



Living in the big city: preference for broad substrates results in niche expansion for urban *Anolis* lizards

Andrew C. Battles¹ · Malcom Moniz¹ · Jason J. Kolbe¹

Published online: 27 July 2018
© Springer Science+Business Media, LLC, part of Springer Nature 2018

Abstract

Persistence of animals in urban habitats, a stark environmental contrast to natural habitats, can be explained through evaluating the mechanisms behind organism-habitat interactions. One of the most notable effects of urbanization is the change in structural habitat; vegetation is removed and modified, favoring large trees and adding artificial structures in cities, which may alter how organismal preferences for aspects of the habitat are realized. We evaluated the mechanisms by which structural habitat changes associated with urbanization alter the available vegetation and substrates on which two species of *Anolis* lizards perch in urban and natural forest sites in Miami, FL. We also experimentally assessed habitat preference in the lab to establish the mechanism behind habitat selection. We found that vegetation was broader in urban areas compared to natural habitats, and artificial structures in urban areas were more than twice the diameter of available natural perches. Lizards expressed their preference for broad perches by selecting broader vegetation and artificial structures compared to their availability in both habitats. With the increased availability of broad substrates in urban areas, perch diameters selected by lizards resulted in an expansion of this aspect of the structural habitat niche for both species. The two species differed, however, in other responses to altered urban habitats. *Anolis cristatellus* tended to avoid artificial substrates, whereas *A. sagrei* used both natural and artificial structures in proportion to their availabilities. This study provides a mechanistic explanation for how urbanization alters structural habitats, leading to niche expansion for organisms living in cities.

Keywords *Anolis cristatellus* · *Anolis sagrei* · Miami · Anole · Structural habitat niche · Perch preference

Introduction

Most species alive today have an evolutionary history that includes persisting through environmental changes and encountering novel habitats to some degree (Thompson 2013). However, ongoing human-induced rapid environmental change (HIREC) is unprecedented in both its rate and magnitude of environmental change on this planet (Palumbi 2001; Hobbs et al. 2006; Sih et al. 2011; Barnosky et al. 2012). Local extinctions and range shifts demonstrate that some organisms are unable to respond successfully in situ to HIREC (Lynch and Lande 1993; McKinney and Lockwood 1999; Brook et al.

2008; Estrada et al. 2015). In contrast, other species persist, and some even thrive, when encountering novel environments produced by human activities (Kowarik 2011; Lowry et al. 2013). To better understand how changing environmental conditions challenge the persistence of populations, we need mechanistic studies that quantify changes in niche dimensions due to global change (Shochat et al. 2006; Sol et al. 2013). Such studies should evaluate changes in resource availability in altered habitats, how organisms respond through their resource use and preferences, and if individuals experience any fitness consequences. This niche-based assessment should yield valuable insight into the role of niche dynamics (e.g. niche contraction or niche expansion) in determining whether populations persist under HIREC (Wingfield et al. 2011).

Urbanization likely alters the niche space available in cities, ultimately determining whether or not populations persist there, yet we know little about the underlying dynamics of how organisms respond to this change. During urbanization, natural vegetation is removed and replaced with novel artificial structures (e.g. walls, pavement, and lamp posts) and managed vegetation assemblages (McDonnell and Pickett

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11252-018-0787-1>) contains supplementary material, which is available to authorized users.

✉ Andrew C. Battles
andrewcbattles@gmail.com

¹ University of Rhode Island, 120 Flagg Rd, Kingston, RI 02881, USA

1990; Forman 2014; McDonnell and Hahs 2015). Habitat changes in cities occur at rates far greater than in natural habitats and in some cases, elicit phenotypic responses distinct from those observed in natural habitats (Winchell et al. 2016; Alberti et al. 2017). These and other selection pressures in urban areas may promote adaptive evolution in traits that improve fitness in cities (Nemeth and Brumm 2009; Atwell et al. 2012; Donihue and Lambert 2014; Weaving et al. 2016; Winchell et al. 2016). New resources in urban habitats may benefit species with adaptations that happen to be useful in urban habitats (i.e. pre-adaptation; McDonnell and Hahs 2015), and previous studies show that urban animal populations exploit a variety of anthropogenic resources (Lowry et al. 2013; Oro et al. 2013; Penick et al. 2015). If urban habitats increase the availability of habitat elements preferred by an organism, urban populations may experience a realized niche expansion (Pearman et al. 2008). A more mechanistic, niche-focused framework that includes organismal preferences, organism-habitat interactions, and comparison of habitat differences between urban and natural environments is needed.

A key axis of diversification for *Anolis* lizards is the structural habitat - the diameter, height, and type of vegetation used by perching lizards (Losos 2009), and strong habitat use-performance relationships drive habitat selection in many species (Rodríguez-Robles et al. 2005; Johnson et al. 2006). Anole structural habitat use varies interspecifically, intraspecifically, and in different environments (Irschick et al. 2005a, b). Furthermore, anole habitat selection is correlated with locomotor performance, a commonly used fitness proxy in anoles (Irschick and Losos 1999; Losos 2009; Gillman and Irschick 2013; Irschick and Higham 2016). Numerous *Anolis* species are found in urban and natural habitats in their native and non-native ranges (Irschick et al. 2005a, b; Marnocha et al. 2011; Kolbe et al. 2016a; Winchell et al. 2016). Two *Anolis* species found in Miami, FL, USA, *Anolis cristatellus* and *Anolis sagrei*, are ideal for evaluating how the habitat alterations caused by urbanization influence structural habitat preferences and selection. Both species inhabit urban and natural forest habitats that occur in close proximity to each other. In their natural forest habitats, these species are commonly found on trunks, branches, leaves, and the ground, making them likely to be sensitive to the structural habitat changes associated with urbanization.

