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Behavioral shifts with urbanization may facilitate biological invasion of a widespread lizard

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Abstract

Understanding how novel environmental conditions presented by urbanization affect the ecology and behavior of species is an important component of global change biology. Behavior is the first way in which organisms respond to novel conditions. We investigated differences in habitat use, movement, and social behavior of invasive adult male Cuban brown anoles (*Anolis sagrei*) in natural and urban areas in Miami, FL. We observed that urban lizards used broader perches and frequented more artificial human-made substrates (e.g. walls) than lizards in a natural forest habitat. Extensive behavioral observations (ca. 1200 min) revealed that urban *A. sagrei* also performed more dewlap displays, changed perches less, and jumped less. Our analysis of the structural environment revealed that urban areas are more open – in other words, have higher visibility at typical lizard perch heights, and have fewer and broader perches than natural areas. An increase in openness may explain why we observed a greater than two-fold increase in the frequency of dewlap displaying – the primary mechanism of visual communication in anoles. Similarly, less perch changes and fewer jumps – a form of locomotion frequently used in perch-perch movement when perches are close – is likely driven by a three-fold decrease in tree density. Understanding how behavior and ecology differ in urban vs. natural ecosystems provides insight into how species persist in urban landscapes, and how such behavioral shifts might facilitate biological invasions.

Keywords *Anolis sagrei* · Florida · Urbanization · Invasive species · Behavior · Urban ecology

Introduction

Global urbanization, the human-driven modification of natural habitats, is presenting many species with novel environmental conditions (Marzluff et al. 2001, Shochat et al. 2006, Hasegawa et al. 2014). Typically, the majority of species decline in abundance with urbanization, with some being driven to local extirpation (Kenneth et al. 2005; Kühn and Klotz 2006). However, some species are able to persist, and those that do may exhibit changes in behavior or ecology in response to the new urban environment (Ditchkoff et al. 2006, Sol et al. 2013). Understanding patterns of behavioral and ecological shifts in response to urbanization may provide insights into the source, strength, and direction of selection on many fitness-related traits, and therefore reveal how urbanization may drive contemporary adaptation (reviewed in McDonnell and Hahs 2015). Another facet of global change in the Anthropocene is a widespread increase in the transport and establishment of non-native species (Simberloff and Rejmánek 2011, Helmus et al. 2014). There are many pathways through which non-native species may be introduced, the majority of which are inherently tied to anthropogenic activities (e.g. pet trade release/escape, cargo stowaway, plant nursery trade, etc.; Simberloff and Rejmánek 2011). As such, many non-native species are introduced into areas of human activity and settlement, which can often comprise a matrix of urban and natural habitats. It has been suggested that similar traits may facilitate both invasion into environments outside of a species natural range, as well as invasion into urban areas

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(Rodda and Tyrrell 2008). Therefore, assessments of the behavior of a non-native species in natural vs. urban environments may provide information on both how species are responding to urbanization, as well as understanding how this may facilitate the establishment and spread of invasive species.

Urbanization generally alters the environment in a few key ways (Sol et al. 2013): i) natural vegetation is replaced by man-made structures and becomes increasingly fragmented, ii) human disturbances increase, and iii) ecosystem structure (e.g. competitors/predators/prey) can change dramatically. Those vegetative patches that do remain are often manipulated for aesthetics, which significantly changes the composition of plant species and structural habitat and may actively stifle natural ecological processes (e.g. succession; Niemelä 1999, McKinney 2002). These factors have been observed to drive shifts in various aspects of organismal behavior compared to populations in natural environments (e.g. Nemeth and Brumm 2009; Sol et al. 2013). For example, in Puerto Rico, urban populations of crested anole (*Anolis cristatellus*) have been observed to use broader and warmer perches (Winchell et al. 2016) and take less risks when presented with novel food resources (Chejanovski et al. 2017), compared to those occurring in natural forest environments.

Anolis lizards, a diverse Neotropical genus also known as anoles, represent an ideal system for studying species' responses to urban environments. Extensive knowledge of phenotype-environment relationships of anoles exist as various aspects of behavior, morphology, physiology, and habitat use have been comprehensively studied (reviewed in Losos 2009). Additionally, anoles are known to rapidly shift behavior in response to changes to the abiotic and biotic environment (Losos et al. 1997; Kolbe et al. 2012). This allows many species to thrive in urban environments, where man-made structures are readily used for basking, foraging, displaying, and as refugia (Henderson and Powell 2001; Perry et al. 2008; Meshaka Jr 2011). This has led to an explosion in the study of anoles in urban ecosystems, where the influence of urbanization on performance (Kolbe et al. 2016a; Winchell et al. 2018), ecology (Aviles-Rodriguez 2015; Tyler et al. 2016; Winchell et al. 2016; Battles et al. 2018), dispersal patterns (Kolbe et al. 2016b), personalities (Lapiedra et al. 2017), foraging behavior (Chejanovski et al. 2017), and morphology (Marnocha et al. 2011; Winchell et al. 2016) has attracted recent research interest.

