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IMPACTS OF URBANIZATION AND INVASIVE SPECIES ON FORAGING BEHAVIOR AND BODY SIZE IN *ANOLIS SAGREI*

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IMPACTS OF URBANIZATION AND INVASIVE SPECIES
ON FORAGING BEHAVIOR AND BODY SIZE IN *ANOLIS*

SAGREI

BY

ZACHARY ALAN CHEJANOVSKI

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE

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DOCTOR OF PHILOSOPHY DISSERTATION

OF

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ABSTRACT

Urbanization dramatically alters the abiotic and biotic environment of cities, favoring species that are pre-adapted or are able to adapt (e.g. through phenotypic plasticity or evolutionary mechanisms) to these novel conditions. While urbanization is widely considered one of the greatest threats to biodiversity worldwide, we still lack a general understanding of the mechanisms underlying organismal responses to human-induced rapid environmental change. The focus of this thesis was to examine how urbanization-induced changes in the abiotic and biotic environment influence the foraging behavior and body size of the brown anole, *Anolis sagrei*. In Chapter 1, we presented anoles from habitats differing in their levels of urbanization with an experimental feeding opportunity to assess differences in foraging decisions. We also manipulated perch availability and the presence of predators to determine whether and how these factors influence foraging decisions. While our manipulations had little effect, we found that anoles from natural forest habitats responded faster and more often to the experimental feeding opportunity compared to conspecifics from urban and suburban populations. In Chapter 2, we utilized gut-content and stable isotope analysis in the same populations as in Chapter 1 (i.e. natural forest, suburban and urban) to identify whether and how changes in the composition of prey and primary producers influence the trophic structure of urban food webs. We found that the differential consumption of prey by anoles among habitat types was only partially consistent with the differences observed among their isotopic niches. Specifically, greater proportional consumption of carnivorous arthropods in natural forest anoles compared to urban and suburban conspecifics was consistent with variation along the

N^{15} axis of their isotopic niche. However, isotopic niches were primarily differentiated along the C^{13} axis, which was not consistent with differences in the proportional consumption of other taxa among habitat types. Furthermore, urban and suburban anoles incorporated substantial amounts of grass-based carbon into their tissues, suggesting that changes in trophic structure were primarily driven by the presence of C_4 grasses in urban areas. In Chapter 3, we assessed the role of abiotic and biotic factors in determining the body size of brown anoles across an urbanized landscape. Given our finding of a positive relationship between anole body size and predator abundance, we then performed a manipulative field experiment and laboratory study to identify the mechanisms behind this pattern. In the field, we presented tethered male brown anoles that varied in body size to predatory curly-tailed lizards (*Leiocephalus carinatus*). Curly-tailed lizards attacked smaller anoles more frequently and at shorter latencies compared to larger anoles. Finally, we conducted a common garden experiment to determine whether body size differences between habitats with and without predators are genetically determined. Male brown anoles from habitats with predators had faster growth rates compared to males from non-predator habitats. However, we found no differences in female growth rate between habitats.

Urban habitats are currently considered hotspots of rapid environmental change and consequently, rapid adaptation of urban taxa. This dissertation demonstrates potential mechanisms through which urbanization can cause organismal change and identifies specific traits that may favor the persistence of taxa in these novel habitats. Yet, our results also emphasize that conditions both within and among urban areas are quite variable over relatively small spatial scales. Urban populations separated by even

short distances are thus likely to experience markedly different selective pressures. This may be why organismal responses to urbanization-induced environmental change have been found to be mostly species and location specific. Indeed, the field of urban ecology has yet to produce conclusions that can be generalized beyond a few taxa, but this should not discourage future work on urban systems. In fact, our ability to predict and mitigate the negative impacts of urbanization is completely dependent on our knowledge of these specific effects. Therefore, we hope this work will encourage others to examine how urbanization influences other taxa and most importantly to determine the specific mechanisms underlying organismal change.

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with lizard storage facilities and experimental arenas. For this, as well as their unconditional love and support, I dedicate this dissertation to them.

PREFACE

This thesis is prepared in the manuscript format and each chapter is preceded by the publication status of each article or the journal intended for submission.

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CHAPTER 1

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.

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 potential predators and fewer refuges for prey (Whittingham and Evans 2004). Vegetative cover influenced escape behavior in the lizard *Psammmodromus 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. 2016), 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. 2016). 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. 2016). 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 minutes 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 minutes. 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; $r=-0.31$, $df=56$, $p=0.758$) or natural forest habitat (Pearson's product-moment correlation; $r=-0.39$, $df=29$, $p=0.708$). 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 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 Soulé 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 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. 2016); 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; Moule et al. 2015).

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. 2016; 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.

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

<i>A. sagrei</i>	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
<i>A. cristatellus</i>	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

Table 2 Summary of statistical tests comparing mean differences between urban and natural forest habitats. Because most values for suburban *A. sagrei* were statistically indistinguishable from those in urban habitats, comparisons between suburban and forest habitats are not shown.

Variable	<i>A. cristatellus</i>			<i>A. sagrei</i>		
	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

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

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

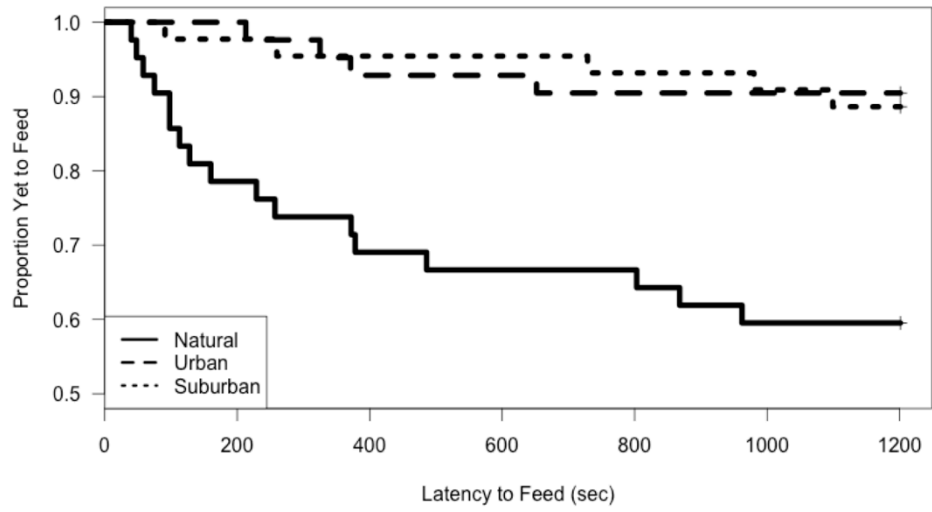


Fig. 1 Survival analysis comparing latency to feed of *A. sagrei* populations from natural forest (n=42), suburban (n=44) and urban habitats (n=42)