In this study, we first compared the structural habitat availability and use by lizards in natural forests and urban areas. This allowed us to evaluate whether lizards are selecting aspects of the structural habitat and if urbanization alters these relationships. After comparing availability, use, and selection in the field, we evaluated preference for a key aspect of the structural habitat – perch diameter – using a laboratory experiment. We predict that urban areas will contain a greater proportion of broad substrates than natural areas due to the removal of smaller trees, branches, and woody debris in urban areas and the addition of artificial substrates, such as walls and posts. We expect

that lizards will prefer larger-diameter perches and non-randomly select wide perches compared to their availability, leading to an expansion of the structural habitat niche in urban sites. Results from our study identify mechanisms behind patterns of organismal responses to urbanization that should improve predictions regarding species and population persistence in our increasingly urbanized world.

Methods

Study species and study sites

We studied two species of *Anolis*, small insectivorous lizards found naturally in southern North America, Central and South America, and throughout the Caribbean (Losos 2009). Several *Anolis* species have been introduced to the Miami metropolitan area (Kolbe et al. 2007), two of which are common in both natural forest and urban areas. *Anolis sagrei* is native to Cuba and the Bahamas, and non-native populations are now widely distributed in the southeastern United States with Miami area populations dating to the 1940–60s (Bell 1953; Salzburg 1984; Kolbe et al. 2004). *Anolis cristatellus* is native to Puerto Rico, and was first documented in Miami in the mid-1970s (Wilson and Porras 1983; Powell et al. 1996; Bartlett and Bartlett 1999; Kolbe et al. 2007). In contrast to the nearly ubiquitous *A. sagrei*, the distribution of *A. cristatellus* is more restricted, radiating out from two independent points of introductions in the Miami area (Kolbe et al. 2016b). Both *A. sagrei* and *A. cristatellus* are classified as trunk-ground habitat specialists, meaning they commonly occupy the ground and perches up to ~2 m (Salzburg 1984; Losos 2009). The larger *A. cristatellus* (snout-vent length, or SVL, up to 75 mm in males and 60 mm in females; mean mass is 8.5 g in males) typically perches higher than the smaller and more terrestrial *A. sagrei* (SVL up to 69 mm in males and 55 mm in females; mean mass is 4.8 g in males).

We studied lizards in four urban and four natural sites throughout the Miami metropolitan area between May and August in 2014. Generally, natural sites were closed-canopy forests on upland hammocks, consisting of hardwood-oak overstory canopy with palmettos and saplings in the understory, and were forest patches within the urban matrix of metropolitan Miami. Urban sites were located within human-altered areas, generally along roadsides with bike paths, canals, and sidewalks. We are unaware of any urban sites in Miami that contain only *A. cristatellus*. Refer to supplementary materials for detailed descriptions of study sites.

Habitat availability, use and selection

Because structural habitat is a key niche axis for anoles, we evaluated the impact of urbanization on the availability of perch sites and perch use by lizards. To understand the relationship

between perch availability and the perch use, we conducted habitat availability transects to quantify the differences between urban and natural sites, and then compared these availabilities to lizard habitat use. We measured the diameter (cm), height (cm), and substrate type of potential lizard perches, denoted further as habitat availability, which includes artificial substrates in urban sites. At all sites, we measured available vegetation (and structures in urban areas) at 0.25 m intervals, from 0 to 2 m vertically. Trunk-ground ecomorphs such as the two *Anolis* species in this study rarely perch higher than 2 m (Losos 2009). We measured one potential perch at each height, within a 0.5-m radius of the sample point. We followed perches that continued outside of the 0.5-m radius but that originated from within it. If a particular height did not have an available perch, such as when vegetation was <2 m (e.g. a low bush), we did not record data at that height. Some transect points had no vegetation within a 0.5 m radius, and in these cases no data were recorded for any height; these were considered ‘open ground’ and used to analyze percent open space. We did not include walls in the perch diameter analyses because we are uncertain on how to quantify accurately these surfaces; very large diameters would skew the results and capping measurements would be inaccurate. Because urban sites were usually along a road, we conducted 6–8 m transects every 30–50 m perpendicular to the road. Exact transect lengths and intervals between transects depended on the length of the site and the distance between the road and the edge, such as the canal edge or building. In natural sites, we conducted two separate transects beginning from haphazard locations within the study plots that followed a random compass heading. Each transect was approximately 20 m in length, with 6-m perpendicular transects at 5-m intervals along the main transect. We collected roughly 2–3 times as many habitat availability observations (not including transect points without vegetation) as lizard perch use observations at each site.

We compared vegetation availabilities to perch use by lizards in the urban and natural sites to determine habitat selection. Using a telescopic pole with a noose, we captured undisturbed adult lizards over a period of 2–5 days in each site and recorded sex, species, and SVL as well as the diameter, height, and substrate of the location where each lizard was perched. Before releasing each lizard, we marked it with a small dot using white-out to ensure we did not re-capture the same individual during the study. We expended equal capture effort in all sites to ensure that we captured a representative sample of the population. We captured males and females totaling approximately 120 adult lizards per species per site (male and female sample sizes in Table S1), evenly collected throughout their activity time during the day (0700 to 1800 h), and never in inclement weather.

