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An experimental evaluation of foraging decisions in urban and natural forest populations of *Anolis* lizards

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Abstract Foraging decisions reflect a trade-off between the benefits of acquiring food and the costs of movement. Changes in the biotic and abiotic environment associated with urbanization can alter this trade-off and modify foraging decisions. We experimentally manipulated foraging opportunities for two *Anolis* lizard species – the brown anole (*A. sagrei*) in Florida and the crested anole (*A. cristatellus*) in Puerto Rico – to assess whether foraging behavior differs between habitats varying in their degree of urbanization. In both urban and natural forest habitats, we measured the latency of perched anoles to feed from an experimental feeding tray. We manipulated perch availability and predator presence, while also taking into account population (e.g., conspecific density) and individual-level factors (e.g., body temperature) to evaluate whether and how these contribute to between-habitat differences in foraging behavior. In both species, urban anoles had longer latencies to feed and lower overall response rates compared to lizards from forests. Urban anoles were also larger (i.e., snout-vent length and mass) in both species and urban *A. sagrei* were in better body condition than the natural forest population. We postulate that the observed patterns in foraging behavior are driven by differences in perceived predation risk, foraging motivation, or neophobia. Although we are unable to identify the mechanism(s) driving these differences, the substantial differences in urban versus forest anole foraging behavior emphasizes the importance of understanding how urbanization influences animal populations and their persistence in anthropogenically-modified environments.

Keywords Foraging behavior · Motivation · Predation risk · Structural habitat · Urbanization

Introduction

Animals must feed to survive, and theory states that organisms maximize fitness by matching their foraging decisions to environmental conditions (Stephens and Krebs 1986; Dall et al. 2005). These decisions reflect a trade-off between the caloric benefits and potential costs of foraging, such as missed mating opportunities or greater predation risk (Lima and Bednekoff 1999; Verdolin 2006). Environmental change can, by altering this cost:benefit ratio, modify foraging behavior. Urbanization, for instance, produces rapid environmental change that dramatically transforms the biotic and abiotic characteristics of populated areas worldwide (Shochat et al. 2006). While these changes are associated with many novel stressors (e.g., habitat fragmentation, human activity, and predators) that may alter foraging decisions in urban habitats, the precise nature of these anthropogenically-driven changes in foraging behavior is still unclear. Furthermore, the ability to modify foraging behavior can determine whether or not animal populations persist in human-modified habitats.

One of the most striking differences between urban and natural areas is their structural habitat. Urban habitats contain fewer trees, lower vegetation (e.g., shrubs and lawns) and more impervious surfaces than natural areas (Blair 1996; Forman 2014). This decrease in structural complexity may heighten perceived predation risk via greater exposure to

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potential predators and fewer refuges for prey (Whittingham and Evans 2004). Vegetative cover influenced escape behavior in the lizard *Psammodromus algirus*, for example, with individuals fleeing from an approaching predator at greater distances in more open areas (Martin and López 1995). Animals may be less willing to forage in urban areas, or may restrict foraging activity to residual vegetated fragments (i.e., green spaces) they perceive as safer (Hodgson et al. 2006). Similarly, small mammals abandoned artificial food patches more quickly in open areas than when the patches were placed nearer to and within vegetation (Bowers et al. 1993; Baker et al. 2015). These studies suggest that habitat structure can mediate the relationship between foraging activity and perceived predation risk. While this research is useful, many studies addressing the topic do not separate out the potentially confounding effects of predation and structural habitat (but see Bouskila 1995). Experiments that do manipulate both factors in urban and natural sites, however, permit assessments of how habitat structure per se influences foraging behavior.