However, understanding how urbanization affects the visual communication system of anoles has previously been overlooked. Anoles are characterized by the presence of a dewlap (i.e. throat-fan; see Fig. 1b) which, when extended and retracted, serves as a primary mechanism for visual communication (Rand and Williams 1970; Leal and Fleishman 2003; Nicholson et al. 2007; Johnson and Wade 2010). Other visual displays such as lateral body presses (pushups) and head-bobs may be performed either independently or in concert with dewlap displays but are often considered secondary mechanisms of communication (Scott 1984; Losos 2009). Dewlap displays, like ornament-driven visual systems in other lizards (Klomp et al. 2016) as well as other taxa (e.g. birds, Prum 2012, 2017; fish, Giery and Layman 2015), are important in intraspecific communication, and are therefore assumed to be central to mediating competitive and social interactions. Dewlap displays, therefore, may influence mate selection and have resulting fitness consequences (Driessens et al. 2013, 2015). The display behavior of anoles may change in response to a number of abiotic and biotic factors. For example, in the presence of a predator, both the rate and amplitude of displays are decreased in an effort to reduce conspicuousness (Simon 2007; Steinberg et al. 2014). This pattern of shifts in display behavior in novel environments has been replicated across many animal species (reviewed in Snell-Rood 2013). Behavioral shifts like these influence the way an animal interacts with its environment, and therefore may change the type of selection pressures that an animal is exposed to (McDonnell and Hahs 2015, Ord et al. 2016).

One major difference between natural vs. urban environments is the degree of structural complexity (Niemelä 1999). Natural environments such as forests are considered to be more structurally complex, or 'cluttered', than their urban counterparts, due to thicker vegetation, a more developed understory, and lack of open space. Due to this, species that persist within urban environments are likely subject to a greater degree of visible distance and scope ('visibility') than those in natural habitats. This aspect of the environment is important for those species which rely heavily on visual communication and has subsequently been observed to influence social behavior in anoles (Butler et al. 2000; Johnson et al. 2010) and other lizards (Stamps 1977), as well as other taxa (e.g. birds, Eason and Stamps 1992; fish, Basquill and Grant 1998).

Changes to the structural environment presented by urbanization may also influence the way animals move about their environment. For example, urban environments are characterized by fewer, broader perching structures (Winchell et al. 2016), which may change the locomotor behaviors displayed by anoles. For example, anoles in complex forest habitats where multiple perches are within jumping distance are more likely to jump than lizards in environments with fewer perches in close proximity (Irschick and Losos 1998). Similarly, jumping tends to occur from narrower perches, as sprint speed – a faster form of locomotion – increases with perch diameter (Irschick and Losos 1998).

In this study, we explore differences in the ecology (microhabitat perch use), movement, and social behavior of invasive Cuban brown anoles (*Anolis sagrei*) in natural-forested and heavily-urbanized environments in Miami, FL USA. Specifically, we collected observational data on microhabitat and thermal microsite use and conducted extensive ethological surveys of focal individuals to assess social and movement behavior rates. Additionally, we conducted detailed quantitative assessments of differences in structural habitat between