Habitat preference

To measure perch-diameter preference, we collected 20 male *A. sagrei* and 20 male *A. cristatellus* from natural sites and

shipped them to the University of Rhode Island (Kingston, RI). In a 1.8 m × 1.8 m × 1.8 m mesh enclosure in the lab, lit with overhead fluorescent lights approximately 3 m above the floor (and no lights or heat sources for basking), we presented individual lizards a choice of six perches (i.e., tree trunks, 1.6 m high) in three duplicated diameters of 2, 7, and 12 cm. These sizes cover the range of mean vegetation diameters observed for availability and use by both species in urban and natural habitats. After a two-minute acclimation period under an opaque cover, lizards were given 15 min to explore the perches. We recorded the proportion of time spent on each perch compared to the total time lizards were on a perch. Lizards usually selected a perch within the first two minutes, sometimes moving between several perches. We arranged the perches in alternating sizes in a circle. Before each trial, we randomized the location of perches in the circle to eliminate a location effect. Each lizard went through the preference experiment two times. Some lizards never selected a perch and were removed from the analysis (*A. sagrei* $N = 1$, *A. cristatellus* $N = 4$); sample sizes in Table S1.

Statistical analyses

We performed all statistical analyses in R (R Core Team 2014), and analyzed species separately for all statistical tests. We compared mean available vegetation diameters of all sites, nested within their site type (urban and natural), using an analysis of variance (ANOVA). We used ANOVA to test for a difference in diameter among vegetation in natural areas, vegetation in urban areas, and artificial structures in urban areas, for both availability and use by males and females. We compared diameters of available substrates (i.e., vegetation and artificial structures) and perch use by sex and site type (urban and natural) with an ANOVA. We also used ANOVA to test for differences in perch height use by sex and site, but did not include availability because nearly all heights were available at each site. To compare the distributions of diameters of available substrates and perches used by lizards between natural and urban environments, we used two-sample Kolmogorov-Smirnov tests. We used Simpson’s index of diversity to calculate the diversity of perches used by each species and sex in both site types; values range from 0 (no diversity) to 1 (infinite diversity). We used chi-squared tests to compare the proportion of artificial and natural perches available in urban habitats to the proportion used by lizards, separately by sex. For all tests, lizards were only compared to availability in the sites that they were found (e.g. *A. cristatellus* for only two of the four urban sites where it was present).

We assessed perch diameter preference from the laboratory experiment using a multinomial mixed model, which accounts for the non-independence of response values, with lizard ID as a random effect to avoid pseudoreplication, and compared the proportions of time spent on small, medium, and large perches for both trials combined using the MCMCglmm package

(Hadfield 2010). The model runs Markov chain Monte Carlo iterations to generate posterior distributions of the response levels. In this case, the mean distributions for time spent on medium and small perches are each compared to time spent on the large perch.

Results

Habitat availability

Urban sites had broader substrates available than natural sites ($F_{1,6} = 154.33$, $p < 0.0001$, Figs. 1a, S2); within natural sites, Montgomery and Matheson had narrower vegetation than Barnes ($F_{6,2816} = 3.26$, $p < 0.01$). Larger mean diameters in urban areas were due to both broader vegetation in urban sites as compared to natural areas and the addition of even broader artificial substrates in urban sites ($F_{2,2896} = 165.7$, $p < 0.0001$, Fig. 1a). These large differences in vegetation and substrate diameters existed despite not including measurements for walls, which account for about 3% of availability in urban areas. The distribution of available substrates in urban areas was shifted away from smaller diameters and toward larger ones compared to natural areas ($D = 0.23$, $p < 0.0001$, Fig. S2). In most instances, the full range of potential perch heights from the ground to at least 2 m was available in both natural and urban sites. Urban habitats also had more open ground than natural areas; about half of the urban survey points lacked vegetation (Fig. 2a, Table S2). Urban habitats had a greater variety of potential perches due to the addition of artificial substrates, such as poles, posts, and walls (Fig. 3), which accounted for about 25% of available substrates (Fig. 2b).

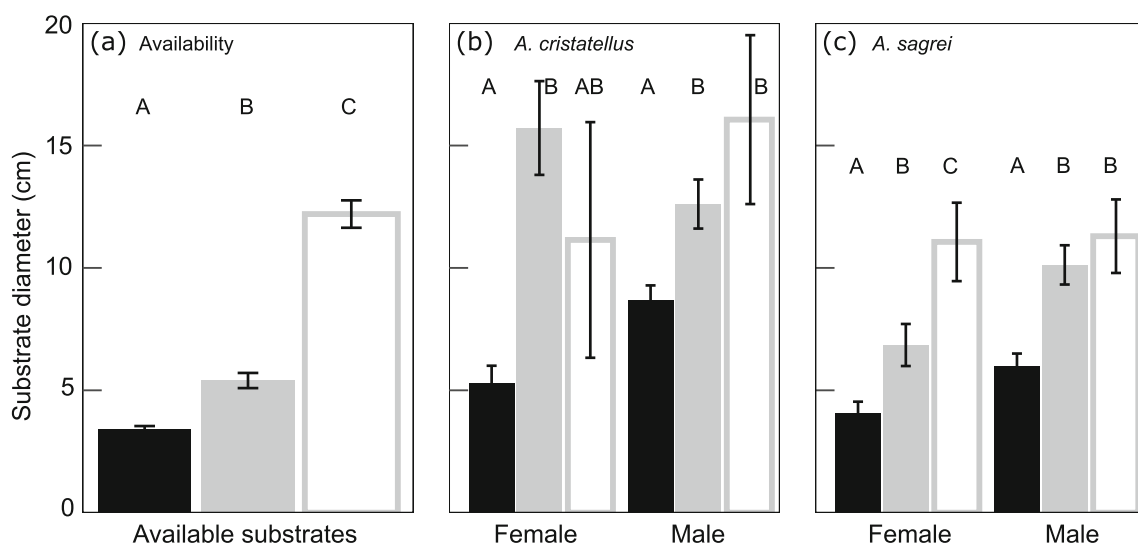


Fig. 1 Mean (\pm SE) for diameters of (a) available vegetation and artificial substrates in natural and urban sites, (b) perches used by *A. cristatellus*, and (c) perches used by *A. sagrei*. Vegetation at natural sites is in black,