Urban habitats containing abundant or novel predators could have higher predation risk than natural areas (reviewed by Fischer et al. 2012). Both feral and domestic cats have been linked to the decline of various urban taxa (e.g., birds: Lepczyk 2003; Baker et al. 2005; lizards: Ditchkoff et al. 2006; small mammals: Sims et al. 2008), and some urban habitats have higher densities of generalist avian predators (Jokimäki and Huhta, 2000; Sorace and Gustin, 2009). Although increases in perceived predation risk may reduce foraging by some urban species, anthropogenic subsidies characteristic of urban areas may decouple the relationship between predator abundance and actual predation risk (Rodewald et al. 2011). Urban mesopredators such as raccoons, for example, readily utilize artificial resources (Prange et al. 2004) that increase their abundance but decrease their need to prey on other species. The fact that studies comparing anti-predator behavior in prey from urban versus natural habitats produce inconsistent results may reflect this decoupling of predator abundance and predation risk. House finches from urban areas escaped at greater distances, suggesting that perceived predation risk is higher in urban versus natural habitats (Valcarcel and Fernández-Juricic 2009). A study of 44 European bird species, however, found shorter escape distances in urban habitats (Møller 2008). The question of whether prey respond appropriately to predation risk in urban environments, and how this response influences foraging behavior, remains unanswered.

Anolis lizards (or anoles) are ideal for research evaluating how structural habitat and predation risk influence foraging in urban and natural environments. Anoles are small, diurnal, mostly insectivorous lizards for whom structural habitat – perch height, diameter and substrate type –is a key niche axis (Losos 2009). Perch attributes such as diameter, inclination and roughness, along with anole morphology, influence locomotor performance (Losos and Sinervo 1989; Irschick and Losos 1999; Kolbe et al.

2015) and thus the ability of anoles to capture prey and evade predators. Anoles utilize elevated perches to survey their territory for potential prey, mating opportunities, and conspecific competitors (Stamps 1977). The fact that perceived risk is inversely related to perch height in anoles (Cooper 2006; Cooper 2010) suggests that elevated perches are perceived as safer than ground perches. For instance, anoles traveling farther on the ground to feed in an experimental setting used more intermediate perches compared to when feeding closer to their original perch (Drakeley et al. 2015). Other studies have also shown that although anoles are primarily ground foragers (Losos 1990; Lapiedra et al. 2017), they become more arboreal in the presence of ground-dwelling predators (Schoener et al. 2002; Losos et al. 2004).

In this study, we experimentally manipulated foraging opportunities for two *Anolis* species – the brown anole (*A. sagrei*) in Florida and the crested anole (*A. cristatellus*) in Puerto Rico – to assess whether foraging decisions differ between habitats varying in their degree of urbanization. During these experiments, we manipulated perch availability and predator presence in each habitat type to determine their effects on perceived predation risk and foraging decisions. We also considered how factors such as perch availability, body temperature, conspecific density and body size, might also contribute to differences in foraging behavior. Our research sought to assess the willingness of lizards to forage in urban and natural forest habitats, and to explore how structural habitat and predator presence influenced foraging decisions.

Methods

Site selection

We examined *Anolis* foraging behavior in populations occupying both urban and natural habitats. All experiments were conducted during warm days (>25 °C during trials) between the hours of 0900 and 1900 when lizards were active. Foraging trials with *A. cristatellus* were conducted in July 2014 in urban and natural forest sites within the San Juan metropolitan area of Puerto Rico. Trials with *A. sagrei* were conducted during April–May 2015 in urban, suburban, and natural forest sites (each replicated twice) in southeast Florida (Broward County). Natural forest habitats were secondary forests characterized by relatively closed canopies, dense vegetation, and little human disturbance. No humans or domestic animals were observed in any of our natural sites throughout the course of these experiments. Urban habitats consisted of sparse vegetation, more open space (typically covered by mown lawn or impervious surfaces), and increased pedestrian traffic compared to natural habitats. Suburban habitats (*A. sagrei* experiments only) were roadside areas intermediate between urban and natural sites in terms of vegetation density, open space, and pedestrian disturbance.

