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Escape in the city: urbanization alters the escape behavior of *Anolis* lizards

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Abstract

Behavioral adjustments may allow organisms to cope with the drastic environmental change caused by urbanization. We compared the escape behavior of *Anolis* lizards during simulated predator approaches on trees in both urban and forest habitats and on artificial structures (i.e., cement walls and metal posts) in urban areas. We found that urban lizards were less wary on trees, likely due at least in part to habituation to humans. In contrast, lizards on cement walls showed greater wariness, which may reflect a behavioral modification when escaping because of poor locomotor performance on this substrate. In both habitats, lizards modulated escape responses in ways consistent with their performance abilities on the various substrates. Escape by jumping decreased when lizards used wider and more isolated perches, which are characteristic of urban sites. Urban lizards squirreled (i.e., moved to the opposite side of a structure) more on wider trees and metal posts, and sprinted more but never jumped from cement walls. These behavioral responses for predator escape are consistent with the structural habitat changes caused by urbanization. Urban habitats had larger diameter trees, sparser ground vegetation, and many artificial structures. We found that urban lizards showed behavioral modulations because of exposure to humans as well as the locomotor constraints of using some artificial structures, such as cement walls. The ability of urban lizards to alter their escape responses and adjust to novel features of the habitat may be important traits of species able to colonize and persist in urban areas.

Keywords *Anolis cristatellus* · Anole · Artificial substrates · Habituation · Flight-initiation distance · Structural habitat

Introduction

Urbanization is one of the most dramatic forms of habitat alteration and disturbance, affecting patterns of species diversity, abundance, and distribution (Shochat et al. 2006; Seto et al. 2012; Ramalho and Hobbs 2012; Forman 2014). The replacement of natural vegetation with buildings, roads, and other artificial structures, leads to urban habitats having generally more open canopies and less complex ground vegetation than natural habitats (Prosser et al. 2006; Uno et al. 2010; Le Roux et al. 2014; Battles et al. 2018). Moreover, urban

parks and yards typically consist of widely spaced mature trees and mowed lawns. A unique feature of urban habitats is the addition of many artificial structures, such as cement walls, wood fences, and metal posts, which may be used as substrate by animals. The structural habitat in cities can have a variety of consequences, yet we know very little about the mechanistic link between habitat modification and its effects on behavior, habitat selection, and performance of animals living in urban areas (Shochat et al. 2006; Sol et al. 2013; Alberti 2015; Kolbe et al. 2016). This is a critically important issue as it directly influences whether or not a species can persist in a city. Urbanization affects habitats in similar ways around the world (McKinney 2006; Hufbauer et al. 2012), thus investigating the mechanisms by which organisms respond to habitat alterations in cities has general importance for interpreting global patterns of species diversity and abundance (Shochat et al. 2006; Sol et al. 2013; Huang et al. 2014; Müller et al. 2014).

Predator escape is one of the most important aspects of behavior because the ability to successfully avoid a predator greatly impacts future fitness (Lima and Dill 1990). To survive in the presence of predators, prey must be able to assess risk

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quickly and adjust escape behavior according to current risk levels (Cooper 2006a). Escape theory predicts that when a predator approaches, the prey should monitor the predator's approach and flee when the fitness cost of not fleeing, due to predation risk, equals the cost of escaping, which includes the loss of opportunities to feed, mate and defend territories (Ydenberg and Dill 1986; Cooper and Whiting 2007; Peckarsky et al. 2008). In urban areas, animals may learn to adjust their escape response to the increase in human activity, which may reduce the costs of wasteful flight effort and maximize resource acquisition time (Oosten et al. 2010; Rodríguez-Prieto et al. 2010).

Anolis lizards, or anoles, are an excellent study system to test hypotheses that address the effect of novel substrates and human activity on escape behavior. Anoles assess risk and adjust their escape responses with increased wariness when predators approach faster (Cooper 2006a), when they are perched in more conspicuous areas (Cooper 2006b) and when there is less human activity (Cooper 2010). Many anole species live in both forest and urban habitats (Kolbe et al. 2016; Winchell et al. 2016), often in close proximity, facilitating the comparison of behavior between anoles in these habitats.

In this study, we evaluated how urbanization alters structural habitats and whether these differences influenced the escape responses of the Crested Anole, *Anolis cristatellus*. Urban escape responses may vary due to differences at both the habitat patch scale (i.e., natural forest v. urban areas) and the local scale within urban sites (i.e., natural v. artificial substrates). Lizards in urban areas are predicted to respond with reduced wariness if predation risk is lower (Cooper 2010) and if they are tolerant to the presence of humans (Cooper 2010; Blumstein 2016). We also evaluated whether perching on artificial structures influences escape responses by comparing lizards using natural (i.e., tree trunks) and artificial (i.e., metal posts and cement walls) structures in the urban habitat. Lizard locomotor performance depends on the properties of the substrates they use, resulting in a trade-off between speed and stability (Spezzano and Jayne 2004; Higham et al. 2010; Kolbe et al. 2016; Winchell et al. 2018), which may influence when and how they escape. For artificial structures, we predicted increased wariness for lizards as a consequence of their decreased locomotor performance on these substrates (Foster et al. 2015), which tend to have smoother and more vertical surfaces resulting in decreased speed and stability for lizards (Kolbe et al. 2016; Winchell et al. 2018). We also predicted that escape mode will differ based on the properties of the substrate used by lizards. For example, in general, lizards should jump more often when occupying narrow diameter vegetation, predicted to be more common in natural habitats, but sprint more on broader diameter substrates characteristic of urban areas (Losos and Irschick 1996; Battles et al. 2018). Lastly, we characterized how two dimensions of the structural

habitat (i.e., perch diameter and number of nearby perches) influenced the escape tactics used by lizards. We also contrasted the vegetation available and used by lizards for perching in natural forests and urban sites to quantify the effects of urbanization. Our study evaluates how multiple factors (i.e., urbanization and substrate variation) influence the way lizards adjust to novel habitats and novel features in their environments. Specifically, urban lizards may increase fitness through behavioral adjustment of escape strategies by both habituating to humans and adjusting escape responses towards more stable locomotion on artificial substrates.