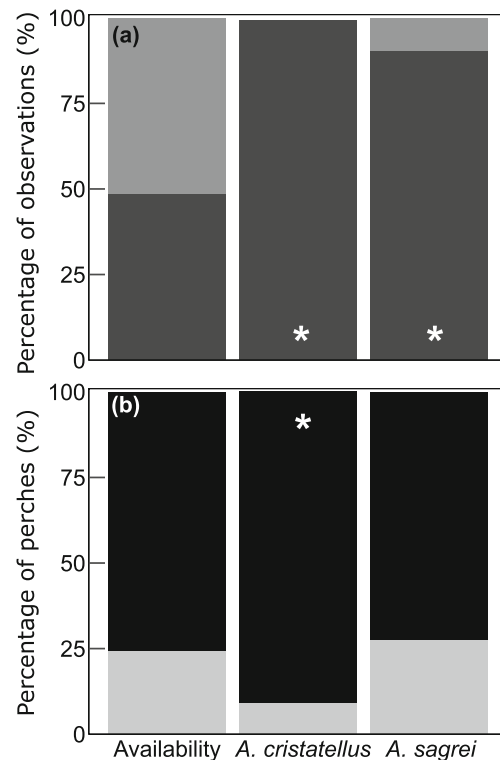


Fig. 2 Panel a) shows the proportion of total observations from habitat availability transects that were open ground (light grey) versus vegetation (i.e., potential perches, dark grey) and the proportion of the time lizards used perches (dark grey) compared to the ground (light grey) (Table S2). Panel b) shows the percentage of natural (black) versus artificial (grey) substrates available and perches used by lizards in urban sites. Sites with and without *A. cristatellus* did not differ in availability/use comparisons and so are pooled for availability columns, and female and male perch use did not differ significantly for either species and were pooled for this figure. * indicates $P < 0.05$ for the chi-squared test of availability versus perch use by lizards

vegetation at urban sites in grey, and artificial substrates in white, with letters indicating significant differences ($P < 0.05$)

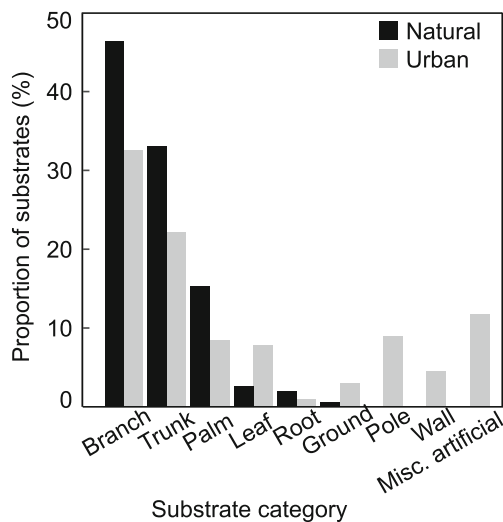


Fig. 3 Frequency of natural and artificial substrate availability at natural forest (black) and urban (grey) sites

Overall, urban areas had broader substrates available (both vegetation and artificial structures) and more open space compared to natural habitats.

Habitat selection

Despite the ubiquity of open ground in urban habitats, lizards were almost always found on vegetation or artificial structures (Fig. 2a). Lizards used wider perches in urban compared to natural areas, and they selected wider perches than were available in both areas (*A. cristatellus*: $F_{5,1914} = 55.657$, $p < 0.001$, Figs. 1 and 4a; *A. sagrei*: $F_{5,2841} = 31.435$, $p < 0.001$, Figs. 1 and 4b). Lizards also used a greater diversity of perches in urban compared to natural areas (Table 1, Figs. S2, S3). The use of broader perches in urban areas was driven by lizards selecting both wider vegetation, which was almost always wider than vegetation used for perching in natural areas, and artificial substrates, which were over twice the diameter of vegetation in urban areas (*A. cristatellus*: $F_{5,517} = 10.27$, $p < 0.001$, Fig. 1b; *A. sagrei*: $F_{5,714} = 9.675$, $p < 0.001$, Fig. 1c). Neither sex of *A. cristatellus* differed in perch height use between urban and natural sites, but females perched lower than males within both sites ($F_{3,523} = 9.152$, $p < 0.0001$, Fig. 4a, S1). Male and female *A. sagrei* perched lower in urban areas than in natural areas and females always perched lower than males ($F_{3,775} = 25.53$, $p < 0.0001$, Fig. 4b, S1). Both sexes of *A. sagrei* used artificial perches at the same frequency as their availability, but female and male *A. cristatellus* used artificial perches at a lower rate (female: $X^2 = 6.80$, $df = 1$, $p < 0.001$; male: $X^2 = 4.93$, $df = 1$, $p < 0.03$, Fig. 2b), suggesting avoidance of artificial substrates by *A. cristatellus* in Miami.