Experimental procedure

We first located male lizards perched in survey posture on a vertical substrate (e.g., tree or wall). Survey posture – head downward, hind limbs extended up the vertical surface, and upper body pushed away from the substrate – indicates an anole receptive to foraging (Stamps 1977); anoles seem to abandon this posture when fed to satiation (Drakeley et al. 2015). After locating an anole, we placed a foraging tray with two mealworms directly in front of this focal lizard at a distance of 1 m from the base of the perch for *A. cristatellus* and five mealworms at a 2-m distance for *A. sagrei*. Mealworms were larvae of the darkling beetle, *Tenebrio molitor*, which have been used successfully as a food resource in previous studies (Drakeley et al. 2015; Lapiedra et al. 2017). These quantities of mealworms elicited the fastest responses for each species in pilot trials conducted near our study sites. Foraging trays were initially covered with an opaque material to prevent lizards from seeing the mealworms before the researcher was able to move to a distance >3 m from the tray (see Drakeley et al. 2015; Lapiedra et al. 2017). Lizards were allowed to habituate for two minutes, after which time the cover was removed by pulling an attached string, signaling the start of the trial. All trials were recorded using a digital video camera placed on a tripod ~1 m from the foraging tray. Latency to feed (in seconds) was measured from these videos as the time from when the cover was removed from the foraging tray to when the first mealworm was captured. Experimental time was limited to 20 min and non-responses were assigned this maximum time.

Half of the foraging trials in each habitat type for each species were experimentally manipulated to test whether perch availability (for *A. sagrei*) and perceived predation risk (for *A. cristatellus*) influenced foraging decisions. For *A. sagrei*, we placed two perches directly between the focal lizard and the feeding tray to increase perch availability in these trials. Perches were ~3 cm in diameter and 1-m tall and constructed using wood collected from the study sites. Lizards readily used these perches in pilot trials. For *A. cristatellus*, we placed a static model of a bird predator ~30 cm behind the foraging tray to increase perceived predation risk. We used a taxidermy specimen of a pearly-eyed thrasher (*Margarops fuscatus*), a bird commonly found in both urban and natural areas of San Juan that has been previously reported to prey upon anoles (Adolph and Roughgarden 1983).

In addition to these experimental manipulations, we also measured a number of variables that could potentially influence latency to feed. Because lizard-accessible perches may serve as refuges or increase the possibility of detecting predators, we measured the number of perches within a 1 m radius of the focal lizard for *A. cristatellus* and within 0.5 m of the line between the feeding tray and focal lizard for *A. sagrei*, not including experimentally-added perches. We standardized these measures by calculating perch density (i.e., number of perches per unit area). Perches were considered as any substrate elevated above

20 cm and >0.5 cm in diameter. We also measured the perch height of the focal lizard at the start of the trial because lizards perched higher may be satiated from previous foraging opportunities (Stamps 1977). Higher perches may also enable lizards to survey a larger area and thus receive more information regarding predation risk (Scott et al. 1976) prior to foraging.

Foraging decisions can also be influenced by temperature. As ectotherms, body temperature greatly affects lizard locomotor performance (Angilletta 2009) and digestive efficiency (Harwood 1979). Because urban areas often act as heat islands (Oke 1973), their higher ambient temperatures relative to nearby natural areas could increase the body temperatures of urban lizards. To estimate body temperature, we placed a copper lizard model at the original position of the focal lizard and allowed temperature readings to stabilize before recording its internal temperature (Hertz 1992; Gunderson and Leal 2015).

While conspecific presence can dilute predation risk (as reviewed by Roberts 1996) or provide cues regarding the quality of a resource patch (Stamps 1987), higher conspecific densities also increase intraspecific competition and the chance of missing foraging opportunities (Drakeley et al. 2015). We measured the number of conspecifics within a 5 m radius of the focal lizard for *A. cristatellus* and within a 3 m radius of the focal lizard for *A. sagrei*. Again, we standardized these measures by calculating conspecific density (i.e., number of conspecifics per unit area). We also recorded whether one or more conspecifics approached the foraging tray during the trial. In laboratory-based staged encounters, larger individuals successfully defended preferred perches from smaller anoles (Tokarz 1985). Because similar outcomes could result during competition for foraging opportunities, we measured body size as snout-vent length (SVL) and mass from a representative sample of each lizard population. We also used these measurements to calculate body condition (i.e., scaled mass index following the methods of Peig and Green 2009) as a proxy for motivation, given that whether a lizard is hungry or satiated (i.e., motivational state) can influence the trade-off between costs and benefits when making a foraging decision. For example, a lizard may be willing to accept greater risk in order to acquire food if it has not fed for an extended period of time or if prey items are rarely encountered. We also calculated body condition for a subset of *A. sagrei* individuals that we were able to capture following their foraging trial (this was not done for *A. cristatellus*). To estimate the original body mass of these individuals, we measured the average weight of each mealworm and subtracted the mass of any mealworms consumed from the mass of each lizard.