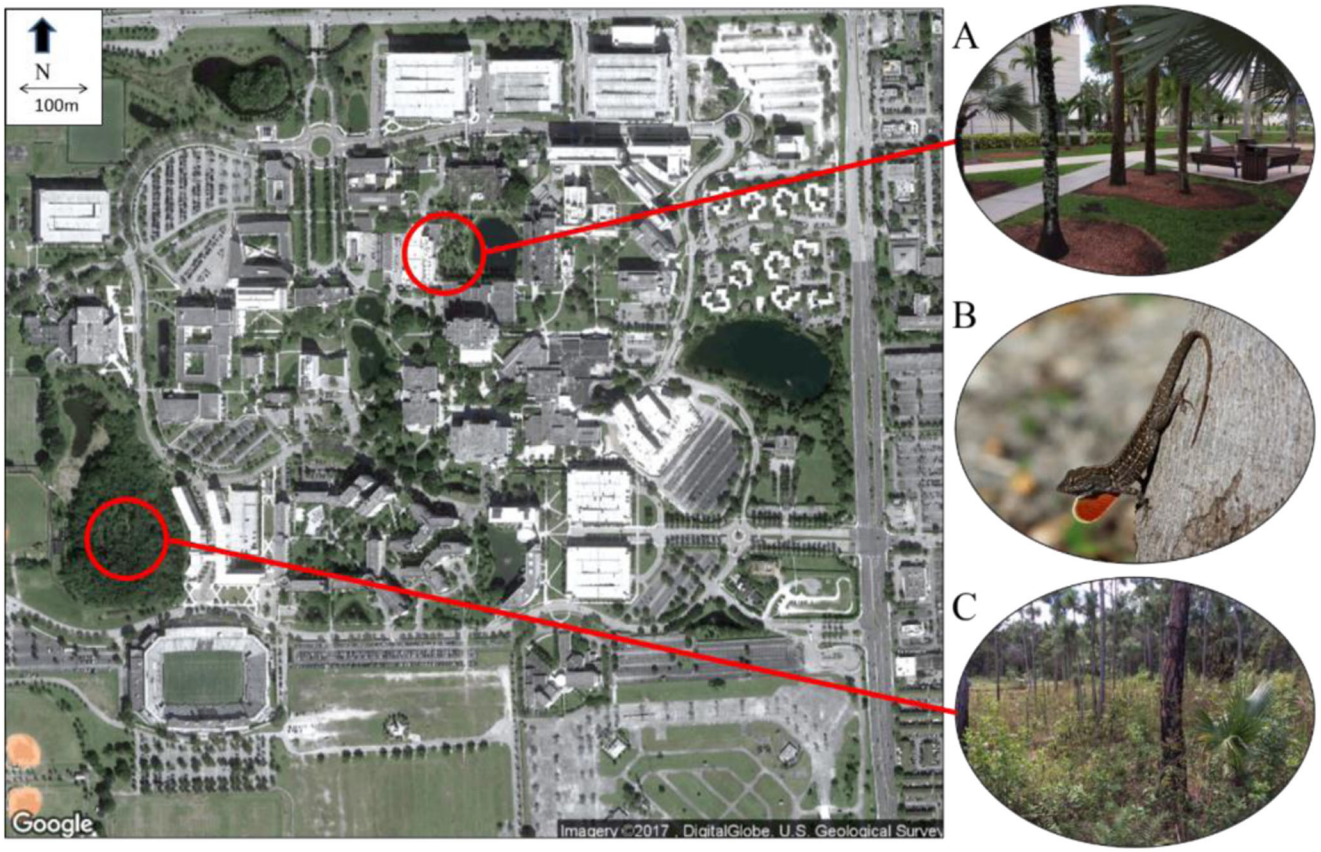

Fig. 1 Aerial view of Florida International University's Modesto el Madique Campus in Miami FL, with the location of the two study sites (Natural and Urban; red circles) where adult male Cuban brown anole behavior was observed. **b** Adult male Cuban brown anole (*A. sagrei*) with fully extended dewlap (throat fan). **a** Urban habitat is characterized by a lack of undergrowth, low tree density, and broader-diameter perches. **c** Natural habitat is characterized by thick undergrowth, high tree density, and thinner perches

urban and natural environments. We predicted that urban environments would differ from natural forest in having fewer trees and a more open understory due to landscaping maintenance, and therefore a higher degree of visibility for anoles. We tested four hypotheses about how urbanization would therefore influence habitat use (i), display behavior (ii), and movement (iii-iv) of *A. sagrei*. Specifically, we predicted that (i) urban lizards would use broader perches than lizards in the forest, and that (ii) urban areas would be more open, leading to increased rates of visual communication displays (i.e. dewlap extensions, head bobs, and pushups) in *A. sagrei.* We also predicted that urban areas would have fewer perches and so *A. sagrei* would be observed to (iii) change perches less frequently, and (iv) jump less frequently – a movement typically used to move between perches in close proximity.

Methods

Species and study site

The Cuban brown anole (*Anolis sagrei*; Fig. 1) is a small, diurnal semi-arboreal lizard endemic to Cuba and the Bahamas. First introduced to south Florida in the 1940s, *A. sagrei* is now well established and continues to rapidly spread, now being found throughout Florida, west to Louisiana and northward into southern Georgia (Parmley 2002; Kolbe et al. 2007). Initial introduction was likely human mediated, with founder populations potentially establishing indirectly via the pet trade or plant nurseries (Kolbe et al. 2007; Losos 2009; Stroud et al. 2017). Many other non-native populations exist both in the USA (Texas and California), the Caribbean (Grand Cayman, Grenada, Barbados, Turks & Caicos, and Jamaica), and in the rest of the world (Hawaii, Taiwan, Costa Rica, and Singapore) (Kolbe et al. 2007, 2017).

We selected two study areas reflecting very different structural environments on a gradient of urbanization. Urban areas (Fig. 1a) were characterized as being surrounded by large buildings, having few trees, with lawn grass, tiled pathways, and other impervious surfaces comprising the majority of the ground. Urban tree species such as royal palm (*Roystonea regia*), paurotis palm (*Acoelorrhaphe wrightii), and coconut palm (Cocos nucifera)* were distributed independently in space, *which is typical of other urban areas in the region. T*he FIU Nature Preserve at FIU MMC was identified as an

un-urbanized "natural" site (Fig. 1c). The preserve is an approximately 40275m^2 area of natural, minimally-managed forest habitat with thick undergrowth. Dominant tree species were slash pine (*Pinus* sp.), live oak (*Quercus* sp.), gumbo limbo (*Bursera simaruba*), wild coffee (*Coffea* sp.) and non-native Brazilian pepper (*Schinus terebinthifolia*). Several other lizard species are present in the study areas, including American green anoles (*Anolis carolinensis*), Hispaniolan bark anoles (*Anolis distichus*), Cuban knight anoles (*Anolis equestris*) and African house geckos (*Hemidactylus mabouia*). All lizard species are found across both habitat types.

Microhabitat use and behavioral assessments

Microhabitat (perch) use of *A. sagrei* of both sexes was collected haphazardly from 10/01/13–05/12/14. Specifically, the height (from ground), diameter, and type (e.g. tree trunk, branch, rock) of perching substrate was recorded, as well as a categorical assessment of basking behavior – i.e., if the lizard was in the shade (0% Sun), filtered sun (>50% shade) or full sun (<50% shade). These are common parameters of ecological importance for *Anolis* lizards (reviewed in Losos 2009). These data were collected during the same study period as the ethological sampling but not while any ethological surveys were being conducted.