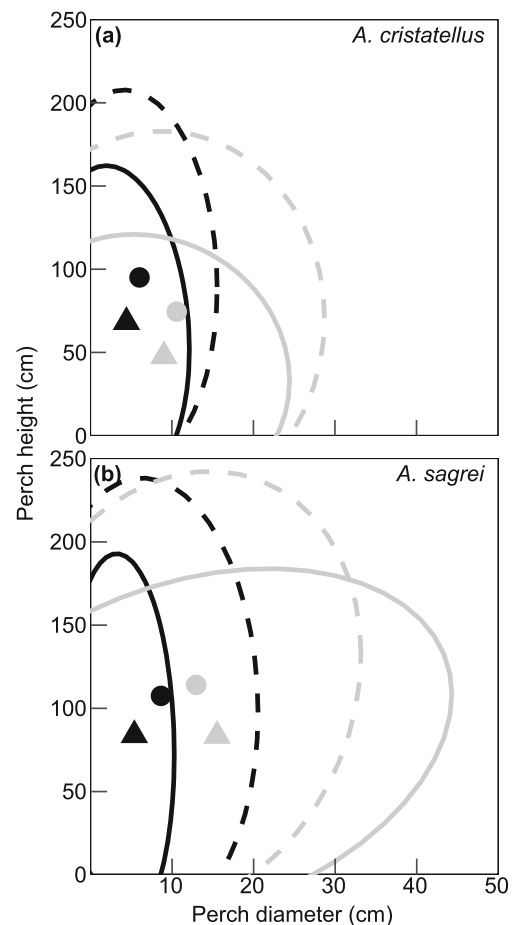


Fig. 4 Urban niche expansion of structural habitat use by (a) *A. cristatellus* and (b) *A. sagrei*. Plots of perch diameter against perch height show means (S.E. error bars do not exceed shape size) and 95% confidence ellipses, separate for males (circles, dashed ellipses) and females (triangles, solid ellipses). Natural sites are in black and urban sites in grey

Habitat preference

In the experimental perch preference trials, *A. cristatellus* and *A. sagrei* spent an average of 53.1 and 66.0% of their time, respectively, on the largest-diameter perches (Fig. 5). *Anolis sagrei* exhibited a stronger preference for broad-diameter perches, preferring the largest perches to both small ($p < 0.001$) and medium ones ($p < 0.001$), whereas *A. cristatellus* preferred only the largest to the smallest perches ($p < 0.001$).

Discussion

We found that lizard habitat preferences interact with habitat availability to drive the expansion of the structural habitat niche of anoles in urban areas (Fig. 4). Lizards selected broader diameter vegetation compared to the availability of potential perches in natural habitats (Fig. 1, S1). Urban habitats had broader substrates compared to natural areas due to a

Table 1 Simpson's index of diversity for the perch diameter classes used by male and female *A. cristatellus* and *A. sagrei* and the Kolmogorov-Smirnov distances, indicating the maximum difference

Species	Sex	Natural site diameter diversity (Simpson's D)	Urban site diameter diversity (Simpson's D)	K-S dist.
<i>A. cristatellus</i>	F	0.42	0.62	0.40
	M	0.71	0.76	0.21
<i>A. sagrei</i>	F	0.40	0.62	0.22
	M	0.54	0.76	0.22

Bold values indicate significance at $p < 0.01$

combination of broader vegetation and the addition of artificial structures (Fig. 3), and lizards still selected broader perches than available (Fig. 1, S1).

Moreover, lizards used a greater diversity of perch diameters in urban sites (Table 1, Fig. S3). Other studies have observed expansion of the realized niche in response to HIREC, particularly in the context of invasive species responding to novel climates in their non-native range (Holt et al. 2005; Broennimann et al. 2007; Fitzpatrick et al. 2007; Pearman et al. 2008; Tingley et al. 2014), but observations of niche expansion in urban environments are limited. Studies of urbanization tend to focus on population- and community-level responses to habitat alterations, which document changes in abundance and diversity that ultimately emerge as a result of underlying niche dynamics (Aronson et al. 2014; Fischer et al. 2015; Boivin et al. 2016). The broad perches encountered by lizards in urban areas were often artificial substrates (i.e.,

smooth, vertical surfaces), amounting to roughly one-quarter of available perches (Fig. 2), and lizard locomotor performance has been shown to decrease on smooth, artificial substrates (Kolbe et al. 2016a). Consequently, preference-driven niche expansion in urban areas may result in urban lizards choosing sub-optimal substrates in terms of locomotor performance. The implications of this paradox in cities range from behavioral changes to fitness losses with the potential to alter selective regimes in urban environments (Kolbe et al. 2016a; Winchell et al. 2016).

Both *Anolis* species in our study preferred the largest diameter perches available, with *A. sagrei* having a stronger preference (Fig. 5), which likely results from a strong association between use of broad perches and increased fitness in natural habitats. Sprint speed, a common fitness proxy in anoles, is faster on wider-diameter perches for long-limbed species, such as the two species in this study (Losos and Sinervo 1989; Irschick and Losos 1998). Large perches, such as tree trunks, may also confer other fitness benefits. To escape predators, anoles will squirrel, or run to the opposite side of a trunk, placing them out of reach and view of a predator (Cooper 2006). Further, flight initiation distance, or the distance between a perceived predator and an anole when the anole flees, decreases with increasing perch diameter in five anole species (Losos and Irschick 1996), suggesting that the benefits of staying on a perch increase as its diameter increases. Tree trunks typically have fewer nearby branches, thereby increasing visibility. This can increase scanning ability to defend territories, identify prey, find and attract mates, and see predators from farther distances (Johnson et al. 2010). Therefore, for these and possibly other reasons, *Anolis* species such as these trunk-ground habitat specialists have developed an innate preference for larger-diameter perches in natural habitats.