Materials and methods

Study sites

We collected data in May–June 2014 in the native range of *A. cristatellus* in San Juan, Puerto Rico and in June–July 2015 in Miami, Florida where this species has established non-native populations (Kolbe et al. 2016). In both regions, we sampled populations from forest and urban habitats that were < 1 km apart. In San Juan, the urban site (18°24′12.8"N, 66°02′33.0"W) was the faculty-housing complex at the University of Puerto Rico, Rio Piedras. This residential area had large open areas dominated by mowed grass and widely spaced, large diameter trees. Most green space was within 10 m of sidewalks and houses. This site had frequent movement of humans, both on foot and by car, and the presence of domestic cats and ground lizards (*Ameiva exsul*), which are potential anole predators. The natural forest site (hereafter forest site; 18°23′02.7"N, 66°02′32.8"W) was a secondary forest in an urban park, the Bosque del Nuevo Milenio. This site was characterized by a dense overstory canopy and understory of various sized trees with leaf litter covering most of the ground. No domestic animals, ground lizards, or humans were observed at the forest site during our study. Lizards were sampled at least 10 m from the forest edge. In Miami, the urban site (25°41′6.3"N, 80°17′4.9"W) was a residential area with houses, fences, roads, schools, walls and an asphalt sidewalk along a canal that was frequently used by people to walk, run, and bike. Grassy areas and widely spaced, large diameter trees were common along the path and in yards. Brown basilisks (*Basiliscus vittatus*), a potential anole predator, were present at this site and found primarily on the ground. The forest site (25°40′36.4"N, 80°15′46.0"W) was located in Matheson Hammock Park and was characterized by a dense overstory canopy with trees of various sizes. We observed people using trails in the forest and therefore sampled lizards at least 20 m away from any trails, with the exception of a subset of lizards specifically sampled at increasing distances from the trail to test for habituation.

Escape distances and habituation

We evaluated the escape behavior of lizards in both forest and urban sites in San Juan and Miami using a standardized protocol. After identifying a lizard perched on a tree trunk or artificial substrate, one researcher (KAR) wearing the same color clothing for all trials approached the lizard at a constant walking speed with an outstretched hand (Cooper 2009). This method of using humans as surrogate predators has been used to study anti-predator responses of a variety of vertebrate taxa, including lizards, birds, and mammals (e.g., Cooper 2006a, b; McCleery 2009; Blumstein 2014; Samia et al. 2015). To avoid re-sampling the same lizards, we followed a unique path through the habitat at each visit. Following Cooper (2005), we measured flight-initiation distance (FID; the distance at which anoles initiate escape), and flight distance (FD; the distance they flee). In pilot trials, we found no difference in FID between a novel threat (i.e., an umbrella modified with large eyes and a gaping mouth) and a human (ANOVA: $F_{1,74} = 0.224$, $P < 0.64$). We therefore used an approaching human.

Body temperature influences the behavior and performance of lizards (Angilletta 2009) and may differ between habitat types. We therefore wanted to account for lizard body temperature variation in our analyses; however, our protocol caused lizards to flee, making them more difficult to capture and potentially altering their initial body temperatures. To estimate lizard body temperatures, we measured the temperature of a copper lizard model fitted with a thermocouple (Hertz 1992) placed at the exact location of the focal lizard immediately after its escape.

To assess whether habituation to humans might influence lizard escape distances, we measured FID for lizards at increasing distances away from a sidewalk or trail. We followed the same methods for measuring FID as stated above for an independent set of lizards at the forest and urban sites in Miami. For each of these trials, we measured the distance of the lizard from the sidewalk at the urban site and the trail at the forest site. This provided a quantitative proxy for exposure to humans. We also counted the number of people using the sidewalk and trail to calculate a human activity rate for each site.

Escape mode and structural habitats

We recorded the escape mode used by lizards, which included squirreling (i.e., moving around the perch and breaking the line of sight with the observer), jumping, and sprinting (Regalado 1998). We evaluated the effect of the structural habitat on escape modes by quantifying the frequency of escape modes used by lizards perched on urban and forest trees and metal posts and cement walls in urban sites. To evaluate

the effect of the structural habitat on the escape mode, we recorded the perch diameter and number of nearby perches for every lizard sampled.

We characterized structural habitat differences between our forest and urban sites by quantifying the availability of key habitat variables along three 20 m long transects within each site. We focused on vegetation diameter and vegetation density because of their importance to lizard locomotion (Pounds 1988; Losos and Irschick 1996). Every 2 m along each transect, we measured vegetation diameters at 0.25 m height increments up to 2 m and counted the number of potential perches (hereafter "number of nearby perches") within a 0.5 m radius. Nearby perches included any substrate sturdy enough to hold a lizard's body weight. Counts of nearby perches maximized unique escape routes lizards could take by jumping to any given perch within the 0.5 m radius. To evaluate structural habitat use by lizards at each site, we measured the perch height, perch diameter, and number of nearby perches for each undisturbed lizard encountered. We quantified the habitat openness in two ways. First, we took hemispherical canopy photographs using a 180° fisheye lens every 3 m along a 30 m transect. We then used GIMP 2 to calculate the percent canopy openness by dividing the area of open sky by the total area (Chianucci et al. 2015). Second, we quantified the percent ground openness by dividing the number of transect points with no vegetation present by the total number of points.

Data analysis

To meet the assumption of normality for ANOVAs, we log transformed FID and FD, adding one to each value before transforming. We used linear regressions to screen for relationships between either FID or FD and estimated lizard body temperatures and perch height. Because FID and FD were related to lizard body temperatures, we used analysis of covariance (ANCOVA) with substrate, perch height, and their interaction as factors and body temperature as a covariate. The final model for FID included substrate, body temperature, and perch height as factors. We used Tukey's Honestly Significant Difference (HSD) post hoc tests to determine which factor levels differed significantly when the overall ANCOVA was significant. We found no significant covariates for FD and therefore used ANOVA to test for differences in FD among substrate types. We investigated the relationship between distance from the sidewalk or trail and FID using linear regressions.

We tested for a difference in the proportion of the three escape modes used for the four substrates using contingency tables. We assessed the overall significance as well as each pairwise contrast between substrates with chi-squared tests. We used multinomial logistic regressions to determine if the

probability of using each escape mode differed with increasing substrate diameter or number of nearby perches. Cement walls were not included in analyses using diameter because no appropriate diameter could be measured on this surface. Separate analyses were conducted for forest and urban sites.