Ethograms were conducted from 10/14/13–05/12/14 at Florida International University's Modesto Madique Campus (FIU MMC), Miami FL, USA (lat: 25.758, long: −80.376). This constitutes the non-reproductive season of *A. sagrei* in Miami (Lee et al. 1989). Urban ethograms were conducted in heavily urbanized areas within the FIU campus, where vegetation was well-maintained by landscapers. No urban surveys were conducted within 500 m of the nature preserve to minimize the opportunity of observing the same individual in both treatments. All "natural" ethological surveys were performed a minimum of 25 m inside the Nature Preserve from the nearest edge.

Each ethogram was constructed to record observed behaviors of a single male lizard during 20 min of continuous focal animal sampling, a period generally agreed to accurately reflect population level patterns of social and movement behavior (Johnson et al. 2010; Johnson and Wade 2010; Baeckens et al. 2018). Male *A. sagrei* were chosen for focal observation in this study as they are abundant, easy to identify and observe, and have high display rates and associated social behaviors compared to both female conspecifics and other sympatric anole species (Scott 1984; Driessens et al. 2013). A suite of behaviors were recorded, focusing primarily on quantification of display (e.g. dewlap extensions, head bob, push-ups) and movement behaviors (e.g. perch changes, jump, run, crawl). A pushup was described as a single up and down torso movement and a head-bob was defined as a single up and down head movement (as in Edwards and Lailvaux 2012), however push-ups and head bobs were ultimately combined into one category as the two behaviors can be difficult to distinguish in the field. Observations of foraging and copulatory activity were also recorded. To account for temporal bias during data collection, sampling was stratified into morning (0800-1100 h) and afternoon (1300-1600 h) sampling sessions.

Observation starting time, location, position of the lizard (e.g., on trunk or rock), and site (natural or urban) was recorded for each sampling event. All ethological data were collected by a single observer (MC) to account for observer acuity. A minimum distance of 4 m from the lizard was maintained during all ethological sampling sessions. Preliminary observations suggested that this was a suitable distance to confidently minimize observer presence bias on lizard behavior (JS *pers. obs.*). If visibility of focal lizards was lost (due to lizard movement), the observer would carefully move location to allow for continuation of data collection. Sampling sessions <10 min (due to loss of lizard sight) were disregarded from final analyses. Interspecific and intraspecific interactions were both observed during this study. Although observations were not described quantitatively, adult male *A. sagrei* did not perform any display behaviors to any other species of lizard, inclusive of all sex, age and size classes. Only one copulation event was observed in ~1200mins of observations. Copulations were, therefore, not included in the final analyses.

Structural habitat assessments

To assess differences in structural habitat between urban and natural treatments, we established random 5 × 5 m quadrats ($n = 20$ per treatment). Within these quadrats we recorded the number of woody-stemmed plants >1 m tall (hereafter trees), the diameter at breast height (DBH; 1.3 m) of all of these trees, and measured visibility by quantifying the complexity of structural vegetation. To measure visibility, we used a 1 m long (5 cm thick) white plastic tube with black lines drawn with a Sharpie pen every 2 cm ($n = 50$ lines). One surveyor would stand on one side of the quadrat while the other stood facing them on the opposite side. The visibility pole was held horizontally at six different heights from the ground (0.25, 0.5, 0.75, 1.0, 1.25, and 1.5 m) and the opposite surveyor would record the number of black bars they could see without obstruction from any vegetation. This value was then doubled to give a percentage visibility (%) score. This process was repeated twice (from both directions across the quadrat, therefore $n =$ 240 visibility assessments conducted per treatment, total $N =$ 480) and the values for each height averaged per quadrat.

Statistical analyses

We calculated rates of all observed behaviors by correcting for time (frequency of behavior divided by time in minutes) as

sampling length varied, and then transformed by log+1 to conform to normality. Initially, a multivariate analysis of variance (MANOVA) was conducted to test for significant differences in multivariate behavior between sampling time (AM vs. PM) and habitat type (natural vs. urban). If significant, further univariate analyses (ANOVA) were performed to assess differences between individual variables. Perch heights and diameters were log transformed to achieve normality. Unpaired t-tests were used to compare mean perch heights and diameters between habitat types for *A. sagrei* (all age and sex classes combined), as well as adult male *A. sagrei* specifically. Additionally, Kolmogorov-Smirnov tests were used to determine if perch height and diameter distributions were different between habitat types. To determine whether lizards used different perching substrates (e.g. tree trunk, branch, rock, wall) between natural and urban areas we used Pearson's Chi-squared (χ^2) test.

To test for overall differences in available structural habitat between natural vs. urban areas we used multivariate analysis of variance (MANOVA) on log+1 transformed data. Further univariate analyses (ANOVA) for each habitat variable were conducted if the initial MANOVA was significant. All statistical analyses were conducted in R version 3.02 (R Core Team 2013) using R-Studio 0.99.483 (RStudio Team 2015).