Preference for larger-diameter perches was consistent with habitat selection by lizards in our study; lizards generally used wider perches than were available in both urban and natural habitats (Figs. 1, S2). Similarly, Wright (2009) found that male and female *A. sagrei* used broader perches added to their habitats (even though these perches were artificial). In natural habitats in our study, the largest perches were tree trunks and

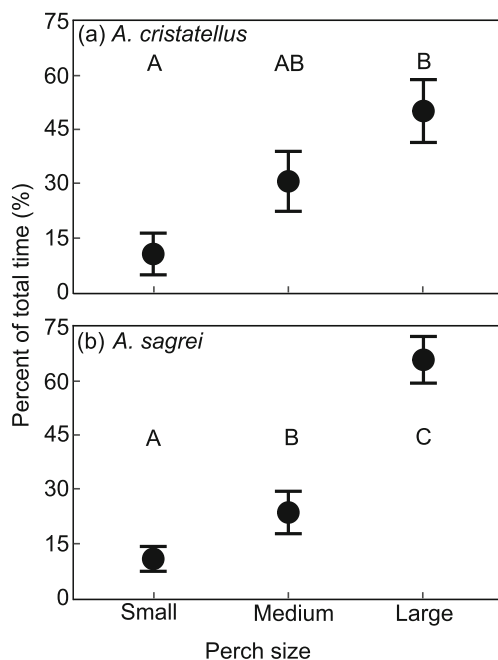


Fig. 5 Mean (\pm SE) percentage of total time that (a) *A. cristatellus* and b) *A. sagrei* spent on small, medium, and large diameter perches during perch preference trials. Letters indicate significant differences ($p < 0.01$), separate for each species

expressing preference for these perches likely confers higher fitness. Because the widest perches available in urban habitats were often artificial (Fig. 1), we would expect both species to occupy broad, artificial structures, especially *A. sagrei*, which had a stronger preference for large perches (Fig. 5). Indeed, in urban habitats we found *A. sagrei* using natural and artificial perches at rates equivalent to their availability (Fig. 2b), suggesting they do not differentiate between artificial and natural structures per se. In contrast, *A. cristatellus*, which exhibited a weaker preference for broad perches in lab trials and tended to avoid artificial substrates in urban areas, using them roughly 10% of the time compared to their 22% availability (Fig. 2b). While artificial structures certainly contribute to the niche expansion, lizards also select broad vegetation for perching in urban areas (Fig. 1b, c). However, smooth substrates, which are rare or absent in natural habitats, may alter the costs and benefits of using broad perches in urban environments (Kolbe et al. 2016a).

If artificial structures confer reduced performance, we can think of two primary reasons why lizards use them without apparent fitness losses. First, behavioral strategies may be used to avoid suboptimal habitat. *Anolis cristatellus* demonstrates that niche expansion in urban areas can still occur without relying upon artificial substrates (Figs. 1 and 2); perch diameter does not differ between artificial and natural perches for this species in urban areas (Fig. 1b). Avoidance of artificial substrates may have occurred because the fitness losses of using artificial substrates are great enough to alter habitat selection cues in urban areas (Schlaepfer et al. 2005). Variation in habitat selection behavior may be adaptive as populations encounter urban environments (Lapiedra et al. 2017). Second, evolutionary adaptation to HIREC, including urbanization, occurs across a wide range of taxa (Nemeth and Brumm 2009; Atwell et al. 2012; McDonnell and Hahs 2015), so specific components of the urban habitat, such as substrate composition are likely to be a selective force. For example, Winchell et al. (2016) showed predictable phenotypic differences (i.e., greater relative hindlimb length and more lamellae) between anoles in urban and natural habitats based on habitat characteristics (such as perch diameter) and demonstrated a genetic basis for these differences, which supports adaptation. Kolbe et al. (2016a) found a performance basis for this morphological variation where *A. cristatellus* with longer limbs proportional to their body size sprinted faster and were more stable on smooth, vertical substrates. Both studies (Kolbe et al. 2016a; Winchell et al. 2016) were conducted in the native range of *A. cristatellus*, where populations have experienced the effects of urbanization for potentially hundreds of generations, whereas the Miami populations in this study were introduced only a few decades ago, so the time exposed to urbanization may influence any potential selective pressures. The extent to which the invasion process alters phenotypes and environmental conditions for non-native populations compared to their source populations needs to be explicitly evaluated in future studies.

In this study, we explored mechanisms by which two species of *Anolis* lizards persist in urban habitats markedly different than their natural habitats, an important task in understanding how HIREC phenomena affect organism-environment interactions (Wingfield et al. 2011). We demonstrated that preference for broad perches and their increased availability in urban habitats interact to facilitate niche expansion of a key component of the structural habitat niche. However, the broadest perches in urban habitats are artificial structures, which are ecologically novel and could reduce fitness (e.g. reduced locomotor performance in Kolbe et al. 2016a). Several factors may allow lizards to minimize the performance losses associated with artificial substrates and therefore not experience population declines in cities. First, artificial structures, though significantly larger than vegetation in urban areas, are not the sole contributor to niche expansion. Second, lizards may avoid reduced-fitness artificial structures, as *A. cristatellus* does, suggesting preference cues may shift from substrate diameter to other features, such as surface roughness. Third, morphology may be under selection in urban areas, resulting in increased performance on artificial substrates. This study demonstrates that the consequences of urbanization for one aspect of the ecological niche, but other factors beyond the structural habitat undoubtedly contribute to fitness in urban areas. For example, increased urban temperatures (i.e., the urban heat island effect) likely affect several traits important for fitness of these ectothermic organisms, such as metabolism, activity and performance (Gunderson and Leal 2012). Urban landscapes provide opportunities for researchers to study how organisms cope with environmental change at relatively accessible scales (e.g. spatial, temporal; McDonnell and Pickett 1991), increasing the power of predictions for organismal response to future change. Future studies should follow a mechanistic framework for evaluating influences of other urban habitat changes to better understand what factors contribute to the persistence of species in cities and how those factors interact.