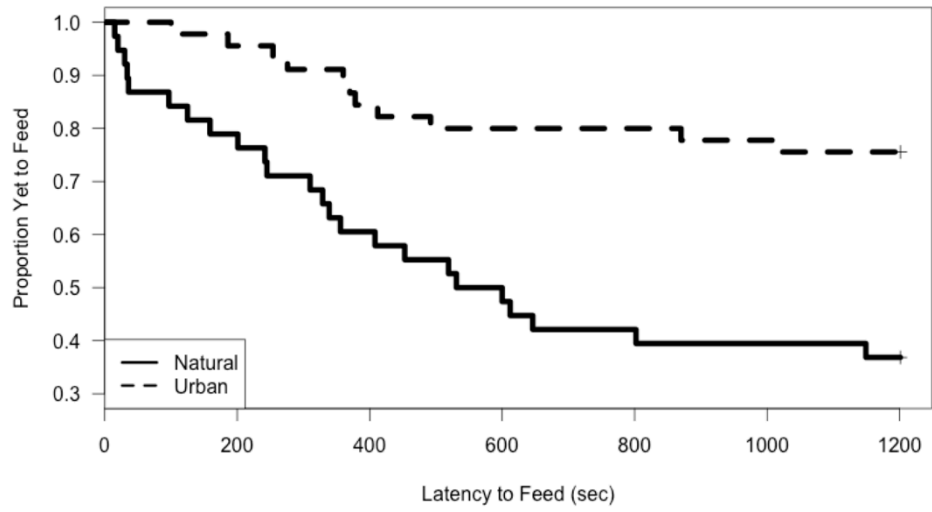


Fig. 2 Survival analysis comparing latency to feed of *A. cristatellus* populations from natural forest (n=38) and urban habitats (n=45)

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CHAPTER 2

IMPACTS OF URBANIZATION ON TROPHIC STRUCTURE AND TROPHIC NICHE OF A COMMON LIZARD, *ANOLIS SAGREI*.

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Abstract

Urbanization is one of the most dramatic forms of environmental change and can thus alter the trophic relationships among organisms that inhabit urban areas. However, there are multiple mechanisms through which urbanization can influence food web structure such as mesopredator release, anthropogenic subsidies, and alteration of basal resources. In this study, we compared brown anole (*Anolis sagrei*) populations from natural forest, suburban, and urban habitats to determine whether and how trophic structure is affected by urbanization. We combined gut-content and stable isotope analysis (C and N) of anole diets with field sampling of arthropods to assess the roles of prey consumption, prey availability, and primary producer composition in driving trophic niche variation of populations from different habitats. Brown anoles consumed proportionately more Coleopterans than were available in all sites, but hymenopterans were consumed more than their availability only in natural forest habitats. Anole isotopic niches among habitat types were primarily differentiated along the $\delta^{13}\text{C}$ axis. However, differences in prey consumption were generally inconsistent with observed patterns in their isotopic niches. IsoError mixing models revealed that nearly half of the carbon in urban and suburban anole tissues was derived from C_4 vegetation. Our results suggest that urbanization-induced variation in the trophic niche of brown anoles is primarily driven by differences in the composition of primary producers and specifically by the presence of grasses in both urban and suburban habitats. It is therefore imperative that future work considers the consequences of such alterations in basal resources for urban taxa and the food webs they comprise.

Introduction

Urbanization, one of the most dramatic forms of environmental disturbance, can alter the trophic relationships among organisms that inhabit urban areas (Faeth et al., 2005). Given that urbanization results in a number of environmental changes, there are multiple routes through which urbanization can influence food web structure. For example, habitat fragmentation has resulted in the disappearance of many apex predators from urban habitats (Estes et al., 2011). Without these predators, the abundance of smaller carnivores increases (i.e. mesopredator release), thereby strengthening their consumptive effects on lower trophic levels (Crooks & Soulé, 2011). However, urban predators may also utilize anthropogenic food subsidies, which can also increase their abundance but lower their need to prey on other taxa (Rodewald et al., 2011; Fischer et al., 2012). Variation in the type and intensity of urban land use can also lead to important changes in basal resources. Though the abundance and composition of both plant and arthropod assemblages have been shown to vary along urbanization gradients (McIntyre, 2000; McKinney, 2008; Williams et al., 2015), whether and how these changes influence urban food web structure remains poorly understood (but see Narango et al., 2017).

The composition of plant communities in native habitats, such as forests, differs markedly from the intensively managed assemblages characteristic of urban areas. Much of these differences can be attributed to the cultivation of non-native species in urban habitats (Turner & Freedman, 2005). In fact, the number of non-native species found in urban habitats can be up to a quarter of the total species

richness (e.g. Aronson et al., 2014). Gardening and other urban landscaping practices often ameliorate environmental stressors that would potentially limit non-native species from becoming established (Niinemets & Peñuelas, 2008). Furthermore, this may explain why areas of moderate development, such as residential gardens, have higher species richness compared to areas that are either more or less urbanized (McKinney, 2008). While the diversity of urban vegetation may be augmented through horticultural practices, these same ideals have led to the widespread proliferation of grass monocultures (Jenkins, 1994). Though lacking in diversity, lawns can influence the trophic structure of urban habitats simply by their abundance. Lawn grass produces significantly more biomass compared to similar vegetation in local prairies and agricultural fields (Golubiewski, 2006). Urbanization can thus lead to very different signals of primary production, such as that from C4 grasses used in lawns. Nonetheless, whether the spatial scale of primary producer variation matches that of primary and secondary consumers will likely determine if these changes transcend into higher trophic levels.

Given that many arthropods rely on vegetation for food, shelter and reproduction, it stands to reason that urbanization and its associated increases (e.g. introduction of non-natives) and decreases (e.g. proliferation of lawns) in plant diversity can cause arthropod richness to increase and decrease, respectively (as reviewed by McKinney, 2008). In addition to differences in species richness, studies have also demonstrated variation in the trophic structure of urban arthropod communities. For example, edge habitats produced by urban development promote higher herbivore abundance compared to taxa belonging to other feeding guilds (e.g.

predators and parasitoids), which is consistent with observations of higher rates of herbivory in these habitats (Christie et al., 2010). Urban mesopredators may then consume more arthropods that occupy lower trophic levels (i.e. herbivores) when compared to conspecifics in natural habitats. Moreover, the trophic level of mesopredators themselves should then be lower in urban habitats compared to natural ones. Even so, this is entirely dependent on the dietary habits and preferences of these mesopredators, and whether they might change in response to urbanization.

In addition to food web structure as a whole, urbanization-induced alterations of basal resources can have important consequences for the trophic niche of species inhabiting urban areas. First, lower prey diversity resulting from habitat fragmentation has been shown to cause contraction of predator trophic niches (e.g. Layman et al., 2007). Therefore, if arthropod diversity is lower in urban habitats relative to natural ones, we might expect narrower trophic niches in urban mesopredators compared to those that forage in natural habitats. However, consumers can exhibit selectivity for certain prey taxa (e.g. Backwell et al., 1998; Cupples et al., 2011; Klecka & Boukal, 2012), which may decouple the relationship between diversity of available prey and trophic niche breadth. Second, in addition to the differences in plant assemblages between urban and natural habitats, the composition of primary producers may also be highly variable both within and among urban habitats (Hope et al., 2003; Kinzig et al., 2005). Such variation within urban habitats can lead to expanded trophic niches, while variation among urban habitats could result in non-overlapping trophic niches among urban consumer populations.