Results

Microhabitat use

The perch use characteristics of a total of 412 *A. sagrei* of both sexes in natural forest and urban environments were recorded in this study. We observed that urban *A. sagrei* used significantly broader diameter perches ($N = 199$, mean = 32 cm, S.E. = 0.02) than forest lizards ($N = 213$, mean = 10 cm, S.E. = 0.07; $t = -14.42$, $df = 356$, $p < 0.0001$) (Fig. 2). This pattern was also true for adult male *A. sagrei* specifically, which perched on significantly broader diameter perches ($n = 61$, mean = 26 cm) than those in the forest ($n = 46$, mean = 12 cm; $t = -5.06$, $df = 94.23$, $p < 0.0001$). There was also a significant difference in the distributions of perch diameter selection for all lizards (D = 0.612, $p < 0.0001$) and for adult males specifically (D = 0.488, $p < 0.0001$), with median perch diameter being larger in urban lizards for both analyses. However, we recorded no significant difference in perch height use of adult male *A. sagrei* ($t = -0.71$, $df = 97$, $p = 0.48$) in forest (mean = 65 cm, $n = 153$) vs. urban (mean = 68 cm, $n = 143$) environments, which was also observed when all lizards were pooled ($t = -1.74$, $df = 373$, $p = 0.083$);. Similarly, there was no significant difference in the distributions of perch heights for all lizards ($D = 0.117$, $p = 0.118$) or only adult males ($D = 0.156$, $p = 0.551$).

There were significant differences in types of perches used between natural and urban lizards ($\chi^2 = 60.67$, $df = 5$, $p < 0.0001$; Fig. 3) – urban lizards perched more frequently on walls and tree trunks and less frequently on branches and rocks compared to forest lizards – but there were no differences in thermal microsite selection ($\chi^2 = 0.07$, $df = 2$, $p = 0.967$; Fig. 4). This pattern was true also for adult males specifically; there was a significant difference in perch substrate ($\chi^2 = 47.51$, $df = 4$, $p < 0.0001$) and also did not differ in thermal microsite selection ($\chi^2 = 2.02$, $df = 2$, $p = 0.364$) between natural and urban environments.

Structural habitat

There were significant differences in habitat structure in forest vs. urban sites (Pillai's Trace = 0.463, F = 2.7, $df = (1,32)$, $p = 0.027$). Univariate F tests (Table 1) revealed that natural forest habitat had significantly higher tree density, whereas urban areas had significantly larger (broader) trees (Table 1). There was a significant difference in perceived levels of visibility between natural forest vs. urban habitats at all sites up to 1 m, although there were no significant differences above that height i.e. at 1.25 m and 1.5 m above the ground; Table 1 and Fig. 5).

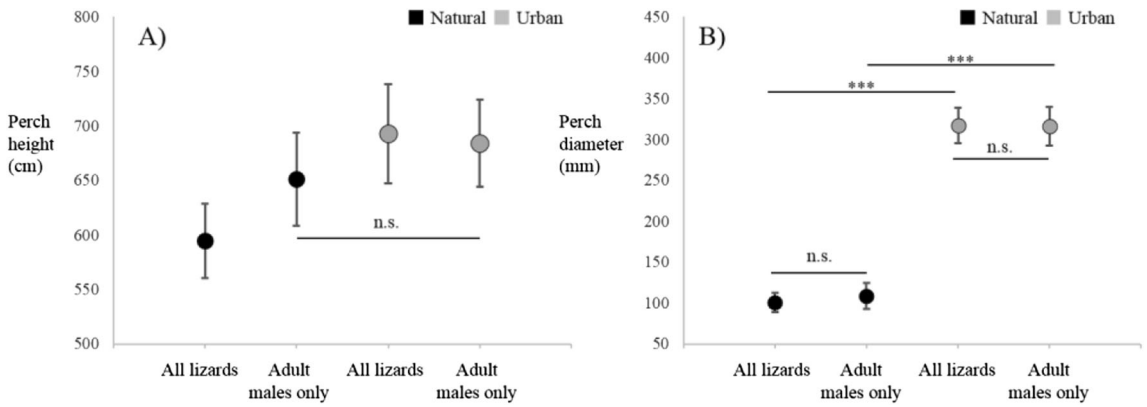

Fig. 2 Perch height and diameter (mean ± 1 S.E.) selection in natural (black) and urban (grey) habitats; data are presented for all sexes and age classes pooled (All lizards) and adult males only

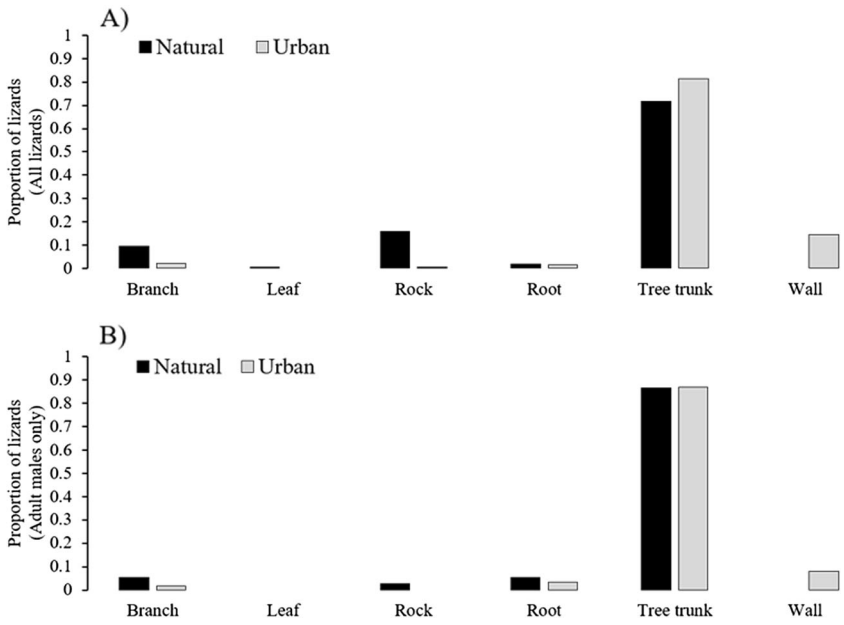

Fig. 3 Microhabitat substrate use of *A. sagrei* in natural (black) vs. urban (gray) habitats of all age and sex class combined (**a**) and only adult males (**b**)