We tested for differences in the two aspects of the structural habitat, vegetation diameter and the number of nearby perches, using three-factor analyses of variance (ANOVAs) with region (San Juan/Miami), site (forest/urban), resource (availability/use by lizards) and their interactions as factors. We used a two-factor ANOVA with site and region to test for differences between percent canopy openness. We tested for differences in ground openness using a generalized linear model with a binomial distribution with factors for site, region, and the site by region interaction. We assessed differences in habitat use by lizards for perch diameter, number of nearby perches, perch height, and estimated lizard body temperature using two-way ANOVAs with region and substrate factors. Preliminary analyses showed structural habitat availability and use by lizards differed substantially between forest and urban sites, but not between San Juan and Miami. Therefore, we pooled the data by site across regions for analyses of escape responses. All analyses were conducted in R (R Core team 2017).

Results

Escape distance and habituation

We assessed the escape response of 166 lizards from urban sites and 250 lizards from forest sites. Although both region (i.e., San Juan and Miami) and the covariate of body temperature were included in the ANCOVA model, their interactions with the main effect of substrate were non-significant and thus we removed them from the final model (Table S1). Lizards perched on forest trees and cement walls had significantly longer FIDs compared to the other substrates ($F_{5,374} = 10.86$, $R^2 = 0.12$, $P < 0.0001$; Fig. 1). Flight-initiation distance was shorter for lizards in San Juan and for lizards with higher body temperatures (Table S1). No potential covariates were correlated with flight distance, which did not differ among the substrates used by lizards ($F_{3,360} = 2.33$, $R^2 = 0.02$, $P < 0.07$).

Flight-initiation distances were shorter for lizards closer to the trail at the forest site in Miami ($R^2 = 0.11$, $P = 0.01$). Lizards at the urban site in Miami showed no relationship between FID and distance from the sidewalk ($R^2 = 0.03$, $P = 0.82$; Fig. 2). At the urban site, the maximum distance from the sidewalk because of the presence of walls surrounding houses and a canal was 8 m. When restricting the sample from the forest to distances up to 8 m, FID was still significantly shorter for lizards closer to the trail ($R^2 = 0.21$, $P < 0.01$; Fig. 2). We encountered over twice as many people on the
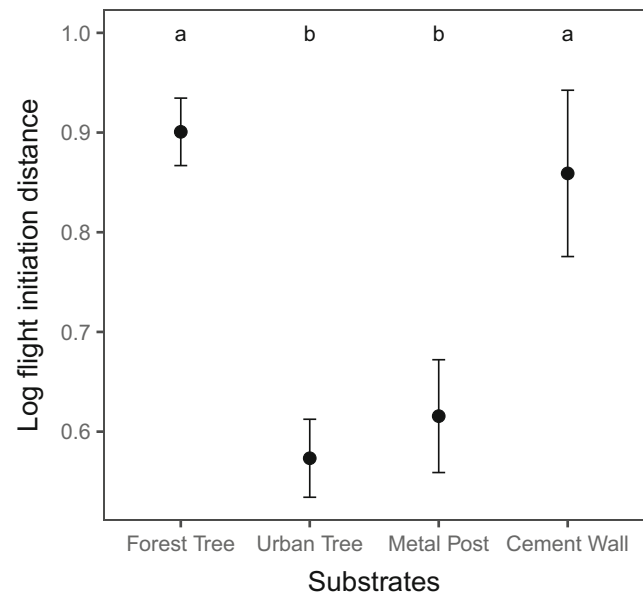

Fig. 1 Mean (± SE) of flight-initiation distance for lizards on the four substrates types (forest tree, $N = 166$; urban tree, $N = 121$; metal post, $N = 67$; and cement wall $N = 62$). FID+1 was log transformed for normality. Letters denote significant differences among substrates based on pairwise Tukey's HSD tests

sidewalk at the urban site (12.2 people per hour; 55 encounters in a 4.5 h survey) compared to on the forest trail (5.0 people per hour; 16 encounters in a 3.2 h survey).

Escape mode and structural habitats

We found that escape mode differed among substrate types ($X^2 = 26.44$, df = 6, $P < 0.01$; all pairwise comparisons differed at $P < 0.05$ except for the urban tree-metal post comparison; Fig. 3). Sprinting was most frequently used on forest trees and cement walls, whereas squirreling was most common for lizards escaping on urban trees and metal posts (Fig. 3). When compared to forest trees, the probability of jumping was lower for lizards on urban trees and metal posts. Lizards on cement walls did not escape by jumping. These differences in escape mode when occupying the various substrates are influenced by the structural habitat differences between natural and urban habitats. Urban areas had broader-diameter vegetation and fewer nearby perches (i.e., sparser vegetation) compared to forest sites, a result consistent across regions (Table S2). Ground vegetation was denser at forest sites (only 4–13% ground openness) in both Miami and San Juan compared to urban sites (69–76% ground openness; $F_{4,1972} = 15.57$, $R^2 = 0.03$, $P < 0.001$; Fig. S1). Tree canopies at urban sites were significantly more open than forests ($F_{2,123} = 72.42$, $R^2 = 0.54$, $P < 0.01$; Fig. S1); the forest site in San Juan was more open than the forest in Miami ($P < 0.01$). Denser forest tree canopies likely contributed to cooler copper lizard model temperatures when compared to the more open urban habitats (i.e., copper model temperatures mean of
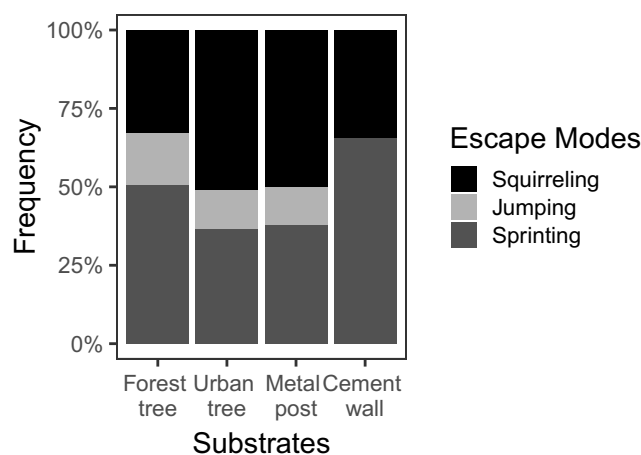
Fig. 2 Relationship between distance from the trail (m) or sidewalk (m) and flight initiation distance at the forest ($N = 34$) and urban sites ($N = 37$) in Miami. FID+1 was log transformed for normality. Note a significant positive relationship also exists between FID and distance from the trail in the forest when including distances up to 30 m ($N = 53$)
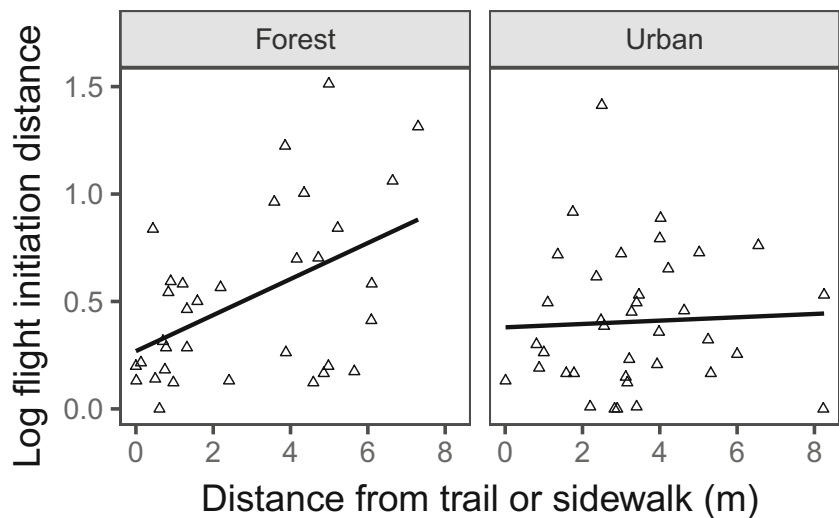
31.0°C and 32.6°C, respectively; $F_{7,375} = 23.3$, $R^2 = 0.30$, $P < 0.001$, Table 1). Overall, we found that urban habitats had broader trees, less dense vegetation, and more open canopies compared to forest habitats.