Studies that utilize urban to rural gradients are often constrained by the limited number of species that occur across the entire gradient (McKinney & Lockwood, 1999). Even the use of closely related species along such gradients is likely to introduce variation that obscures habitat-specific patterns. However, when a single species can be found in both urbanized and natural habitats, this enables a more accurate assessment of how the trophic niche of that species, and food web structure in general, varies in response to urbanization. In this study, we compare populations of the brown anole (*Anolis sagrei*) inhabiting natural forest, suburban, and urban habitats (see methods for habitat descriptions) to determine whether and how trophic structure changes due to urbanization. We utilize gut content analysis coupled with arthropod sampling in the field to assess potential differences in prey use and availability among habitat types. We also perform stable isotope analysis to quantify and compare the isotopic niche of brown anoles across habitats. Lastly, we combine these two approaches to examine whether variation in the isotopic niche among brown anole populations is explained by differences in prey consumption, primary producer composition, or both.

Materials and methods

Study system

The brown anole is a small, semi-arboreal lizard found in both urbanized and natural habitats across its non-native range in Florida (Lapiedra et al., 2017). This species utilizes a sit-and-wait foraging strategy where individuals typically scan for potential prey while perched on the lower portion of tree trunks (typically no more

than ~2 meters high) and often descend to the ground during prey capture (Chejanovski et al., 2017). Brown anoles are considered dietary generalists and primarily consume insects and other arthropods (Losos, 2009). Indeed, multiple studies have described the dietary habitats of *A. sagrei*, though this work has primarily focused on insular populations in the Bahamas (Kartzinel & Pringle, 2015 and references therein). However, studies investigating the trophic dynamics of mainland *A. sagrei* are rare (but see Giery et al., 2013).

We compared food webs of brown anole populations inhabiting urban, suburban, and natural forest habitats (each replicated twice) in southeast Florida (Broward County). Urban habitats were characterized by high human traffic, high impervious surface cover, and little canopy cover compared to natural forest habitats that consisted of large fragments of secondary forest, little to no human traffic, and relatively closed canopies. Suburban habitats were long stretches of continuous vegetation found along roadsides chosen to represent an intermediate between natural forests and urban habitats in terms of human traffic, impervious surface cover and canopy cover (GPS coordinates for each site in Supplementary Materials).

Diet and Arthropod Availability

Twenty male brown anoles from each of our six sites were captured, measured (i.e., snout-vent length and mass), and collected. Males were used for this study due to their conspicuousness and ease of capture in the field. In the lab at the University of Rhode Island, we dissected each lizard, removing the entirety of the digestive tract (i.e., stomach and intestine) for gut-content analysis. Arthropod prey fragments were

identified to Order and counted for each lizard. In addition to prey abundance, we also calculated the proportion of each prey category within the stomach of each lizard. Diversity of prey taxa was calculated using Simpson's Index of Diversity for both prey found within the stomach of each lizard and prey taxa pooled for each site.

To estimate food availability from ground arthropod abundance, we deployed four pitfall traps in each site at random intervals between 10-20 meters along an established transect (transect length was no more than 100 meters). Each pitfall trap was filled with a solution of soap and water to prevent arthropods from escaping. We collected pitfall traps after 24 hours and arthropods were preserved in isopropyl alcohol and transported to the lab for identification. We identified arthropods to Order and our classifications of potential prey generally matched the taxa considered in previous studies on brown anole diets (e.g., Schoener, 1968; Lister, 1976; Spiller & Schoener, 1990; Giery et al., 2013; Kartzinel & Pringle, 2015; Stroud et al., 2017). We included absolute and proportional abundance, as well as taxonomic diversity as measurements of food availability, which were averaged for each site (for comparisons to prey consumption) and across habitat types (for comparisons among habitat types).

Stable Isotope Analysis

Stable isotopes, particularly those of carbon and nitrogen, have been used extensively in studies of trophic ecology and the factors influencing trophic structure (Layman et al., 2007; Boecklen et al., 2011). Nitrogen is used to assess trophic level such that higher ratios of N^{15}/N^{14} ($\delta^{15}N$) are indicative of species that feed at higher

trophic positions (e.g. predators; Post, 2002). Carbon is used to provide information regarding basal resources. For example, grasses using the C₄ metabolic pathway and organisms that consume these grasses contain elevated ratios of C¹³/C¹² ($\delta^{13}\text{C}$) compared to the relatively depleted signatures of C₃ plants and their consumers (Layman et al., 2012). Together, these isotopic ratios can represent a time-integrated measure of the trophic niche compared to other methods, such as gut-content analysis that instead provide a brief snapshot of ongoing trophic dynamics (Tieszen et al., 1983; Dalerum & Angerbjörn, 2005). However, studies that make use of both gut-content and stable isotope analysis can provide insight into which trophic levels (i.e., primary producers versus consumers) are responsible for changes in trophic structure. Therefore, we collected tail-tips from each lizard for analysis of isotopic composition of carbon and nitrogen. Additionally, we collected 3-5 leaves from each of the dominant primary producers at each site for stable isotope analysis (see below).

Statistical Analysis

We tested for differences in the proportional availability and consumption of arthropods within each site using Welch's two-sample t-tests. We also compared the proportional availability, diversity and consumption of arthropods among habitat types using Kruskal-Wallis Rank Sum Tests and Dunn's test for multiple comparisons with Bonferroni correction post hoc given that these data were not normally distributed. Hymenoptera and Coleoptera represented the majority of gut contents (>50% across sites; >80% across habitats) in most individual anoles and were well sampled by our pitfall traps. Therefore, we restricted most of our analyses to these two groups. We

suspect that Dipterans may have been attracted to the liquid in our pitfall traps and were likely oversampled. Also, our pitfall traps may have poorly sampled spiders given that many of these taxa are arboreal. Therefore, we did not compare Dipteran and spider availability to consumption, but rather only compared availability (except spiders) and consumption of these taxa among habitat types. However, all taxa were included in calculations of diversity.

Isotopic niches were generated using bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using the SIBER package (Jackson et al., 2011) available in R. We used the “standard.ellipse” function that employs maximum-likelihood estimators to produce ellipses that encompass approximately 40 percent of the bi-plot data within each site, thereby reducing the impact of outliers. This function also provides calculations of the area of each ellipse (corrected for small sample size) as a measure of isotopic niche width, which we compared among sites and habitat types. To test for specific differences along each axis of the isotopic niche (i.e., carbon and nitrogen), we compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among habitat types using Kruskal-Wallis Rank Sum Tests and Dunn’s test for multiple comparisons with Bonferroni correction post hoc. Prior to this analysis, we standardized $\delta^{15}\text{N}$ values by subtracting the mean $\delta^{15}\text{N}$ value of primary producers in a given site from the $\delta^{15}\text{N}$ of each brown anole from that site. Variable lipid content has been shown to influence $\delta^{13}\text{C}$ values of consumers (Post et al., 2007). However, we have no reason to expect lipid content to vary among anoles from different habitat types and thus we do not account for this in our analyses. Similarly, discrimination factors are also likely to be similar in anoles from different habitat types and thus we do not use any discrimination factors in our analyses. We also used

the $\delta^{13}\text{C}$ values of our urban and suburban primary producers to calculate the proportion of C_3 and C_4 based carbon contributing to the diet of brown anoles in each site through IsoError mixing models (Phillips & Greg, 2001; Giery et al., 2013).

