches most often, urban *A. sagrei* exhibited an exceptionally strong preference for wood substrates and never used the metal perches (Fig. 2). We discuss these findings in the context of how habitat preferences influence habitat selection and fitness-related locomotor performance of lizards in human-altered environments, such as cities.

We expect natural selection to generate a positive relationship between organismal preferences and their fitness value. For example, a laboratory study allowing gravid *A. sagrei* to choose among 5 moisture levels for oviposition revealed females strongly preferred nesting substrates with high moisture content. Eggs incubated under these conditions led to high hatching success, large offspring size, and increased offspring survival, all important components of fitness (Reedy et al., 2013). In terms of the structural habitat niche, most anoles sprint faster, and are more stable when moving on broader surfaces (Losos and Sinervo, 1989; Losos, 1990; Irschick and Losos, 1999; Spezzano and Jayne, 2004). Thus, the overall preference for larger diameter perches found in this and previous studies (Fig. 1; Wright, 2009; Langford et al., 2014; Battles et al., 2018) is

consistent with a proxy of fitness (i.e., better locomotor performance on broader perches). Most habitat selection studies have found that anoles perch on broader vegetation compared with the distribution of available perches based on random sampling of the habitat (e.g., Rodríguez-Robles et al., 2005; Kolbe et al., 2012; Battles et al., 2018; but see Winchell et al., 2017). We infer anoles in natural forest habitats will be better poised to sprint faster to pursue potential prey, defend their territories, and escape predators when perching on broader vegetation (Irschick and Losos, 1999).

Urban areas, in contrast to natural forest habitats, have a different distribution of potential surfaces for anoles to use, including a greater availability of broader diameters and smoother substrates (Battles et al., 2018; Avilés-Rodríguez and Kolbe, 2019). Thus, the preference cues that anoles use in natural habitats may have different fitness consequences in human-modified habitats (Robertson et al., 2013). For example, the broad-diameter substrates preferred by anoles may be houses, poles, or walls in urban areas in addition to large-diameter trees (Kolbe et al., 2016a; Battles et al., 2018). These artificial substrates tend to be smooth and vertical, and anoles run slower and slip and fall more often on these substrates compared with natural vegetation (Kolbe et al., 2016a; Battles et al., 2019). Despite these potentially negative fitness consequences, anoles from natural forest and urban habitats in Miami do not show any consistent differences in their perch diameter preferences (Fig. 1). In contrast, urban *A. sagrei* showed a very strong preference for wood substrates over 2 types of smooth, artificial substrates (i.e., PVC and metal) on which lizards slipped and fell during trials compared with natural forest *A. sagrei* (Kolbe et al., 2016a; Fig. 2). This suggests the possibility of learned or evolved preferences in some urban populations for substrates on which anoles perform better. Given the variability in perch-diameter-preference trials, more substrate preference trials are needed to assess the consistency of these results among populations and species. Perhaps the nonnative populations of these *Anolis* species in South Florida have not experienced the divergent pressures in natural forest and urban habitats long enough to shape multiple aspects of their structural habitat preferences. Future studies of preferences for different aspects of the structural habitat could contrast findings from this study with populations experiencing consistent, long-term differences in urbanization, such as in the native ranges of these species (e.g., *A. cristatellus* in Puerto Rico; Winchell et al., 2016).

This study extended previous findings by comparing perch diameter preferences of anoles from 2 different habitats, assessing substrate preferences, and conducting both laboratory and mesocosm trials. Although some variation among trials existed (Tables 1–4; Fig. 1), there were no consistent differences in perch diameter preference between the two species, natural forest and urban habitats, or laboratory and mesocosm trials. Anoles in this study preferred larger diameter perches. Variation among trials could be related to some unmeasured aspect of these populations, and researchers should be cautious when using preferences measured for one population to represent the preferences of a different population or species. For instance, we did not measure the availability and use of perch diameters and substrates for all the populations in this study. Preferences could be influenced by the relative frequency with which lizards experience perches with different characteristics. Moreover, although perch type availability was constant for each trial (1 or 2 perches of each diameter depending on the trial), broader perches offered greater habitat surface area relative to thinner

perches. Future studies may consider exploring the interaction between habitat surface area and availability to further disentangle the causal mechanisms underlying habitat choice. Studies should also explore other potential sources of variation, including quantifying aspects of natural forest and urban environments not captured by assigning them to discrete categories. Moreover, individual consistency in perch preference behavior is little known, yet several studies have shown repeatable behavior in multiple dimensions of anole personalities (e.g., Lapiedra et al., 2017, 2018). Repeated preference trials for individual lizards may help to reduce variation in analyses (see Battles et al., 2018) and potentially reveal consistent individual-based behavior.

Future studies should explore the extent to which preferences exist for other aspects of the ecological niche of anoles and other lizards as well as whether preferences differ between males and females and different life stages (see Langford et al., 2014; Delaney and Warner, 2016). Studies of thermoregulation routinely assess preferred temperatures using thermal gradients in the laboratory and apply these data to evaluate the precision of thermoregulatory behavior in the field using field body temperatures from lizards and operative temperatures from nonthermoregulating lizard models (Hertz, 1992; Hertz et al., 1993). Preferences in other niche dimensions are less often studied; for example, few diet studies have conducted preference trials for food items and nest-site selection studies rarely use experimental approaches to assess preferred conditions in the laboratory (but see Reedy et al., 2013). The role of thermal, food, and structural habitat preferences in competitive interactions between sympatric species is another area of future research. Some evidence exists for competition between *A. cristatellus* and *A. sagrei* in South Florida (Salzburg, 1984; Losin, 2012; Kolbe et al., 2016b; Stroud, 2018) and their shared preference for large-diameter perches should increase the strength of competition on this niche axis. Additionally, our current knowledge of preferences for the structural habitat (i.e., diameters and substrates) is limited to 2 species of trunk-ground anoles. The structural habitat is a key axis of niche differentiation in anoles, so it would be informative to determine whether *Anolis* ecomorphs have consistent preferences for perch diameters and substrates.

In conclusion, we found that anoles in this study generally prefer broader diameter perches in laboratory and mesocosm trials, and lizards from natural forest and urban habitats did not differ in this regard. These results for trunk-ground anoles are consistent with previous studies using the same species (Wright, 2009; Battles et al., 2018), and support habitat selection and locomotor performance studies indicating that these anoles select broader perches and perform better on them in natural forest habitats. The addition of artificial substrates to urban habitats may alter the performance-based benefits of preferring broader diameters (Kolbe et al., 2016a). Urban anoles appear to have the capacity to alter their preferences in ways that favor locomotor performance, as indicated by the strong preference of urban *A. sagrei* for wood substrates on which they run faster and are more stable (Kolbe et al., 2016a). The extent to which these and other niche-related preferences vary among populations and species is a key direction for future research.

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LITERATURE CITED

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