Multinomial logistic regression results showed that narrow diameter perches (i.e., smaller than 15 cm) at both forest and urban sites favored escape by jumping (Forest: $X^2 = 34.0$, df = 2, $P < 0.01$; Urban: $X^2 = 31.6$, df = 2, $P < 0.01$; Fig. 4). Lizards in all sites selected significantly broader diameter perches compared to the diameters of available vegetation in each habitat (Table S3). However, forest lizards used 15-cm diameter or narrower perches more frequently than broader perches (Fig. S2), likely influenced by the increased availability of smaller diameter vegetation in forests. Lizards in urban sites used broader diameter substrates compared to forest sites ($F_{2,347} = 32.29$, $P < 0.001$; Table S3). These substrates consisted of urban trees that were three times broader on average than trees used by lizards in forests, and metal posts that were twice as broad as forest trees. The probability of squirreling increased

Fig. 3 Proportion of escape modes used across different substrate types (forest tree, $N = 166$; urban tree, $N = 121$; metal post, $N = 67$; and cement wall $N = 62$). Note that lizards never jumped from cement walls

with perch diameter in both habitats. For lizards perched on trees, forest lizards escaped by squirreling less than urban lizards likely due to the use of narrower-diameter perches. The broader perch diameters used at urban sites likely facilitated both sprinting and squirreling, which had similar probabilities across perch diameters. This was in contrast to forest sites where the probability of sprinting decreased to zero for perches larger than about 20 cm, although lizards in the forest rarely used perches of this diameter or larger (Fig. S2). The effect of the number of nearby perches on escape mode did not differ between forest and urban sites. The probability that lizards would escape by jumping increased in both habitats with increasing number of nearby perches (Forest: $X^2 = 15.57$, df = 2, $P < 0.01$; Urban: $X^2 = 19.68$, df = 2, $P < 0.01$; Fig. 5). Lizards tended to use perches surrounded by more vegetation (i.e., a greater number of nearby perches) compared to that available, although this was only significant for the urban site in San Juan (Fig. S3). The number of nearby perches tended to be lower for metal posts and was lowest for cement walls (Table 1). Lizards perched on cement walls had 75% fewer nearby perches compared to trees in both habitats, and lizards never jumped from cement walls.

Discussion

We found that lizards differed in their escape behavior between forest and urban habitats and when occupying artificial substrates within urban habitats. Specifically, urban lizards had shorter FIDs when escaping on trees compared to lizards in the forest, likely due to habituation to humans. Other studies have also reported shorter FIDs in habitats with higher exposure to humans (Samia et al. 2015, 2017; Lapiedra et al. 2017). However, few studies have evaluated differences in FID within urban habitats as consequence of using artificial structures that can reduce locomotor ability in lizards (Kolbe et al. 2016;

Table 1 Sample size and mean (± SE) for lizard structural habitat use and estimated body temperatures at forest and urban sites in San Juan and Miami

		N	Perch diameter (cm)		Number of nearby perches		Perch height (cm)		Copper lizard model temperature (°C)	
			Mean ± SE	Tukey HSD	Mean ± SE	Tukey HSD	Mean ± SE	Tukey HSD	Mean ± SE	Tukey HSD
San Juan	Forest tree	97	7.95 ± 1.28	B	2.32 ± 0.16	A	103.94 ± 4.18	A	31.35 ± 0.07	B
	Urban tree	71	24.12 ± 2.78	A	2.22 ± 0.34	AB	111.94 ± 4.48	A	32.32 ± 0.08	A
	Metal Post	41	15.7 ± 2.65	A	1.34 ± 0.17	BCD	115.83 ± 7.22	A	32.74 ± 0.15	A
	Cement Wall	30	NA	NA	0.56 ± 0.14	D	112.60 ± 11.91	A	32.31 ± 0.17	AB
Miami	Forest tree	69	7.67 ± 0.88	B	1.49 ± 0.16	BCD	106.48 ± 3.58	A	30.48 ± 0.24	C
	Urban tree	50	17.86 ± 2.55	A	2.10 ± 0.31	ABC	96.52 ± 5.34	AB	33.00 ± 0.22	A
	Metal Post	26	26.65 ± 5.47	A	1.58 ± 0.23	ABCD	74.88 ± 6.72	B	32.85 ± 0.36	A
	Cement Wall	32	NA	NA	1.06 ± 0.17	CD	110.39 ± 8.75	A	32.91 ± 0.40	A

Letters denote significant differences in mean values among substrates based on Tukey's HSD test. Most pairwise comparisons between the regions were non-significant. Note that perch diameter could not be measured for cement walls, but this substrate consisted of very broad, vertical surfaces

Winchell et al. 2018). We found that lizards on cement walls had longer FIDs compared to other substrates in urban sites, which may indicate locomotor deficiencies when fleeing on this novel substrate. Furthermore, we found that forest lizards perching closer to trails frequently used by humans had lower FIDs. Both urban and forest lizards likely modulate FID by reducing responsiveness to humans and adjust their escape behavior in response to the properties of substrates on which they perch. In the forest, we showed that a fraction of the population exposed to higher frequency of humans had decreased wariness in their escape response. The ability to adjust escape behavior in accordance with human activity, substrate type, and habitat likely contributes to the success of this species in urban areas and perhaps as an invasive species.