Results

Coleopterans were consumed by brown anoles in greater proportions than were available in all sites (Table 1; $p < 0.001$ for all comparisons using Welch's two-sample t-test). Hymenopterans were consumed in greater proportions than were available only in natural forest sites (Fern Forest: $t = 4.107$, $df = 8.125$, $p = 0.003$; Markham: $t = 4.528$, $df = 20.894$, $p = 0.0002$), but urban and suburban anoles consumed them in proportion to their availability. Urban anoles consumed proportionately more coleopterans when compared to natural and suburban anoles (Dunn's test for multiple comparisons; $X^2 = 10.901$, $df = 2$, $p < 0.01$), which did not differ from each other (Fig. 1A). Urban anoles also consumed proportionately less hymenopterans compared to anoles from natural forest habitats ($X^2 = 6.624$, $df = 2$, $p = 0.018$; Fig. 1B). Dipterans were consumed in similar proportions across habitat types ($X^2 = 3.179$, $df = 2$, $p = 0.204$). Spiders were consumed in larger proportions by natural forest anoles (MEAN = 0.079, SD = 0.175) compared to those from urban habitats (MEAN = 0.012, SD = 0.031; $X^2 = 5.069$, $df = 2$, $p = 0.046$), but suburban anoles (MEAN = 0.047, SD = 0.111) were similar to those from both urban and natural forest habitats. The proportional availability of Coleopteran, Hymenopteran and Dipteran taxa did not differ among habitat types ($X^2 = 2.403$, $df = 2$, $p = 0.3006$; $X^2 = 3.012$, $df = 2$, $p = 0.2218$; $X^2 = 4.051$, $df = 2$, $p = 0.132$, respectively; Fig. 1D-E, Dipteran data not shown due to low proportional values). We found no differences

in the mean gut-content diversity of individuals among habitat types ($X^2=4.237$, $df=2$, $p=0.1202$; Fig. 1C), as well as no difference in diversity when consumed taxa were pooled by site ($X^2=0.286$, $df=2$, $p=0.870$). However, urban habitats had higher arthropod diversity compared to natural and suburban habitats ($X^2=8.322$, $df=2$, $p=0.020$), but natural and suburban habitats did not differ in diversity (Fig. 1F).

We observed significant differences in the mean values for all pairwise comparisons among the three habitat types for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of anoles ($p<0.05$ for all comparisons using Dunn's test). $\delta^{13}\text{C}$ values among habitat types indicated that suburban anoles incorporated the most grass-based carbon into their tissues, followed by urban anoles, and lastly natural forest anoles where no grasses were observed. $\delta^{15}\text{N}$ values among habitat types indicated that natural forest anoles occupy the highest trophic levels, followed by urban, and then suburban anoles (Fig. 2).

On average, isotopic niche widths were widest in urban habitats (mean = 2.92) and suburban and natural habitats were similar (1.72 and 2.03 respectively; Fig. 3). Moreover, the two urban sites had non-overlapping ellipses indicating greater among site variation as compared to the natural forest and suburban sites. Primary producers from both urban and suburban habitats had distinct carbon signatures: C_4 grasses (i.e. St. Augustine Grass, *Stenotaphrum secundatum*) had $\delta^{13}\text{C}$ values that were relatively enriched (mean=-13.438, $SD=0.527$) compared to C_3 vegetation (mean=-28.804, $SD=1.334$). Also, the mean $\delta^{15}\text{N}$ values for our primary producers were significantly different among all habitat types ($X^2=49.245$, $df=2$, $p<0.01$; results not shown). Lastly, IsoError mixing models showed a substantial contribution of grass-based carbon to the diet of both suburban and urban anoles (56% and 43%, respectively).

Discussion

We compared the prey use and isotopic niches of six brown anole populations in habitats differing in their level of urbanization to determine whether and how urbanization influences trophic structure. While there were no differences in the availability of arthropod prey (i.e. Coleoptera, Hymenoptera, and Diptera) across habitats (Fig. 1D,E), brown anoles consistently selected Coleopterans (i.e. beetles), consuming them in greater proportions than were available in all sites. Additionally, anoles from natural habitats showed selectivity for Hymenopterans (i.e. ants and bees) as well. The greater proportional consumption of spiders by natural forest anoles compared to those from other habitats was consistent with variation in $\delta^{15}\text{N}$ among habitat types. However, isotopic niches were primarily differentiated along the $\delta^{13}\text{C}$ axis (Fig. 3) and almost half of the carbon in urban and suburban lizard tissues was derived from C_4 grasses, as indicated by the IsoError mixing models. While this is consistent with differences in primary producer composition between natural forest and urban/suburban habitats, these isotopic patterns did not match those regarding the differential consumption of prey taxa (Fig. 1A,B). Our results suggest that urbanization-induced variation in the trophic niche of brown anoles is primarily driven by differences in the composition of primary producers and specifically by the presence of grasses in urban habitats.

Many lizards, including anoles, are considered opportunistic generalists and as such, the composition of their diets is expected to fluctuate along with prey availability (Pianka, 1973). For example, Kartzinel & Pringle (2015) found that the

composition of brown anoles diets in the Bahamas varied among seasons, which they suggest may be due to different availabilities of prey species in wet and dry periods. Such seasonal variation in diet composition has also been shown in other anoles (e.g., Lister 1981; Bullock et al., 1993). However, there is increasing evidence suggesting that lizards, in general, may be more selective of their prey than previously recognized (Carretero, 2004). Brown anoles in Taiwan, for example, had similar prey items in their stomachs from month to month (Norval et al., 2010). In our study, differences in the proportional consumption of prey among habitat types were not explained by differences in availability. Coleopterans were similarly available among habitat types, while urban anoles consumed proportionately more of them compared to suburban and natural forest anoles (Fig. 1). Coleopterans were also consumed in greater proportions than were available in all sites, further supporting that brown anoles may be exhibiting prey selection. Coleopterans have been reported in previous studies to comprise a significant proportion of brown anole diets (e.g., Schoener, 1968; Lister, 1976; Spiller & Schoener, 1990). Therefore, while brown anoles may not necessarily specialize on beetles, characterizing them as dietary generalists may not be entirely accurate.

Many factors can contribute to variation in the isotopic niche among populations including competitive interactions (e.g. Comas et al., 2014), behavioral differences (e.g. Cherel et al., 2007), and prey consumption, prey availability and primary producer composition as considered in this study. Proportional prey consumption was similar between suburban and natural forest anoles, but differed for urban lizards. In contrast, the isotopic niches of these anoles were significantly different among all habitat types and were primarily differentiated along the $\delta^{13}\text{C}$ axis.

C₄ grasses in our urban and suburban sites exhibited enriched $\delta^{13}\text{C}$ signatures compared to that of C₃ vegetation (see Results). Since grasses were not found in our natural forest habitats, it is unsurprising that the lizards from these habitats had the lowest $\delta^{13}\text{C}$ values of around -26.1%, demonstrating dependence on prey that consume C₃ vegetation. Urban and suburban anoles, however, exhibited enriched $\delta^{13}\text{C}$ signatures of approximately -22.1% and -21.0%, respectively, indicating greater reliance on grass-based carbon compared to natural habitats. Indeed, IsoError mixing models showed that a substantial proportion of the carbon in urban and suburban anole tissues is derived from C₄ vegetation. These results are in agreement with previous studies showing incorporation of grass-based carbon, when available, by anoles and other lizards (Magnusson et al., 2001; Giery et al., 2013). Furthermore, Magnusson et al. (2001) found that the proportion of C₃ based carbon in lizards' tissues was positively related to the proportional cover of these types of plants. Though we did not measure the percent cover of grasses relative to other C₃ plants in our study sites, suburban habitats generally had more grass compared to urban habitats, whereas grasses were not observed in forested sites. Therefore, we suspect that the relationship between anole $\delta^{13}\text{C}$ values (Fig. 2), the proportion of grass-based carbon in urban/suburban anole tissues, and increasing levels of urbanization reflects similar patterns in the abundance of C₄ grasses in these habitats. Increases in material and energy flux across habitat boundaries can aid in the stabilization of food webs (Huxel & McCann, 1998). In our urban and suburban habitats, anoles couple understory (i.e. grass) and canopy food webs by consuming arthropods from these two habitats. Previous work has shown that such coupling results from the movement of prey, rather

than the movement of predators, among these habitats (Giery et al., 2013). Urban food webs may thus benefit from the stabilizing effects of such allochthonous inputs compared to those of natural forest habitats, in which such energy flows are absent.