Statistical analysis

We tested for statistical differences in latency to feed by performing survival analysis. We used a Cox proportional hazards model available in the R-package "survival" (Therneau

and Lumley 2015). This semi-parametric model is capable of dealing with right-censored data such as those obtained by limiting our foraging trials to a maximum of 20 min. Model selection was based on AICc scores (Burnham and Anderson 2004) and only significant (or marginally non-significant) factors were retained in the best models. Following Burnham and Anderson (2004), the model with the fewest factors was favored when models differed by less than two units from the best model. Differences in mean SVL, mass, body condition, estimated body temperature, conspecific density and perch availability among habitat types were tested using t-tests or analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) post hoc tests when data were normally distributed (as determined from Shapiro-Wilks test of normality). When data could not be normalized, differences were tested using Kruskal-Wallis rank sum tests (pairwise) or Dunn's test (multiple comparisons; R-package "dunn.test"; Dinno 2016) using rank sums with Bonferroni correction. For the subset of *A. sagrei* individuals we were able to measure following their foraging trial, we tested the relationship between body condition and latency to feed using Pearson's product moment correlation. All analyses were performed using R statistical software (R Development Core Team 2015).

Results

For *A. cristatellus*, lizards from forest habitats fed faster than those from urban habitats (coeff. = −0.82, $z = -2.12$, $p = 0.034$, Fig. 1) and had an overall greater response rate (63% in forest vs. 26% in urban). Similarly, *A. sagrei* from forests fed faster than those in either suburban (coeff. = −1.50, $z = -2.95$, $p = 0.003$) or urban habitats (coeff. = −1.67, $z = -3.01$, $p = 0.003$). Forest *A. sagrei* also had a greater response rate (38%) than those from urban (10%) or suburban (11%) habitats. However, latency to feed did not differ between urban and suburban habitats for *A. sagrei* (coeff. = −0.17, $z = -0.25$, $p = 0.799$, Fig. 2). Habitat type was the only factor in the best model for *A. sagrei*, whereas habitat type, perch height, and conspecifics present at the foraging tray were significant factors for *A. cristatellus* (Table 1). Specifically, higher-perching *A. cristatellus* individuals took longer to feed than those perched nearer to the ground (coeff. = −0.01, $z = -3.48$, $p < 0.001$), and focal lizards tended to have shorter latencies when a conspecific attempted to feed from the tray (coeff. = 0.74, $z = 1.87$, $p = 0.06$).

At the habitat level, there were more perches available in natural forests compared to urban habitats for *A. cristatellus* (Kruskal-Wallis rank sum test; $X^2 = 20.42$, df = 1, $p < 0.001$; Table 2). The number of available perches for *A. sagrei* was also higher in natural habitats compared to both urban (Dunn's test using rank sums; $z = -4.12$, df = 2, $p < 0.001$) and suburban (Dunn's test using rank sums; $z = -4.87$, df = 2, $p < 0.001$) habitats, but urban and suburban habitats did not differ (Dunn's test using rank sums; $z = 0.71$, df = 2, $p = 0.720$). Forest *A. sagrei* were smaller (SVL) and weighed less than suburban and urban populations (Table 2), but urban and suburban lizards did not differ. Urban *A. sagrei* had better body condition compared to forest lizards (Table 2), but suburban lizards did not differ from either urban (Dunn's test using rank sums; $z = 1.17$, df = 2, $p = 0.122$) or forest populations (Dunn's test using rank sums; $z = 1.00$, df = 2, $p = 0.160$). The relationship between latency to feed and body condition for *A. sagrei* captured following a foraging trial was not significant for either the urban/suburban (Pearson's product-moment correlation; $t = -0.31$, df = 56, $p = 0.758$) or natural forest habitat (Pearson's product-moment correlation; $t = -0.39$, df = 29, $p = 0.708$). Forest *A. cristatellus* were also smaller (SVL) and weighed less compared to urban lizards, but body condition did not differ between these populations (Table 2).