The largest difference in FID was between lizards occupying trees in urban and forest habitats (Fig. 1), a comparison that controlled for the substrate type to focus on the effect of the habitat. When escaping an incoming predator, lizards respond in accordance with the costs of flight in their habitats (Cooper 2003, 2005; Cooper and Whiting 2007). For example, *Anolis sagrei* from forest habitats reacted with increased wariness compared to urban counterparts during simulated predator attacks in captivity (Lapiedra et al. 2017). When predators are abundant, the costs of not fleeing from incoming threats are high because of greater risk of incurring injury or predation (Ydenberg and Dill 1986; Downes 2001) and thus animals should have longer FID. Shorter FID of urban animals may correspond in some instances to predator release (e.g. Rodewald et al. 2011). Previous studies have shown higher injury rates for clay models of anoles in forest habitats compared to urban habitats (Shepard 2007; McMillan and Irschick 2010), suggesting greater predation risk in forests. Whether the higher FIDs associated with forest lizards in our study are because of greater predation risk requires additional data on predators. We did not assess the composition or abundance of predators at our sites. However, a recent study found higher caudal autonomy for *A. cristatellus* in urban compared to forest sites in Puerto Rico (Tyler et al. 2016) suggesting greater frequency of predatory encounters in cities. A comparison of tail regeneration in the brown anole (*Anolis sagrei*) among sites in Florida with no cats, feral cats (considered efficient predators), and pet cats (considered inefficient predators because they were well fed) found the highest tail loss (25%) rate was due to pet cats (Bateman and Fleming 2014). This suggests that some urban predators might be less efficient at capturing prey (Rodewald et al. 2011; Orros and Fellowes 2012), which could contribute to lower FIDs for lizards in urban habitats.

Habituation to human activity may also explain why urban lizards had shorter FIDs. Other studies have reported longer FIDs in forest habitats as opposed to more open and urban-like habitats (Burger et al. 2004; Irschick et al. 2005; Grolle et al. 2014; Lapiedra et al. 2017). Irschick et al. (2005) showed that anoles had longer FIDs in a habitat that was relatively undisturbed by people and had complex vegetation. Furthermore,
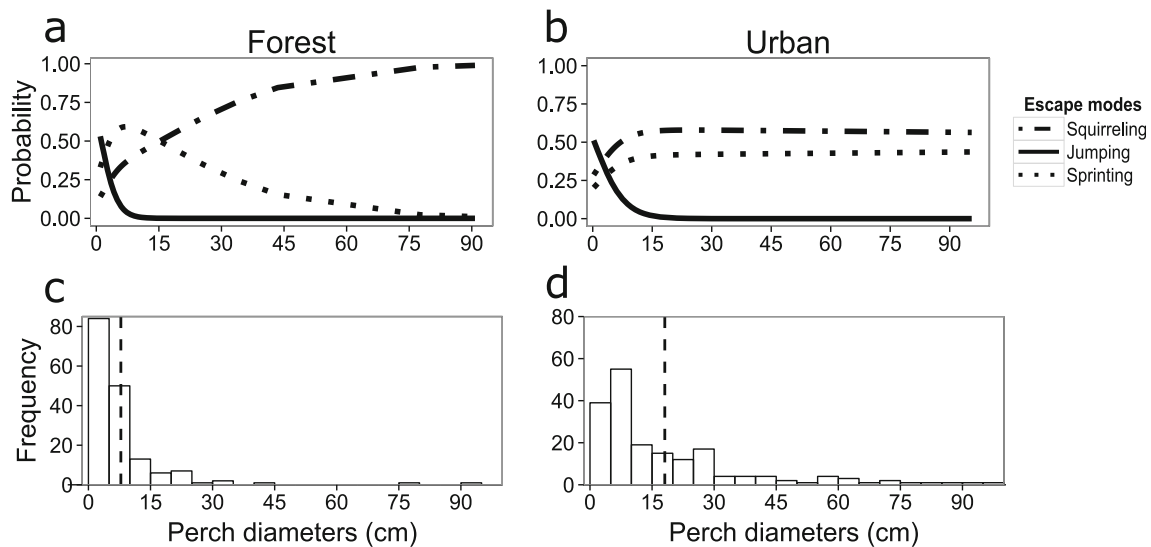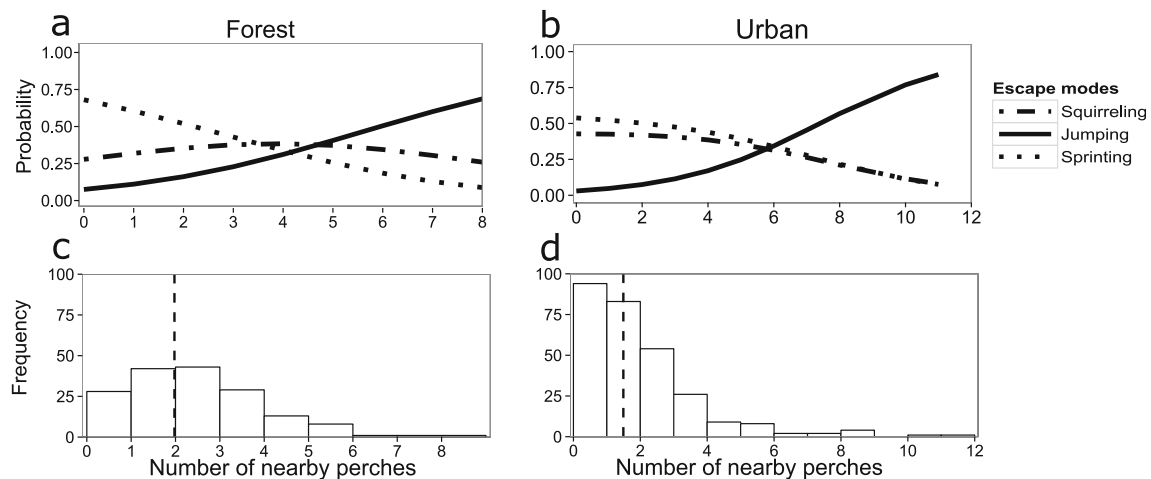
Fig. 4 Results from multinomial logistic regressions assessing the probability of using each escape mode with increasing perch diameters for the **a**) forest sites (*N* = 166) and **b**) urban sites (*N* = 250). Histograms show the frequency of perch diameters used by lizards at **c**) forest sites and **d**) urban sites. The dashed vertical line shows the mean perch diameter used by lizards in each habitat. Data from San Juan and Miami are combined for the forest and urban sites and cement walls are excluded from the urban sites because perch diameters did not apply to this substrate