In addition to the presence of C₄ grasses, the spatial heterogeneity of urban habitats can also be an important driver of trophic structure. Urban brown anoles had wider isotopic niches compared to those inhabiting natural forest or suburban habitats (see results; Fig. 3), which were driven by a greater dispersion of individuals in isotopic niche space (i.e., the space within the bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) within each urban site. There was no overlap in isotopic niches between the two urban sites compared to the partial overlap observed among the pairs of suburban and forest sites, which suggests that urban habitats may be more variable in primary producer composition across sites. Indeed, the species richness of urban plant assemblages has been shown to be highly variable and linked to factors such as differential land use and socioeconomic status (Hope et al., 2003; Kinzig et al., 2005). Given that male brown anoles maintain small territories and exhibit high site fidelity (Calsbeek, 2009), their isotopic niches could accurately represent this fine-scale spatial variation in primary producer composition, as well as variation in prey composition within each site. If we had instead used a study organism that forages more broadly, this may have masked the patterns observed in isotopic niches among habitats. We therefore suggest that future research on the trophic structure of urban communities consider whether the scale at which resources are used by an organism matches the scale at which they vary in the environment.

While the isotopic niches of brown anoles among habitat types primarily varied along the $\delta^{13}\text{C}$ axis, we also detected significant variation in $\delta^{15}\text{N}$. Specifically, $\delta^{15}\text{N}$ was enriched in natural forest lizards compared to urban and suburban conspecifics and this variation could result from a number of factors. First, if primary producers in urbanized habitats contain elevated $\delta^{15}\text{N}$ values, this could lead to the elevation of $\delta^{15}\text{N}$ values for all subsequent trophic levels. $\delta^{15}\text{N}$ values were significantly different among habitats both before and after correcting for differences in primary producer $\delta^{15}\text{N}$ values. Thus, differences in $\delta^{15}\text{N}$ values of primary producers among habitat types may only partially explain the differences in anole $\delta^{15}\text{N}$ values. Furthermore, the potential causes of increased $\delta^{15}\text{N}$ in primary producers are numerous and often complex. For example, in a global study, foliar $\delta^{15}\text{N}$ values were significantly related to climatic factors (i.e. mean annual temperature and precipitation), nitrogen availability, and associations with mycorrhizal fungi (Craine et al., 2009). Second, anoles may occupy higher trophic levels in natural forest habitats by consuming carnivorous arthropods rather than those that feed on plant matter. Spiders represent the only strictly carnivorous prey taxa considered in this study. Anoles from natural forest habitats consumed proportionately more spiders compared to urban and suburban anoles, although the latter comparison was not significant. These results support a role for spider consumption in the elevated trophic position of natural forest anoles. Had we accurately measured the availability of spiders among habitats, this may have lent support to the hypothesis of greater abundance and consumption of herbivorous arthropods in edge (i.e. urban and suburban) habitats compared to natural ones (Christie et al., 2010). Therefore, habitat type may influence

anole trophic level and food chain length through alterations in the composition of arthropod feeding guilds. However, more research is needed to confirm these observations, and we suggest using sampling strategies that specifically target arthropods from these various feeding guilds.

We demonstrate that urbanization can have dramatic effects on trophic structure through alterations to the composition of primary producer communities. Our results suggest that the incorporation of grass-based carbon into the diet of urban and suburban brown anoles is primarily responsible for the differentiation of their isotopic niches. Grasses are a fundamental part of most urbanized habitats in North America (Melesi et al., 2005), and thus our results likely apply to a number of insectivorous and herbivorous taxa inhabiting or foraging in urban areas. Furthermore, the area of urban land cover is projected to triple by 2030 (Seto et al., 2012), and so we can expect similar increases in the cover of these grasses. It is therefore imperative that future work considers the consequences of such alterations in basal resources for urban taxa and the food webs they comprise.

Table 2 Mean (SD) proportion and abundance of available and consumed arthropod prey identified from pitfall traps and brown anole gut-contents respectively.

	Habitat	Coleoptera		Hymenoptera		Diptera	
		Proportion	Abundance	Proportion	Abundance	Proportion	Abundance
Available	Natural	0.005 (0.011)	0.333 (0.516)	0.010 (0.091)	3.000 (2.828)	0.839 (0.125)	57.500 (72.644)
	Suburban	0.026 (0.035)	5.375 (8.651)	0.323 (0.221)	60.625 (50.014)	0.631 (0.242)	118.875 (67.030)
	Urban	0.064 (0.095)	0.875 (1.126)	0.308 (0.259)	5.500 (5.555)	0.532 (0.333)	16.125 (23.811)
Consumed	Natural	0.405 (0.287)	5.875 (6.153)	0.440 (0.297)	6.225 (9.883)	0.008 (0.034)	0.100 (0.304)
	Suburban	0.411 (0.253)	2.750 (1.446)	0.390 (0.279)	4.450 (6.590)	0.015 (0.041)	0.150 (0.427)
	Urban	0.590 (0.280)	6.500 (5.875)	0.278 (0.261)	5.875 (9.274)	0.045 (0.111)	0.375 (0.868)