Social and movement behavior

Ethological assessments of focal individuals were conducted in urban ($n = 30$) and natural forest ($n = 30$) habitats, resulting in cumulative observation times of 601 and 599 mins respectively and mean survey lengths of 20.03mins (Urban; 18–21 min) and 19.59 mins (Natural; 12–29 min). There were no significant differences in multivariate behavior between individuals observed in the morning and afternoon (Pillai's Trace = 0.159, $F = 1.202$, $df = (1,58)$, $p = 0.317$), so morning and afternoon observations were subsequently pooled for analysis. There was a significant difference in the movement and social behavior of adult male *A. sagrei* between natural and urban habitats (Table 2; Pillai's Trace = 0.308, $F = 2.83$, $df = (1,58)$, $p = 0.011$). Specifically, anoles in urban habitats performed significantly more dewlap displays than those in natural forest ($F = 4.39$, $df = (1,58)$, $p = 0.04$). Urban lizards also changed perches less ($F = 7.50$, $df = (1,58)$, $p < 0.01$) and jumped less ($F = 8.02$, $df = (1,58)$, $p < 0.01$; Table 2) compared to lizards in natural areas.

Discussion

Understanding how behavior may change in response to novel environmental conditions, such as those presented to species through urbanization or to a non-native species introduced to a new area, is an important component of global change

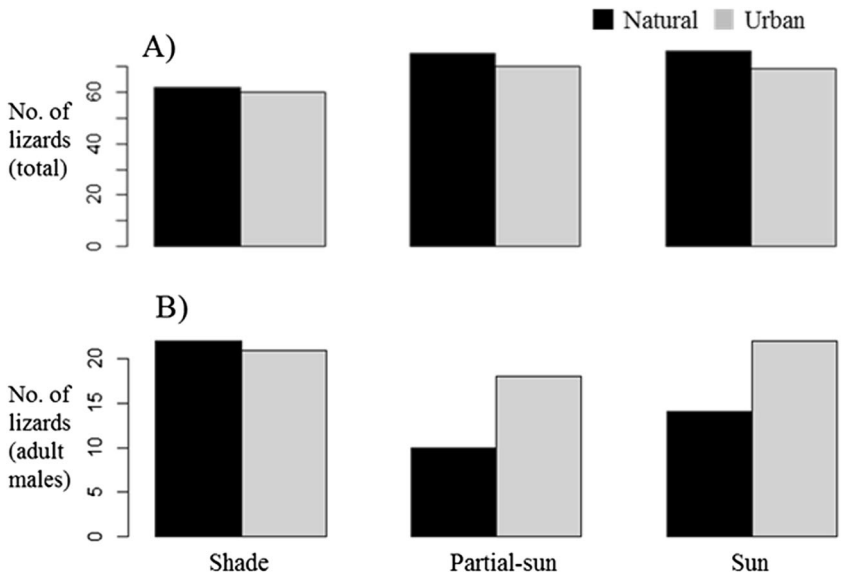

Fig. 4 Thermal microsite use of *A. sagrei* in urban (black) vs. natural (grey) habitats of all age and sex classes (**a**) and only adult males (**b**)

Table 1 Univariate *F* tests of structural habitat characteristics of urban vs. natural areas surveyed in this study

Habitat variable	Treatment	Mean	St. Dev	df	*F*	*p* value	
Tree density (no. trees/m^2)	Natural	0.19	0.19	1,32	15.30	**<0.001**	***
	Urban	0.06	0.04				
Tree diameter (cm)	Natural	6.53	7.32	1,32	12.45	**<0.005**	**
	Urban	20.37	17.61				
Visibility @ 0.25 m (%)	Natural	17.05	18.88	1,32	15.55	**<0.001**	***
	Urban	31.89	16.11				
Visibility @ 0.50 m (%)	Natural	18.58	18.16	1,32	10.89	**<0.005**	**
	Urban	31.39	16.54				
Visibility @ 0.75 m (%)	Natural	19.55	18.01	1,32	9.46	**<0.005**	**
	Urban	31.29	17.23				
Visibility @ 1.00 m (%)	Natural	21.98	16.25	1,32	5.17	**0.029**	*
	Urban	32.50	18.96				
Visibility @ 1.25 m (%)	Natural	24.93	13.32	1,32	0.62	0.438	
	Urban	30.61	19.87				
Visibility @ 1.50 m (%)	Natural	26.53	13.90	1,32	0.11	0.737	
	Urban	29.82	21.45				

All significant differences between treatments are highlighted in bold

biology. Here we contribute to our understanding of how urbanization may influence global biodiversity by documenting divergence in habitat use, movement, and social behavior of a widespread invasive lizard, the Cuban brown anole (*A. sagrei*). Specifically, lizards found in urban environments moved less frequently around their habitat than lizards in natural environments but had a significantly higher rate of visual displays (i.e. dewlap extensions). The structural habitat experienced by *A. sagrei* was significantly different between study areas and was characterized by urban areas having fewer, but much broader, trees, and an almost absent understory allowing for greater visibility (Table 1).