Discussion

Anoles in urban habitats took longer to feed than those in forest habitats, a result consistent across two species in two geographically distinct locations. Moreover, a large proportion of urban lizards (80–90%) never responded to foraging opportunities in our experimental trials. This is contrary to

Fig. 1 Survival analysis comparing latency to feed of *A. sagrei* populations from natural forest ($n = 42$), suburban ($n = 44$) and urban habitats ($n = 42$)
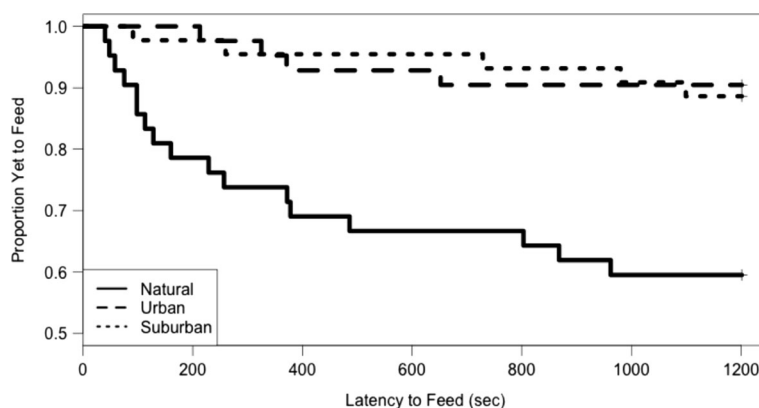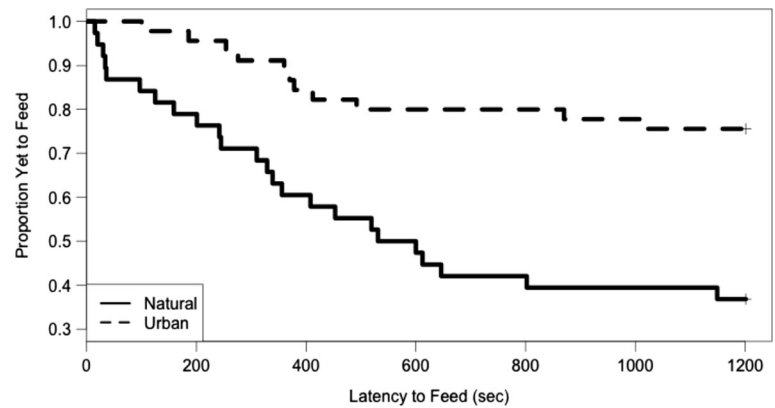
Fig. 2 Survival analysis comparing latency to feed of *A. cristatellus* populations from natural forest (*n* = 38) and urban habitats (*n* = 45)

research on birds and mammals in which greater foraging activity was observed in experimental food patches placed in urban habitats compared to natural ones (Bowers and Breland 1996; Shochat et al. 2004). While such studies are rare in lizards, a recent study on delicate skinks (*Lampropholis delicata*) found no differences in foraging-related behaviors between urban and forest populations (Moulé et al. 2015). Although our experimental manipulations of perch availability and predator presence did not affect anole foraging, *A. cristatellus* had shorter latencies to feed when perched lower and when conspecifics attempted to forage. The difference in anole foraging between urban and natural habitats could result from variation in at least three factors: perceived predation risk, motivation of lizards to forage, or neophobia.