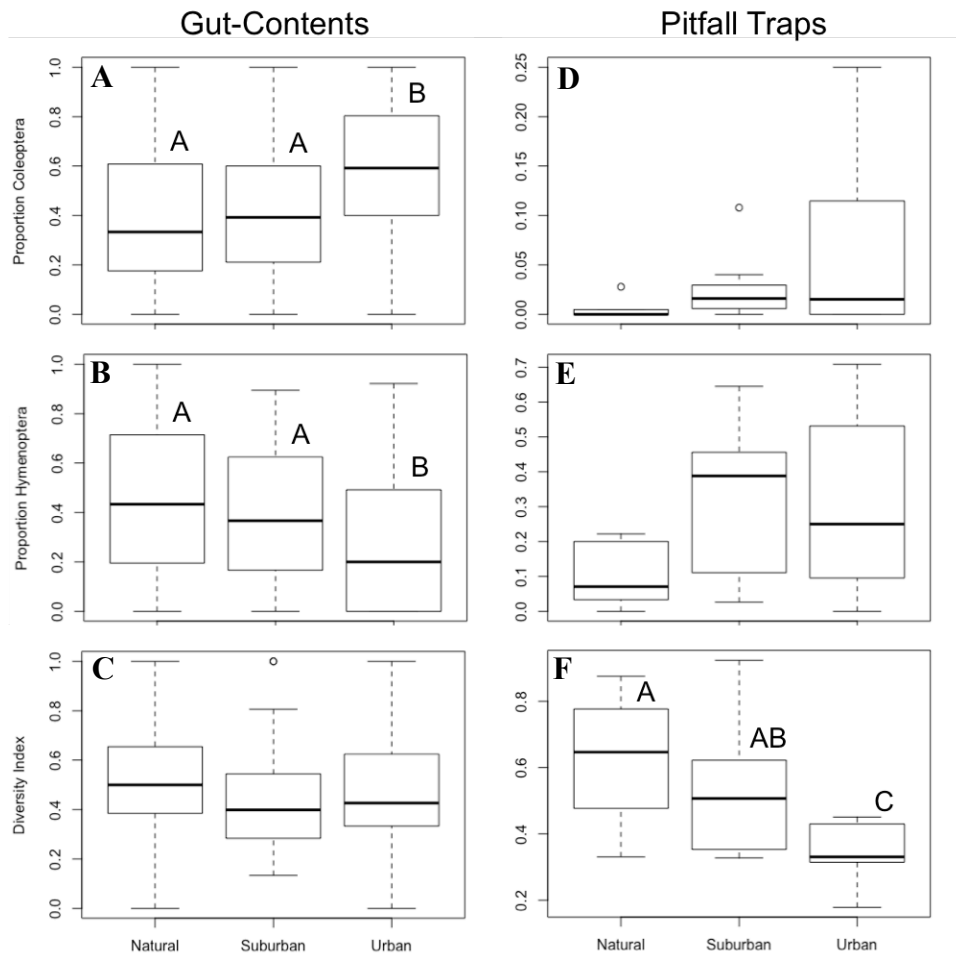


Figure 1 Proportional consumption (A-B) and availability (D-E) of arthropod prey among natural, suburban, and urban habitats. Also shown are the Simpson's Index of Diversity calculated from brown anole gut-contents (C) and pitfall traps (F). Letters denote significant differences among habitat types as indicated from Dunn's test for multiple comparisons with Bonferroni correction. Note that lower values of Simpson's Index of Diversity indicate higher species richness.

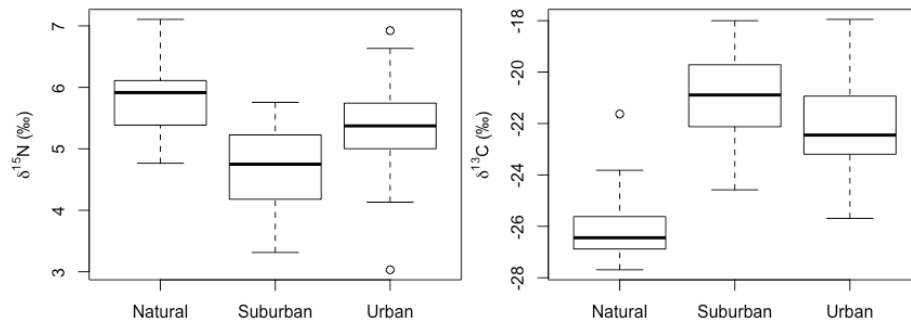


Figure 2 Differences in δC^{13} and δN^{15} for brown anoles inhabiting natural forest, suburban and urban habitats. Anole δN^{15} values were standardized by subtracting the mean δN^{15} values of primary producers from that of anoles in each site. All habitats were significantly different from each other for both δC^{13} and δN^{15} .

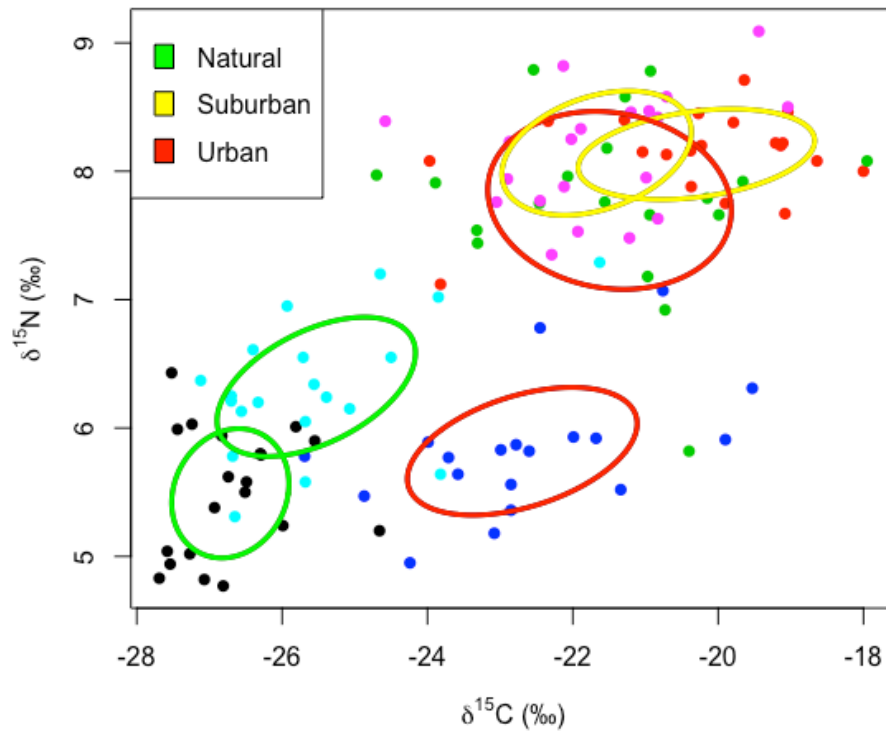


Figure 3 Bi-plot of δC^{13} and δN^{15} of brown anoles inhabiting natural forest, suburban and urban habitats each replicated twice. We used the “standard.ellipse” function in the R package SIBER that employs maximum-likelihood estimators to produce ellipses that encompass approximately 40 percent of the bi-plot data within each site. Point colors represent different sites, whereas ellipse colors represent habitat types.

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CHAPTER 3

PREDATORS INFLUENCE PREY BODY SIZE VARIATION IN AN URBAN
LANDSCAPE.

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Abstract

1. Body size is a key trait linked to many aspects of an organism's life history, physiology, and behavior. Variation in body size can thus have important fitness consequences across a broad range of ecological contexts.
2. We examined the relationship between body size in brown anoles (*Anolis sagrei*) and multiple abiotic and biotic factors across 38 randomly selected urban sites in southern Florida (Broward County). We simultaneously assessed a suite of factors that represent major hypotheses regarding body size variation in ectotherms and other animal groups: temperature, food availability, conspecific abundance and predator abundance. Given our findings of a positive relationship between brown anole body size and predator abundance and no support for the other hypotheses, we performed a tethered intruder experiment to determine whether predator attack behavior depends on prey body size. Lastly, we conducted a common garden experiment to examine whether body size differences between predator and non-predator habitats are genetically determined.
3. Predator abundance was the primary predictor of brown anole body size for both males and females. Body size increased with increasing predator abundance, while body size variation decreased. Additionally, predators attacked larger lizards less often and at longer latencies compared to smaller lizards. Finally, male brown anoles from habitats with predators had faster growth rates in the lab compared to those from habitats without predators.