fence lizards had significantly shorter FIDs at sites with nearly constant foot traffic near lizards (Grolle et al. 2014). These findings suggest that lizards can become habituated to the presence of humans and reduce their escape response to humans near their perches. We quantified the influence of human exposure on FID by sampling at varying distances from trails and paths used by humans in each habitat. When we analyzed FID in conjunction with the distance from trails and sidewalks used by humans, we found that forest lizards close to the trail had shorter FIDs compared to lizards farther from the trail (Fig. 2), even when limiting the maximum distance from the trail to 8 m. In contrast, FIDs for urban lizards showed no relationship with the distance from the sidewalk.

The short distance from the sidewalk (a maximum of 8 m) in conjunction with the openness of the urban habitat meant that lizards were visually detecting human activity even at the longest possible distances from the sidewalk. In the forest, denser vegetation limited the field of vision for lizards perched farther from the trail, thus limiting exposure to human activity. A similar trend was found for populations of black iguanas, where groups that were exposed to a higher frequency of human activity had shorter FID (Burger and Gochfeld 1990). We expect that repeated exposure to low-risk predators, including humans and possibly domestic pets, should decrease FIDs, minimizing costly escapes and maximizing time for foraging and reproduction (Grolle et al. 2014).

Fig. 5 Results from multinomial logistic regressions assessing the probability of using each escape mode with increasing number of nearby perches for the **a**) forest sites (*N* = 166) and **b**) urban sites (*N* = 250). Histograms show the number of nearby perches for lizards at **c**) forest sites and **d**) urban sites. The dashed vertical line shows the mean number of nearby perches for lizards in each habitat. Data from San Juan and Miami are combined for the forest and urban sites

Although urban populations showed a reduction in FID on trees, lizards on cement walls had much longer FIDs. Because the habitat is the same, the increase in FID likely reflects a behavioral adjustment associated with perching on this particular substrate. Therefore, lizards adjust their escape responses by risk-assessment decisions based on differences in habitat (i.e., urban v. forest) and also their immediate perching location. Stability during locomotion has been shown to influence escape performance in the natural habitat (Mattingly and Jayne 2004), and novel substrates like cement walls may be challenging to traverse. Longer FIDs on this substrate may reflect behavioral modulation, lizards need to reduce speed to increase stability (Kolbe et al. 2016), but this means starting to escape when predators are at a longer distance. Anole lizards sprinting on cement race-tracks at a nearly vertical inclination had a 45% reduction in sprinting velocity and slid backwards during locomotion a significantly greater proportion of the time compared to race-tracks made of tree bark (Winchell et al. 2018). Cement walls potentially impact the ability of lizards to run at maximal speed, particularly when these substrates are also smooth, which was common at our study sites. Because maximum acceleration is vital for escaping predators (Walker et al. 2005; Higham et al. 2010), lizards on cement walls may increase their FID to compensate for performance limitations on this substrate. Further work should follow individual lizards to determine whether they are flexible in their locomotor behavior, including FID, when they occupy natural and artificial perches in the urban environments.

Escape modes used by lizards also differed between habitats and between the use of natural and artificial substrates. Differences in escape modes likely correspond to adjustments to maximize locomotor efficiency during escape (Losos and Irschick 1996). Perch diameter had the most dramatic effect on the probability of jumping, which quickly decreased from a probability of 0.5 to zero going from a perch diameter of 1 cm to around 10 cm (Fig. 4). When jumping, anoles typically position the main axis of their body perpendicular to the substrate, such as a branch or trunk, and then push off the substrate (Losos and Irschick 1996; Losos 2009). This is more easily accomplished when the substrate is narrow. What is more, squirreling and sprinting are infrequent on these narrow-diameter perches, whereas they are common on broader perches. In terms of perch diameters, metal posts and trees used by lizards in urban areas were 2–3 times broader on average than trees in the forest (Table 1), and the probability of escaping by squirreling increased with perch diameter (Fig. 4). Consequently, urban lizards escaped when on metal posts and trees by squirreling about 50% of time, significantly more than lizards on narrower trees in the forest. About 80% of the trees in the forests had diameters <5 cm (Fig. S2), and such narrow diameters are unlikely to conceal fully a squirreling adult male *A. cristatellus*, making this escape behavior ineffective in these circumstances. Moreover, squirreling

was the lowest probability escape mode at narrow diameters in the forest, and it was not until perch diameters exceeded 15 cm that squirreling became favored over sprinting in the forest. Consistent with previous studies showing most anoles run relatively slow on narrow diameter perches and sprint speed increases with substrate diameter (Losos and Sinervo 1989; Losos and Irschick 1996), the probability of sprinting increased from the narrowest perch diameters to a maximum at around 7–10 cm (Fig. 4). Limb posture during strides begins to resemble movement on flat surfaces as diameters increase and the curvature of the surface becomes less relevant for these relatively small lizards (Spezzano and Jayne 2004). Thus, sprinting performance gains resulting from increased substrate diameters should be negligible above some threshold, which is likely around 10–15 cm for male *A. cristatellus*. Escape mode on cement wall was significantly different from all other substrates. Lizards on cement walls escaped more by sprinting and did not jump. This substrate was the broadest in diameter (although not quantified) and had the fewest nearby perches (Table 1). For optimal jumping, lizards must take off at angles between 39° and 42° (Toro et al. 2003), and very wide diameter perches and vertical cement walls may constrain the ability of lizards to maneuver into a position to jump at this takeoff angle. Thus, the combination of broader diameter perches and fewer nearby perches, which reduces the number of locations to which lizards could jump (Pounds 1988; Losos and Irschick 1996; Gilman and Irschick 2013; Fig. 3), produced conditions unfavorable for jumping. This likely explains the lack of jumping to escape when on cement walls in urban areas. Differences in the structural habitat caused by urbanization impact the escape modes used by lizards, and this could also factor into their decision of when to escape.