If anoles perceive greater predation risk in urban versus forest habitats, this could explain why most urban anoles were unwilling to forage. Perceived risk could be increased by reduced perch availability in urban areas, thereby increasing exposure to potential predators. Perch density in each of our urban foraging trials was at least 50% lower than in forest trials (Table 3). Previous work has linked decreased vegetative cover to an increase in predation pressure using mesocosms (Finke and Denno 2002) and clay models (Shepard 2007). However, perch availability was not a significant factor influencing latency to feed, even when experimentally increased in *A. sagrei* foraging trials.

An increase in perceived predation risk could also reflect higher predator abundance in urban habitats (Sorace 2002).

The extirpation of top predators from urban areas can increase mesopredator abundance (Soulé et al. 1988; Rogers and Caro 1998; Crooks and Soule 1999). Many potential predators of anoles have successfully colonized urban areas, including birds (Clergeau et al. 1998; Croci et al. 2008), mammals (Ordeñana et al. 2010) and other lizards (Smith et al. 2004). Although this study did not assess predator abundance, we saw multiple bird species, including great egrets (*Ardea alba*) and yellow crowned night-herons (*Nyctanassa violacea*), searching for and consuming anoles in urban habitats (Z. Chejanovski, *pers. obs.*). Anoles likely detect such predators via movement; movement of a model snake, for instance, elicited a deterrent response from anoles in Puerto Rico (Leal 1999). The lack of any response by *A. cristatellus* to our model predator likely reflects the absence of any movement; during one trial, a lizard actually perched on the model's head. This lack of response emphasizes the importance of coupling life-like models with movement to simulate the presence and hunting strategy of a particular predator.

The urban-forest difference in foraging behavior may also reflect habitat-linked variation in the motivational state of each lizard population. Although we attempted to control for among-individual differences in motivation by only selecting anoles found in survey posture (see Methods; Drakeley et al. 2015), perch height may also indicate anole foraging motivation. Perch height negatively influenced willingness to feed for *A. cristatellus* (Table 1), and Stamps (1977) observed that female anoles perched higher after being fed to satiation. If

Table 1 Results of the best Cox proportional hazards model for each species summarizing the effects of each factor on latency to feed relative to natural habitats

A. sagrei	Variable	Coeff.	Exp(coef)	SE(coef)	Z	*P*-value
	Suburban	-1.50	0.22	0.51	-2.95	0.003
	Urban	-1.67	0.19	0.56	-3.01	0.003
A. cristatellus	Urban	-0.82	0.44	0.39	-2.12	0.034
	Conspecifics Present	0.74	2.10	0.40	1.88	0.061
	Perch Height	-0.01	0.99	0.01	-3.48	< 0.001

Latency to feed did not differ between urban and suburban habitats for *A. sagrei* ($z = -0.254$, $p = 0.799$)

Table 2 Summary of statistical tests comparing mean differences between urban and natural forest habitats

	A. cristatellus			A. sagrei		
Variable	Statistic	df	P	Statistic	df	P
Perch Height	$t = -2.53$	75.67	0.013	$z = -3.17$	2	<0.001
Conspecific Density	$X^2 = 0.18$	1	0.668	$z = 2.89$	2	0.002
Body Temperature	$t = -11.21$	79.69	<0.001	$q = 42.41$	2	0.999
Perch Availability	$X^2 = 20.42$	1	<0.001	$z = -4.12$	2	<0.001
SVL	$t = 3.89$	33.54	<0.001	$z = 4.43$	2	<0.001
Body Mass	$t = 3.43$	37.96	<0.001	$z = 5.03$	2	<0.001
Body Condition	$X^2 = 19$	19	0.457	$z = 2.27$	2	0.012