These results provide both support to other studies of urban *Anolis* ecology, and in Miami specifically, as well as offering novel insights into how urbanization is affecting anole biology. The differences we observed in the structural environment of urban areas compared to natural forest may explain our observed support for our social hypothesis of urbanization; a greater visibility in urban areas due to a less complex understory resulted in an elevated rate of visual communicative displays in anoles. Support for this relationship between dewlap displays in anoles and structural habitat complexity, i.e. visibility, has been suggested before (Johnson et al. 2010), although only in the frame of differences between forest types.

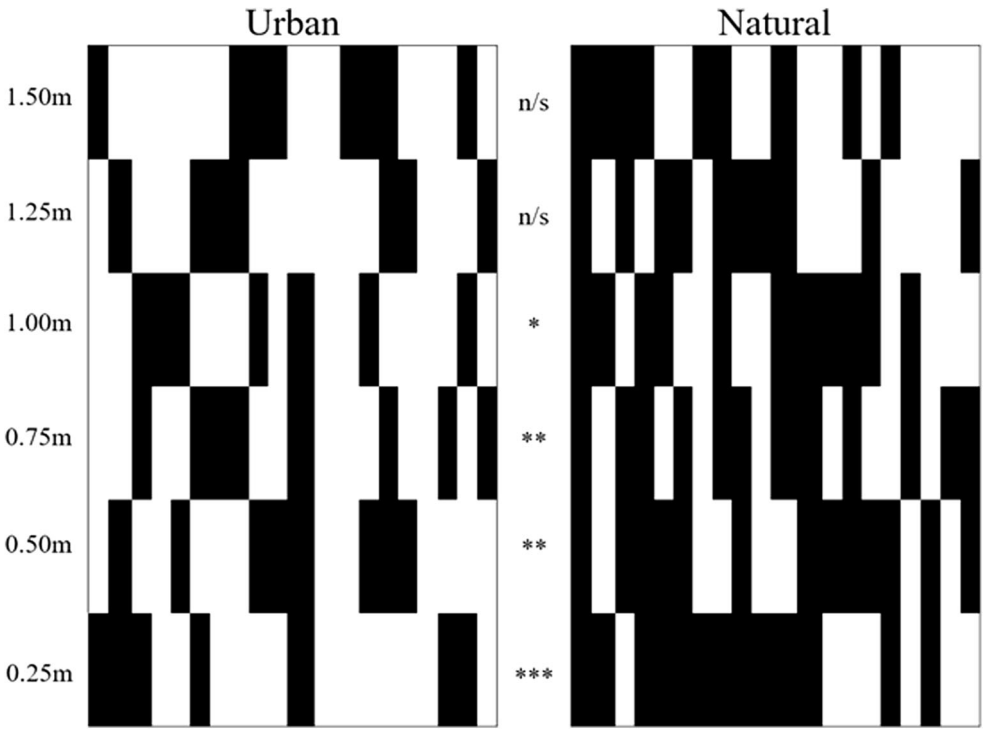

Fig. 5 A representation of differences in habitat complexity, and therefore apparent visibility, between urban and natural environments. Black squares indicate visible obstruction, white squares indicate no visible obstruction. Grid layout was calculated from a random sequence generator using mean values for each height (see Table 2 for full details), and therefore is likely more random than realistic in pattern. Significant differences in visibility at each height are shown as follows n/s not significant, *$p < 0.05$, **$p < 0.005$, ***$p < 0.001$

Table 2 Time-corrected frequencies of movement, display and foraging behaviors of adult male Cuban brown anoles (*A. sagrei*) during timed ethological surveys

	1. Dewlap extensions	2. Push-ups/headbobs	3. Perch changes	4. Run	5. Crawl	6. Jump	7. Eat
Natural ($N = 30$)	7.50	25.47	2.67	1.23	4.80	2.47	0.63
(St. Err)	(1.40)	(5.45)	(0.44)	(0.27)	(0.68)	(0.36)	(0.21)
Urban ($N = 30$)	15.97	35.10	1.20	1.80	7.10	1.13	0.40
(St. Err)	(3.79)	(6.00)	(0.31)	(0.36)	(1.26)	(0.30)	(0.15)
Univariate *F* tests							
df	1,58	1,58	1,58	1,58	1,58	1,58	1,58
F-value	4.40	1.41	7.50	1.59	2.57	8.02	0.81
p value	**0.040***	0.240	**0.008****	0.213	0.114	**0.006****	0.371

There was a significant difference in multivariate behavior between Natural and Urban treatments (MANOVA; $p < 0.05$); subsequent univariate *F*-tests (above) revealed anoles significantly increased rates of (1.) dewlap extension displays, and significantly decreased rates of (3.) perch change and (6.) jumping

Our results suggest that this visibility-display relationship may be extended to forest-urban environmental comparisons, which are much more extreme than variations between forest types. Through this change in the vegetative environment, urban areas may increase both the distance that a signal can be broadcasted, as well as increasing its efficacy to individuals within close proximity.