Our results indicate that a highly successful urban colonizer (*A. cristatellus*) adjusts escape responses to both the presence of humans and the use of artificial structures as perches. Urban anoles modulated their escape behavior when perched on cement walls, potentially to compensate for a reduction in their ability to move at high speeds without falling or slipping on this smooth surface (Kolbe et al. 2016; Winchell et al. 2018). On one hand, this could reduce the strength of selection acting to increase performance on this novel substrate. On the other hand, the behavioral decision to use artificial substrates, regardless of any behavioral modulation, likely exposes lizards to novel selection pressures related to an important morphology-performance relationship. Under these circumstances, urban habitats should favor longer limbs and larger toepads for increased stability moving on smooth, vertical surfaces (Kolbe et al. 2016; Winchell et al. 2018), and longer limbs for faster sprinting to minimize the time spent on the ground traveling between vegetation (Goodman 2009) and during foraging bouts (Drakeley et al. 2015; Lapiedra et al. 2017). Consistent with this prediction, urban *A. cristatellus* in Puerto Rico have longer limbs and more lamellae than their forest counterparts (Winchell et al. 2016) and *A. sagrei* in the Bahamas have longer limbs in human-modified

habitats (Marnocha et al. 2011). Thus, the behavioral decision to use artificial substrates likely exposes lizards to novel selective pressures, favoring morphology that increases performance on artificial substrates. Although we are only beginning to understand how urban environments alter behavior (e.g. Ditchkoff et al. 2006; Sol et al. 2013; Lapiedra et al. 2017), behavioral responses to humans and urban environments likely have fitness consequences, making urbanization a potent force influencing ecological persistence and evolutionary trajectories of populations (Hendry et al. 2011; Sih et al. 2011).

References

Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol Evol 30:114–126. https://doi.org/10.1016/j.tree.2014.11.007

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York

Bateman PW, Fleming PA (2014) Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? J Zool 294:93–98. https://doi.org/10.1111/jzo.12156

Battles AC, Moniz M, Kolbe JJ (2018) Living in the big city: preference for broad substrates results in niche expansion for urban Anolis lizards. Urban Ecosyst 21:1087–1095. https://doi.org/10.1007/s11252-018-0787-1

Blumstein DT (2014) Attention, habituation, and antipredator behaviour: implications for urban birds. In: Gil D, Brumm H (eds) Avian urban ecology: behavior and physiological adaptations. Oxford University Press, Oxford, pp 41–53

Blumstein DT (2016) Habituation and sensitization: new thoughts about old ideas. Anim Behav 120:255–262. https://doi.org/10.1016/j.anbehav.2016.05.012

Burger J, Gochfeld M (1990) Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. J Comp Psychol 104:388–394. https://doi.org/10.1037//0735-7036.104.4.388

Burger J, Jeitner C, Jensen H, Fitzgerald M, Carlucci S, Shukla S, Burke S, Ramos R, Gochfeld M (2004) Habitat use in basking northern water (*Nerodia sipedon*) and eastern garter (*Thamnophis sirtalis*) snakes in urban New Jersey. Urban Ecosyst 7:17–27. https://doi.org/10.1023/B:UECO.0000020169.86700.76

Chianucci F, Puletti N, Giacomello E, Cutini A, Corona P (2015) Estimation of leaf area index in isolated trees with digital photography and its application to urban forestry. Urban For Urban Green 14:377–382. https://doi.org/10.1016/j.ufug.2015.04.001

Cooper WE (2003) Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. Ethology 109:617–626. https://doi.org/10.1046/j.1439-0310.2003.00912.x

Cooper WJ (2005) When and how do predator starting distances affect flight initiation distances? Can J Zool 83:1045–1050. https://doi.org/10.1139/z05-104

Cooper WE (2006a) Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. Ethology 112:858–864. https://doi.org/10.1111/j.1439-0310.2006.01240.x

Cooper WE (2006b) Risk factors affecting escape behaviour by Puerto Rican *Anolis* lizards. Can J Zool 84:495–504. https://doi.org/10.1139/z06-018

Cooper WE (2009) Theory successfully predicts hiding time: new data for the lizard *Sceloporus virgatus* and a review. Behav Ecol 20:585–592. https://doi.org/10.1093/beheco/arp035

Cooper WE (2010) Escape tactics and effects of perch height and habituation on flight initiation distance in two Jamaican anoles (Squamata: Polychrotidae). Rev Biol Trop 58:1199–1209

Cooper WE, Whiting MJ (2007) Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. Ethology 113:661–672. https://doi.org/10.1111/j.1439-0310.2007.01363.x

Ditchkoff SS, Saalfeld ST, Gibson CJ (2006) Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosyst 9:5–12. https://doi.org/10.1007/s11252-006-3262-3

Downes S (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82:2870–2881. https://doi.org/10.1890/0012-9658(2001)082[2870:THAFFS]2.0.CO;2

Drakeley M, Lapiedra O, Kolbe JJ (2015) Predation risk perception, food density and conspecific cues shape foraging decisions in a tropical lizard. PLoS One 10:e0138016. https://doi.org/10.1371/journal.pone.0138016

Forman R (2014) Urban ecology: science of cities, 1st edn. Cambridge University Press, Cambridge

Foster KL, Collins CE, Higham TE, Garland T (2015) Determinants of lizard escape performance: decision, motivation, ability, and opportunity. In: Cooper WEJ, Blumstein DT (eds) Escaping from predators: an integrative view of escape decisions. pp 287–321. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9781107447189.012

Gilman CA, Irschick DJ (2013) Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. Funct Ecol 27(2):374–381

Goodman BA (2009) Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. J Evol Biol 22:1535–1544. https://doi.org/10.1111/j.1420-9101.2009.01766.x