4. Brown anole body size variation among populations may result in higher survival of larger lizards during predatory confrontations, and this trait is at least partially heritable in males. Therefore, our results suggest that predators may be important agents of natural selection in urban habitats. Future research should focus on predation and species interactions in general given the lack of information regarding their importance in urban habitats.

Introduction

Body size is a key trait linked to many aspects of an organism's life history, physiology, and behavior. A number of important body size relationships generalize to a diverse array of taxa. For example, nearly every measure of fecundity is highly correlated with body size in most vertebrate and invertebrate groups (Blueweiss et al., 1978; Honěk, 1993). Body size is also tightly linked to the daily energy requirements of many animals. In a study of hundreds of vertebrate species, body size explained over 70 percent of the variation in field metabolic rate (Nagy, 2005). As such, larger individuals have higher food requirements. Body size also appears to play a role in determining consumer diets in that the majority of feeding interactions within a food web involve a larger predator consuming smaller prey (Cohen et al., 1993). Even in non-predator-prey systems, body size can determine the result of both intra- and interspecific interactions. Larger organisms often dominate and displace smaller ones, enabling better access to food, mates, and preferred habitat (Morse, 1974; French & Smith, 2005). Variation in body size can thus have important fitness consequences across a broad range of ecological contexts. This has resulted in a large research effort

aimed at identifying the factors that may contribute to body size variation both within and between species (Peters, 1986; Dmitriew, 2011).

Both abiotic and biotic factors have been posited to drive patterns of body size variation at various geographic scales. Globally, studies have related latitudinal trends in body size with climatic factors, such as temperature and precipitation. Body size in temperate organisms is often larger compared to those inhabiting more tropical areas, perhaps owing to an increased ability of larger organisms to retain heat and thus persist in colder climates (e.g. Bergmann's Rule; Meiri & Dayan, 2003). At the local scale, colder temperatures experienced by ectotherms during development can slow growth rates and increase size at maturity (Angiletta et al., 2004). Additionally, precipitation and temperature together may correlate with primary productivity, which may serve as a proxy for food availability (Yom-Tov & Geffen, 2006). The dependence of growth on food availability is straightforward from an energy-acquisition perspective. However, when food is limited, organisms may face a trade-off between the energy allocated to somatic growth versus that devoted to other traits such as immune function or reproduction (Van Noordwijk & Jong, 1986, van der Most et al., 2011). With regard to biotic factors, both competition and predation have been hypothesized to influence body size. For example, body size has often been considered in studies of ecological character displacement across taxa (Dayan & Simberloff, 2005). Changes in body size can thus be the result of divergent natural selection generated by inter- or intraspecific competition between similarly sized individuals. Additionally, when competition is high and food resources are limited, this may favor smaller individuals with lower energy requirements (Peters, 1986). Predators can also

mediate competition for limited resources by depressing population densities through prey consumption and thus indirectly influence competition-driven selection on body size (Wootton, 1994). Predators can also directly cause shifts in body size distributions if they are limited to or prefer prey of certain size classes (Persson et al., 1996; Urban, 2008). Whether biotic or abiotic factors are considered, they are most often evaluated in isolation, which makes determining their relative or habitat-specific effects on body size difficult (but see Peckarsky et al., 2001). Given that several abiotic and biotic factors likely influence body size, we need a study system that captures landscape-scale variation in multiple factors to determine their relative effects.

Urbanization produces considerable variation in many of the abiotic and biotic factors hypothesized to influence body size variation (Foreman, 2014). Temperatures are often higher in cities compared to less developed areas due to both increased canopy openness and impervious surface cover (i.e., the urban heat island effect; Yuan & Bauer, 2007). Moreover, surface temperature variation within urban areas can be substantial and urban surface temperatures are driven primarily by heterogeneity in vegetative cover (Weng et al., 2004; Chen et al., 2006; Buyantuyev & Wu, 2010). Arthropods that rely on such vegetation vary in their abundance and community structure among different urban land use types (McIntyre et al., 2001). Since arthropods form the basal food resource for many taxa, urban areas may contain fine-scale variation in food availability. Invasive species are also prevalent in urban habitats and the non-continuous nature of their spread often results in patchy distributions (With, 2002). These discontinuous distributions can generate variation in both competition and predation regimes within a city (Shochat et al., 2010; Fischer et

al., 2012). Such high variability across relatively small spatial scales makes urban areas ideal for testing whether and how these factors interact to influence body size.

Lizards of the genus *Anolis* (or anoles) are an appropriate system to test how urbanization-induced alterations of the environment may contribute to body size differences among populations. Several *Anolis* species, including the brown anole (*Anolis sagrei*) used in this study, are widespread in urban habitats and often occupy a gradient from natural forests to highly disturbed urban cores (Battles et al., 2013; Kolbe et al., 2016; Winchell et al., 2018). Moreover, urbanization has been shown to modify both anole morphology and behavior. Urban anoles have longer hind limbs, more lamellae and faster growth compared to forest conspecifics (Winchell et al., 2016; Hall & Warner, 2017). Other studies have demonstrated differences in foraging behavior, risk-taking behavior, and body size between urban and forest anoles (Chejanovski et al., 2016; Lapiedra et al. 2017). Yet, while these and many other studies compare populations that occupy opposing ends of the urbanization gradient, they do not address trait variation among localities within an urban habitat. There may be substantial variation in both biotic and abiotic conditions among urban localities, which may produce selective pressures on body size that differ in magnitude and direction. Furthermore, changes in anole morphology, including body size, have been shown to result from both plastic responses to differing environmental conditions and genetic differences between populations (e.g., Bonneaud et al., 2016; Hall & Warner, 2017). Therefore, by using anoles to study body size variation we can also test whether plasticity or genetic differences are responsible for body size differences among populations.

In this study, we simultaneously assess a suite of factors that are likely to exhibit high variation across an urbanized landscape and represent major hypotheses regarding body size variation in ectotherms and other animal groups: (1) temperature, (2) food availability, (3) conspecific abundance and (4) predator abundance. First, the metabolic rate of ectotherms is highly sensitive to even minor temperature variation (Gillooly et al., 2001; Angilletta book). Increased temperatures in cities may then lead to elevated metabolic rates and enable faster growth assuming food is readily available (Dillon et al., 2010). When food is limited, such temperature-induced increases in metabolism may cause declines in physiological condition and result in the need for higher rates of food acquisition to meet higher energetic demands (e.g., Lienart et al., 2014). Second, while increased temperatures may exacerbate the negative consequences of food limitation, reductions in food availability generally inhibit growth in most animals, though this may vary depending on when food shortage occurs during ontogeny (Sebens, 1987). Third, even if food is initially available, increases in population density can increase competition and result in resource limitation. Additionally, male-male competition can produce selection for larger sizes (Hunt et al., 2009), suggesting intraspecific competition as a mechanism of body size evolution independent of food availability. Lastly, predators have been shown to alter the body size of their prey. Shifts toward larger prey size occur when predators can only consume smaller prey (i.e., gape-limited predators) or when larger prey size confers greater ability to escape from predatory attacks (e.g. Janzen, 1993; Mattingly & Butler, 1994; Blomberg & Shine, 2000; Allen, 2008). Conversely, shifts toward smaller individuals can occur when larger prey are more conspicuous and thus suffer

higher mortality through increased detectability by predators (Cote et al., 2008; Mascaro et al., 2003).