Because most values for suburban *A. sagrei* were statistically indistinguishable from those in urban habitats, comparisons between suburban and forest habitats are not shown

higher-perching *A. cristatellus* are more likely to be satiated, lower-perching lizards may be more receptive to ground-dwelling prey. Consistent with the "motivational state" hypothesis, we found that urban lizards in both species were larger (SVL and mass) and, for *A. sagrei*, in better body condition than their forest-dwelling conspecifics (Table 3). Body condition may represent a measure of the energy stores available to an organism, acquired from previous foraging opportunities (Jakob et al. 1996). In ground squirrels (*Spermophilus beldingi*), for instance, individuals with lower body condition spent more time foraging under risky conditions (Bachman 1993). Additionally, Allenby's gerbils (*Gerbillus andersoni allenbyi*) supplemented with food (thus increasing condition of these individuals) allocated more time surveying for predators and less time foraging under predation risk (Kotler et al. 2004). If forest anoles are more food-limited, they may choose to feed on the ground despite the risk. Such "risky" behavior occurs when the costs of a missed opportunity exceeds those caused by predation (Lima and Dill 1990), which is often the case when food is scarce. Lizards alter their behavior in relation to food availability, and may take more risks when resources are scarce; anoles, for instance, responded faster to feeding trays containing less food than to trays with more food

(Drakeley et al. 2015). *Podarcis* lizards decreased flight-initiation distance in response to increasing food abundance (Cooper et al. 2006), highlighting their ability to weigh the costs of predation risk against the benefits of resource acquisition. Nonetheless, in our study, the relationship between latency to feed and body condition was not significant in either urban/suburban or natural forest populations of *A. sagrei*.

Neophobia, the tendency of an animal to avoid novel food resources or objects, could also explain the response of urban anoles to our foraging trays. While neophobic behaviors protect animals from the dangers associated with unfamiliar stimuli (Greenberg 1990; Greenberg and Mettke-Hofmann 2001), they can also hinder the ability of animals to exploit novel food resources, a trait central to the success of some urban species (Sol et al. 2011). The fact that the mealworms used in this study are not a common food resource in urban areas may have deterred the anoles. In a previous study, however, a majority of anoles from similar urban habitats responded when mealworms were presented without a feeding tray (Lapiedra et al. 2017); this suggests that the feeding tray itself may elicit neophobia in urban anoles. However, other herpetological studies comparing urban and natural conspecifics found no differences in neophobia (Candler and Bernal 2015; Moulé et al. 2015).

Table 3 Summary of variables (mean ± SE) hypothesized to influence latency to feed for each species in each habitat type

	A. cristatellus		A. sagrei		
Habitat Type	Natural	Urban	Natural	Suburban	Urban
N	38	45	42	44	42
Perch Height	137.33 ± 9.12	167.39 ± 1.13	116.48 ± 8.03	89.61 ± 7.29	83.79 ± 6.84
Conspecific Density	0.04 ± 0.0006	0.04 ± 0.0004	0.02 ± 0.005	0.05 ± 0.008	0.05 ± 0.006
Body Temperature	30.58 ± 0.02	32.66 ± 0.02	30.87 ± 0.33	30.77 ± 0.44	30.85 ± 0.40
Perch Availability	3.73 ± 0.28	1.82 ± 0.24	3.15 ± 0.32	1.23 ± 0.30	1.36 ± 0.24
N	20	20	31	26	32
SVL	65.4 ± 0.45	68.5 ± 0.66	52.58 ± 0.91	58.23 ± 0.88	58.09 ± 0.65
Body Mass	8.63 ± 0.30	10.12 ± 0.31	3.60 ± 0.20	5.24 ± 0.25	5.37 ± 0.18
Body Condition	9.30 ± 0.41	9.08 ± 0.37	4.98 ± 0.08	5.07 ± 0.11	5.30 ± 0.11

Our results demonstrate clear differences in foraging behavior between anoles from urban and forest habitats. These patterns could result from differences in perceived predation risk, motivation to forage, neophobia, or a combination of these factors. Although selection pressures in urban and natural habitats likely favor different behavioral strategies (Hendry et al. 2008; Audet et al. 2016; Lapiedra et al. 2017; reviewed in Sol et al. 2013), we are far from understanding how urbanization alters animal behavior (Shochat et al. 2006). Furthermore, it is pivotal that future research address whether changes in foraging and other behaviors can allow animal populations to persist in urban environments, which is critical to predict and mitigate potential changes in biodiversity.

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