Adult male anoles perform dewlap displays for a variety of biotic reasons, although its primary purpose is generally accepted to be for intraspecific communication (reviewed in Losos 2009); for example, to mediate agonistic interactions, as well as to display to potential mates (Scott 1984; Losos 2009). The higher rate of dewlap displays we observed in urban *A. sagrei* therefore suggests that urban lizards may be experiencing a higher rate of intraspecific visual interactions. In *A. sagrei*, rates of dewlap displays by adult males have been observed to be higher in courtship displays towards potential mates (i.e. mature females) than in agonistic interactions with other males (Simon 2007), suggesting an increased level of heterosexual interaction in urban environments. Alternatively, display rates might increase as a result of lizards feeling more exposed due to the lack of structural habitat complexity (i.e. an increase in "openness"), rather than a direct increase in visual conspecific interactions.

Divergence in dewlap display rate could also be due to other biotic factors, such as interspecific interactions or predator deterrence. However, the composition of the biotic community did not differ between our study sites, and no urban *A. sagrei* in our focal observations was ever observed performing directed dewlap displays at a heterospecific *Anolis*. Similarly, we did not observe significant differences in the rates of other (secondary) forms of visual communication, such as head-bobs and push-ups, between urban and forest lizards. Head-bob display rates in *A. sagrei* have been observed to decrease with increasing predation pressure (Steinberg et al. 2014), suggesting that anoles in this study may not have experienced (or perceived) differences in predator encounter rates (there were no significant difference in head-bob display rates; Table 2), despite urban areas being frequently associated with increased predation (Fischer et al. 2012).

We observed no difference in mean perch height of *A. sagrei* between urban and natural habitats. This observation supports those of Kolbe et al. (2016b), who observed that perch heights of *A. sagrei* vary little across different habitat types in the Miami metropolitan area, and Winchell et al. (2016) who observed no difference in perch height of *Anolis cristatellus* – an ecomorphologically similar species to *A. sagrei* – in urban vs. natural habitats in Puerto Rico. However, while perch height remained consistent across habitat types in our study, urban lizards were found on significantly broader perches. This is likely due to urban areas having generally broader perches than natural forest (Table 1), such as palm trunks and man-made surfaces (e.g. walls; Fig. 3). An increase in mean perch diameter was also observed in urban populations of *A. sagrei* in the Exumas (Marnocha et al. 2011), as well as in Puerto Rican *A. cristatellus* (Winchell et al. 2016). We did not, however, observe any differences in patterns of thermal microsite use in natural vs. urban lizards, despite other studies finding urban anoles are frequently hotter than those occurring in forest habitat (Battles 2018; Battles and Kolbe 2018). There are two reasons why we may have observed this pattern; (i) despite urban areas being less structurally complex and therefore lizards may be exposed to more solar radiation, lizards may have behaviorally managed thermal exposure to maintain preferred internal body temperature (i.e. thermoregulatory behavior), or (ii) our qualitative assessment of thermal biology was not accurate enough to identify differences in the thermal biology of these populations, a more detailed approach (e.g. internal body temperature, as in Gunderson and Leal 2015) may have elucidated different and more cryptic patterns.

In addition to differences in dewlap displays and perch use, we also observed differences in movement behavior between urban and natural sites. Lizards in urban sites jumped less and changed perches less than lizards in natural areas. Jumping in anoles is often most frequently used when individuals are

either on a narrow perch, have multiple perches within jumping distance, or both (Irschick and Losos 1998). Urban anoles in this study more frequently used perches that were broader and more isolated than those in natural environments, therefore providing one possible explanation for the lower rates of jumping we observed. Similarly, a decreased frequency of jumping may be explained by the absence of a complex understory into which lizards may jump into as natural refugia during safety retreats, for example from approaching predators. Other studies have highlighted differences in predator avoidance behavior in urban anoles. Urban anoles; for example, have shorter flight initiation distances (FID) – the distance at which an approaching 'predator' would provoke the anole to move out of sight. Additionally, urban anoles are more likely to exhibit 'squirreling' behavior – shifting to the other side of the same perch and out of view of a predator – than to jump and change perches (Blamires 1999; Aviles-Rodriguez 2015). However, this shift in squirreling behavior may simply be an effect of perch use; squirreling on narrow perches, such as those used in forests, is unlikely to result in a lizard being visually hidden from the approaching predator. The degree to which anoles respond to a perceived predator by shortening its FID is likely due to habituation of visual interactions with many perceived 'predators'. A shorter FID by urban lizards may indicate increased 'boldness', which could represent a selective advantage for animals in urban areas, allowing them better feeding opportunities in the presence of humans (i.e. perceived predators) that may pose little actual threat (Greenberg and Mettke-Hofmann 2001, Greggor et al. 2016; although see Lapiedra et al. 2017).

The ability of *A. sagrei* to persist in a range of different habitat types could be an important factor explaining its successful establishment in multiple non-native locations around the world. Our findings in this study suggest that by diverging in its behavior, *A. sagrei* is capable of responding to changes in the environment, such as those experienced when introduced to a new location or when an area undergoes urbanization. Understanding how urbanization influences changes in behavior of species may, therefore, also lead to a better understanding of why some species are more likely to become invasive than others. This synthesis could be extremely powerful as human-induced global changes continues to advance.

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