Acknowledgements We thank the Miami-Dade Parks and Recreation department for permission to use Miami-Dade parks as study sites, Z. Chejanovski and J. Stroud for collecting and shipping lizards, and P. Griffith and the Montgomery Botanical Center for research sites and support. We thank E. Preisser and the Kolbe lab group for helpful comments on drafts on this manuscript.

Compliance with ethical standards

Protocols for use of lizards were approved by the URI Institutional Animal Care and Use Committee (AN11–09–005). This work was funded by grants from the National Geographic Society, the National Science Foundation (DEB-1354897), and the University of Rhode Island Enhancement of Graduate Research Award as well as funds from the University of Rhode Island. A. Battles was a National Science

Foundation graduate research fellow. M. Moniz participated in the URI Coastal Fellows Program during this project. We can think of no conflicts of interest for this work.

References

- Alberti M, Correa C, Marzluff JM, Hendry AP, Palkovacs EP, Gotanda KM et al (2017) Global urban signatures of phenotypic change in animal and plant populations. *PNAS* 114:8951–8956. <https://doi.org/10.1073/pnas.1606034114>
- Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *P Roy Soc B-Biol Sci* 281:20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Atwell JW, Cardoso GC, Whittaker DJ, Campbell-Nelson S, Robertson KW, Ketterson ED (2012) Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav Ecol* 23:960–969. <https://doi.org/10.1093/beheco/ars059>
- Barnosky, AD, Hadly, EA, Bascompte, J, Berlow, EL, Brown, JH, Fortelius, M, et al (2012) Approaching a state shift in Earth's biosphere. *Nature*:486, 52–58. <https://doi.org/10.1038/nature11018>
- Bartlett, RD, & Bartlett, PP (1999) A field guide to Texas reptiles and amphibians (vol. 22). Gulf Pub Co
- Bell LN (1953) Notes on three subspecies of the lizard *Anolis sagrei* in southern Florida. *Copeia*:63. <https://doi.org/10.2307/1440256>
- Boivin NL, Zeder MA, Fuller DQ, Crowther A, Larson G, Erlandson J. M., ... Petraglia M. D. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions *PNAS* 113:6388–6396. <https://doi.org/10.1073/pnas.1525200113>
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecol Lett* 10:701–709. <https://doi.org/10.1111/j.1461-0248.2007.01060.x>
- Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends Ecol Evol* 23:453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Cooper WE (2006) Risk factors affecting escape behaviour by Puerto Rican *Anolis* lizards. *Can J Zool* 84:495–504. <https://doi.org/10.1139/z06-018>
- Donihue CM, Lambert MR (2014) Adaptive evolution in urban ecosystems. *Ambio* 44:194–203. <https://doi.org/10.1007/s13280-014-0547-2>
- Estrada A, Meireles C, Morales-Castilla I, Poschlod P, Vieites D, Araújo MB, Early R (2015) Species' intrinsic traits inform their range limitations and vulnerability under environmental change. *Glob Ecol Biogeogr* 24:849–858. <https://doi.org/10.1111/geb.12306>
- Fischer JD, Schneider SC, Ahlers AA, Miller JR (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conserv Biol* 29:1246–1248. <https://doi.org/10.1111/cobi.12451>
- Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Global Ecol and Biogeogr* 16:24–33. <https://doi.org/10.1111/j.1466-8238.2006.00258.x>
- Forman R (2014) *Urban ecology: science of cities*. Cambridge University Press, New York
- Gillman CA, Irschick DJ (2013) Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. *Funct Ecol* 27:374–381. <https://doi.org/10.1111/1365-2435.12063>
- Gunderson AR, Leal M (2012) Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. *Funct Ecol* 26:783–793. <https://doi.org/10.1111/j.1365-2435.2012.01987.x>
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw* 33:1–22. <https://doi.org/10.18637/jss.v033.i02>
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr* 15:1–7. <https://doi.org/10.1111/j.1466-822X.2006.00212.x>
- Holt RD, Barfield M, Gomulkiewicz R (2005) Theories of niche conservatism and evolution. In: Sax DF, Stachowicz JJ, Gaines SD (eds) *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates Incorporated Sunderland, MA, pp 259–290
- Irschick DJ, Higham TE (2016) *Animal athletes: an ecological and evolutionary approach*. Oxford University Press
- Irschick DJ, Losos JB (1998) A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219–226. <https://doi.org/10.2307/2410937>
- Irschick DJ, Losos JB (1999) Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in caribbean anoles. *Am Nat* 154:293–305. <https://doi.org/10.1086/303239>
- Irschick DJ, Carlisle E, Elstrott J, Ramos M, Buckley C, Vanhooydonck B et al (2005a) A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol J Linn Soc* 85:223–234. <https://doi.org/10.1111/j.1095-8312.2005.00487.x>
- Irschick DJ, Vanhooydonck B, Herrel A, Meyers J (2005b) Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol J Linn Soc* 85:211–221. <https://doi.org/10.1111/j.1095-8312.2005.00486.x>
- Johnson MA, Kirby R, Wang S, Losos JB (2006) What drives variation in habitat use by *Anolis* lizards: habitat availability or selectivity? *Can J Zool* 84:877–886. <https://doi.org/10.1139/Z06-068>
- Johnson MA, Revell LJ, Losos JB (2010) Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* 64:1151–1159. <https://doi.org/10.1111/j.1558-5646.2009.00881.x>
- Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–181. <https://doi.org/10.1038/nature02807>
- Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB (2007) Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. *Conserv Biol* 21:1612–1625. <https://doi.org/10.1111/j.1523-1739.2007.00826.x>
- Kolbe JJ, Battles AC, Avilés-Rodríguez KJ (2016a) City slickers: poor performance does not deter *Anolis* lizards from using artificial substrates in human-modified habitats. *Funct Ecol* 30:1418–1429. <https://doi.org/10.1111/1365-2435.12607>
- Kolbe JJ, VanMiddlesworth P, Battles AC, Stroud JT, Buffum B, Forman RTT, Losos JB (2016b) Determinants of spread in an urban landscape by an introduced lizard. *Landsc Ecol* 31:1795–1813. <https://doi.org/10.1007/s10980-016-0362-1>
- Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. *Environ Pollut* 159:1974–1983. <https://doi.org/10.1016/j.envpol.2011.02.022>
- Lapiedra O, Chejanovski Z, Kolbe JJ (2017) Urbanization and biological invasion shape animal personalities. *Glob Change Biol* 23:592–603. <https://doi.org/10.1111/gcb.13395>
- Losos J (2009) *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles* (vol. 10). In: University of California Press
- Losos JB, Irschick DJ (1996) The effect of perch diameter on escape behaviour of *Anolis* lizards : laboratory predictions and field tests. *Anim Behav* 51:593–602. <https://doi.org/10.1006/anbe.1996.0063>