Grolle EK, Lopez MC, Gerson MM (2014) Flight initiation distance differs between populations of Western fence lizards (*Sceloporus occidentalis*) at a rural and an urban site. Bull South Calif Acad Sci 113:42–46. https://doi.org/10.3160/0038-3872-113.1.42

Hendry AP, Kinnison MT, Heino M, Day T, Smith TB, Fitt G, Bergstrom CT, Oakeshott J, Jørgensen PS, Zalucki MP, Gilchrist G, Southerton S, Sih A, Strauss S, Denison RF, Carroll SP (2011) Evolutionary principles and their practical application. Evol Appl 4:159–183. https://doi.org/10.1111/j.1752-4571.2010.00165.x

Hertz PE (1992) Evaluating thermal resource partitioning - by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. Oecologia 90:127–136. https://doi.org/10.1007/BF00317818

Higham TE, Korchari P, Mcbrayer LD (2010) How to climb a tree: lizards accelerate faster, but pause more, when escaping on vertical surfaces. Biol J Linn Soc 102:83–90. https://doi.org/10.1111/j.1095-8312.2010.01564.x

Huang S-P, Porter WP, Tu M-C, Chiou C-R (2014) Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a high-elevation lizard. Oecologia 175:25–35. https://doi.org/10.1007/s00442-014-2882-1

Hufbauer RA, Facon B, Ravigne V et al (2012) Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote

invasions. Evol Appl 5:89–101. https://doi.org/10.1111/j.1752-4571.2011.00211.x

Irschick DJ, Carlisle E, Elstrott J et al (2005) 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

Kolbe JJ, Battles AC, Avilés-Rodríguez KJ (2016) 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

Lapiedra O, Chejanovski Z, Kolbe JJ (2017) Urbanization and biological invasion shape animal personalities. Glob Chang Biol 23:592–603. https://doi.org/10.1111/gcb.13395

Le Roux DS, Ikin K, Lindenmayer DB et al (2014) Reduced availability of habitat structures in urban landscapes: implications for policy and practice. Landsc Urban Plan 125:57–64. https://doi.org/10.1016/j.landurbplan.2014.01.015

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Losos JB (2009) Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley

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

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

Mattingly WB, Jayne BC (2004) Resource use in arboreal habitat: structure affects locomotion of four ecomorphs of *Anolis* lizards. Ecology 85:1111–1124. https://doi.org/10.1890/03-0293

Mccleery RA (2009) Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. Landsc Ecol 24:483–493. https://doi.org/10.1007/s10980-009-9323-2

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McMillan DM, Irschick DJ (2010) Experimental test of predation and competition pressures on the green anole (*Anolis carolinensis*) in varying structural habitats. J Herpetol 44:272–278. https://doi.org/10.1670/08-196.1

Müller J, Bae S, Röder J, Chao A, Didham RK (2014) Airborne LiDAR reveals context dependence in the effects of canopy architecture on arthropod diversity. For Ecol Manag 312:129–137. https://doi.org/10.1016/j.foreco.2013.10.014

Oosten JE, Magnhagen C, Hemelrijk CK (2010) Boldness by habituation and social interactions: a model. Behav Ecol Sociobiol 64:793–802. https://doi.org/10.1007/s00265-009-0896-1

Orros ME, Fellowes MDE (2012) Supplementary feeding of wild birds indirectly affects the local abundance of arthropod prey. Basic Appl Ecol 13:286–293. https://doi.org/10.1016/j.baae.2012.03.001

Peckarsky BL, Abrams PA, Bolnick DI et al (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator prey Interactions. Ecology 89:2416–2425. https://doi.org/10.1890/07-1131.1

Pounds JA (1988) Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. Ecol Monogr 58:299–320. https://doi.org/10.2307/1942542

Prosser C, Hudson S, Thompson MB (2006) Effects of urbanization on behavior, performance, and morphology of the garden skink, Lampropholis guichenoti. J Herpetol 40:151–159. https://doi.org/10.1670/38-05A.1

R Core team (2017) R: A language and environment for statistical computing. R foundation for statistical computing. In: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. Trends Ecol Evol 27:179–188

Regalado R (1998) Approach distance and escape behavior of three species of Cuban *Anolis* (Squamata, Polychrotidae). Caribb J Sci 34:211–217

Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator–prey relationships. Ecol Appl 21:936–943

Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2010) Habituation to low-risk predators improves body condition in lizards. Behav Ecol Sociobiol 64:1937–1945. https://doi.org/10.1007/s00265-010-1004-2

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT (2015) Increased tolerance to humans among disturbed wildlife. Nat Commun 6:8877. https://doi.org/10.1038/ncomms9877

Samia D, Blumstein DT, Díaz M et al (2017) Rural-urban differences in escape behavior of European birds across a latitudinal gradient. Front Ecol Evol 5:1–13. https://doi.org/10.3389/fevo.2017.00066

Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc Natl Acad Sci U S A 109:16083–16088. https://doi.org/10.1073/pnas.1211658109

Shepard DB (2007) Habitat but not body shape affects predator attack frequency on lizard models in the brazilian cerrado. Herpetologica 63:193–202

Shochat E, Warren PS, Faeth SH et al (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. Anim Behav 85:1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Spezzano LC, Jayne BC (2004) The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). J Exp Biol 207:2115–2131. https://doi.org/10.1242/jeb.00995

Toro E, Herrel A, Vanhooydonck B, Irschick DJ (2003) A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. J Exp Biol 206:2641–2652. https://doi.org/10.1242/jeb.00473

Tyler RK, Winchell KM, Revell LJ (2016) Tails of the city : caudal autotomy in the tropical lizard, *Anolis cristatellus*, in urban and natural areas of Puerto Rico. J Herpetol 50:435–441. https://doi.org/10.1670/15-039

Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosyst 13:425–441. https://doi.org/10.1007/s11252-010-0136-5

Walker JA, Ghalambor CK, Griset OL et al (2005) Do faster starts increase the probability of evading predators? Funct Ecol 19:808–815. https://doi.org/10.1111/j.1365-2435.2005.01033.x

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

Winchell KM, Maayan I, Fredette JR, Revell LJ (2018) Linking locomotor performance to morphological shifts in urban lizards. Proc R Soc Biol 285:20180229. https://doi.org/10.1098/rspb.2018.0229

Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Study Behav 16:229–249. https://doi.org/10.1016/S0065-3454(08)60192-8