- Losos JB, Sinervo B (1989) The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J Exp Biol* 145:23–30 Retrieved from <http://jeb.biologists.org/content/145/1/23.abstract>
- Lowry H, Lill A, Wong BM (2013) Behavioral responses of wildlife to urban environments. *Biol Rev* 88:537–549. <https://doi.org/10.1111/brv.12012>
- Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: Karieva M, Kingsolver JG, Huey RB (eds) Biotic interactions and global change, pp 234–250
- Marnocha E, Pollinger J, Smith TB (2011) Human-induced morphological shifts in an island lizard. *Evol Appl* 4:388–396. <https://doi.org/10.1111/j.1752-4571.2010.00170.x>
- McDonnell MJ, Hahs AK (2015) Adaptation and adaptedness of organisms to urban environments. *Annu Rev Ecol Evol S* 46:261–280. <https://doi.org/10.1146/annurev-ecolsys-112414-054258>
- McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71:1232–1237. <https://doi.org/10.2307/1938259>
- McDonnell MJ, Pickett STA (1991) Comparative analyses of ecosystems along gradients of urbanization: opportunities and limitations. *Comparative Anal Ecosyst* Springer New York:351–355
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol and Evol* 14:450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- Nemeth E, Brumm H (2009) Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *An Behav* 78:637–641. <https://doi.org/10.1016/j.anbehav.2009.06.016>
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínex-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16:1501–1514. <https://doi.org/10.1111/ele.12187>
- Palumbi SR (2001) Humans as the world's greatest evolutionary force. *Science* 293:1786–1790. <https://doi.org/10.1126/science.293.5536.1786>
- Peaman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. *Trends Ecol Evol* 23:149–158. <https://doi.org/10.1016/j.tree.2007.11.005>
- Penick CA, Savage AM, Dunn RR (2015) Stable isotopes reveal links between human food inputs and urban ant diets. *Proc Royal Soc B* 282:20142608. <https://doi.org/10.1098/rspb.2014.2608>
- Powell, R, Henderson, RW, Adler, K, & Dundee, HA (1996) An annotated checklist of West Indian amphibians and reptiles. *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*, 51–93
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Available at: <http://www.R-project.org/>
- Rodríguez-Robles JA, Leal M, Losos JB (2005) Habitat selection by the Puerto Rican yellow-chinned anole, *Anolis gundlachi*. *Can J Zool* 83:983–988. <https://doi.org/10.1139/Z05-082>
- Salzburg MA (1984) *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. *Ecology* 65:14–19. <https://doi.org/10.2307/1939453>
- Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. *Ecol Lett* 8:241–246. <https://doi.org/10.1111/j.1461-0248.2005.00730.x>
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21:186–191. <https://doi.org/10.1016/j.tree.2005.11.019>
- Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evol Appl* 4:367–387. <https://doi.org/10.1111/j.1752-4571.2010.00166.x>
- Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. *An Behav* 85:1101–1112. <https://doi.org/10.1016/j.anbehav.2013.01.023>
- Thompson JN (2013) *Relentless evolution*. University of Chicago Press, Chicago
- Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a global biological invasion. *PNAS* 111:10233–10238. <https://doi.org/10.1073/pnas.1405766111>
- Weaving MJ, White JG, Isaac B, Rendall AR, Cooke R (2016) Adaptation to urban environments promotes high reproductive success in the tawny frogmouth (*Podargus strigoides*), an endemic nocturnal bird species. *Landscape Urban Plan* 150:87–95. <https://doi.org/10.1016/j.landurbplan.2016.03.001>
- Wilson, LD, & Porras, L (1983) *The ecological impact of man of the South Florida Herpetofauna*. Lawrence: University of Kansas: Museum of Natural History
- Winchell KM, Reynolds RG, Prado-Irwin SR, Puente-Rolón AR, Revell LJ (2016) Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution* 70:1009–1022. <https://doi.org/10.1111/evo.12925>
- Wingfield JC, Kelley JP, Angelier F, Chastel O, Lei F, Lynn SE, et al. (2011) Organism-environment interactions in a changing world: a mechanistic approach. *J of Ornithol* 152:279–288. <https://doi.org/10.1007/s10336-011-0668-3>
- Wright AN (2009) Niche breadth, disturbance specialization, and behavioral flexibility in an invasive lizard, *Anolis sagrei*. PhD dissertation, Department of Biology. In: University of California: Davis, Davis, California