To evaluate these hypotheses, we compare populations of brown anoles occurring across an urbanized landscape in south Florida (i.e., southwest Broward County) to determine the relative effects of the thermal environment, food availability, conspecific abundance, and predator abundance on body size variation. Overall, we predict that male and female anole body size will increase with increases in each of these factors -- temperature, food, competitors and predators. To further investigate the effect of predator abundance on brown anole body size, we also examine the relationship between anole body size and the attack behavior of predatory curly-tailed lizards (*Leiocephalus carinatus*) using a tethered-intruder experimental design. These predators are known to be gape-limited (Schoener et al., 1982) and thus we expect larger brown anole lizards to experience lower attack rates. Finally, we conduct a common garden laboratory experiment to test whether brown anole body size differences among sites are genetically based.

Materials and methods

Body Size Variation Across an Urbanized Landscape

Site Selection

Our body size variation study was conducted from June-August 2016 across 38 sites located within the urban matrix of Broward County, Florida. We first generated random GPS points within cities in southwest Broward County using qGIS (QGIS Development Team, 2017). Any point < 1 km from a previously established site or

deemed inaccessible (e.g. private property or water bodies) was excluded. We then surveyed the area within a 300-m radius of each point to delimit relatively continuous habitat and determine whether brown anoles were present. Sites mostly included urban parks and roadsides (see Supplementary Materials for GPS coordinates and descriptions for each site).

Land-Cover Measurements

Line transects were used to measure percent cover of grass, bushes, bare ground, and impervious surfaces at each site. Five parallel transects were placed along the site at random intervals between 10 and 20 m. Transect length varied depending on the site (e.g. roadside habitat transects ended at the road), but each was no more than 10 m (mean: 9.3 m; range: 3.5-10 m). Percent cover for each site was then calculated as the sum of the distance covered by each land-cover type among the five line transects, divided by the total distance of these transects multiplied by 100.

Arthropod Food Availability

To estimate arthropod availability, we used a sweep net to collect arthropods from vegetation at each site. We only collected arthropods from vegetation found < 50 m from where lizards were sampled (see Lizard Measurements below). Vegetation was swept during three time-periods to account for any potential daily variation in arthropod abundance: 0900-1000 (morning), 1300-1400 (afternoon), and 1800-1900 (evening). Grasses (most commonly *Stenotaphrum secundatum*) and bushes were swept separately, with approximately 50 sweeps for each vegetation type during each

time period. After collection, arthropods were immediately placed in a kill jar charged with acetone and then frozen until returned to the lab for sorting. In the lab, small pieces of vegetation were removed using a dissecting microscope. Arthropods were then placed on a paper towel to remove any excess moisture and weighed (i.e., wet mass) to the nearest 0.0001g using a digital balance. Biomass was measured as grams per sweep for each vegetation type within each time period. We found no differences in biomass between time periods among each vegetation type as well as no differences between vegetation types (p-values > 0.05 using Dunn's test of multiple comparisons and Wilcoxon rank sum test respectively) and thus we calculated total biomass per site as the sum of all individual samples collected during the three time periods from both vegetation types.

Conspecific and Predator Abundance

Visual encounter surveys (VES) were conducted at each site to estimate relative abundance of brown anoles and curly-tailed lizards, which are well-documented predators of anoles (Schoener et al., 2002; Losos et al., 2004, 2006). Surveys consisted of walking the site at a constant pace and recording every individual lizard observed. We also measured the perch height of each brown anole observed using a laser distance meter that was placed at the lizards' original position and aimed at the ground. We performed these VES along the same route within each site during three time periods: 0800-0900 (morning), 1400-1500 (afternoon), and 1800-1900 (evening) given previous work showing marked differences in daily activity times between brown anoles and curly-tailed lizards in similar habitats to this study

(Lapiedra et al., 2017; also see Kolbe et al. 2008). These routes were left undisturbed for at least 30 minutes prior to each survey. Each survey was limited to a maximum of 10 minutes (discounting time taken to record observations), though some were shorter depending on the amount of habitat available and number of lizards observed. To standardize these measures, we calculated the number of lizards observed per minute for each survey. For brown anoles, males and females are easily distinguished in the field and were thus counted separately. Relative abundance for both brown anoles and curly-tailed lizards in each site was measured as the maximum number of individuals observed per minute among the three time periods.

Lizard Morphology and Habitat Measurements

In between VES, we captured 14-20 brown anoles of each sex as encountered at each site using a noose affixed to a telescopic fishing pole. We measured the internal body temperature of each lizard immediately upon capture using a thermocouple placed into the lizard's cloaca. Any lizard that moved from sun to shade or vice versa during capture was not used. Additionally, lizards were only captured between the hours of 0930-1800, the time of day when brown anoles are active and attain relatively stable body temperatures (Battles et al., In Review). We then measured body size of each lizard as snout-vent length (SVL) to the nearest mm and mass to the nearest 0.01 g using a digital balance. We included only sexually mature adult lizards for this study, corresponding to a minimum size of 42 mm SVL for males and 36 mm SVL for females (Lee et al., 1989). Lastly, we measured canopy openness of each site to assess potential differences in microclimatic among sites.

Hemispherical photographs were taken of the canopy from each lizard's original position (i.e., before capture) using a digital camera with a 360° fish-eye lens. From these photos, canopy openness was calculated for each image using Gap Light Analyzer (GLA) Version 2.0 (Frazer et al., 1999) and then averaged for each site.

Statistical Analyses

We used linear mixed-effect models with site as a random effect to determine the abiotic and biotic factors that contribute to body size variation among sites. Specifically, we included body temperature (with time of day as a covariate), impervious surface cover and canopy openness as measures of the thermal environment, as well as food availability, conspecific abundance and predator abundance as fixed effects in the model. We used the total abundance of both male and female brown anoles as our measure of conspecific abundance in our analysis given that the abundances of males and females were highly correlated (corr: 0.53, $p < 0.001$). Because brown anoles are sexually dimorphic with regard to body size, we modeled the body size of each sex separately. Additionally, SVL measurements were squared to improve the normality of model residuals. Previous studies have shown that brown anoles increase their perch heights in response to the experimental introduction of curly-tailed lizards (Schoener et al., 2002; Losos et al., 2004, 2006). Therefore, we also tested for a positive correlation (Pearson's product-moment correlation) between curly-tailed lizard abundance and brown anole perch heights. We used only brown anole perch heights obtained from the afternoon VES as this is when curly-tailed lizards are most active and thus when brown anoles are most likely to shift their perch

heights in response to curly-tailed lizards. Furthermore, perch height has been observed to differ between the sexes of *A. sagrei* and other anoles (Butler & Losos, 2002), and therefore we analyzed males and females separately. We calculated correlations for all sites (n=38) and a reduced set of sites including only those with predators present (n=19). All analyses in this and the following studies were performed using R statistical software (R Core Team, 2017).

Tethered-Intruder Experiment

Experimental Design

We performed a field experiment in May 2017 to test whether larger brown anole body size results in lower attack rates by predatory curly-tailed lizards. We utilized a tethered-intruder experimental design (Reedy et al., 2017; Wu et al., 2018) in which we presented male brown anoles of varying size to free ranging curly-tailed lizards and measured the latency (in seconds) of curly-tailed lizards to attack. Trials were performed in areas of high curly-tailed lizard abundance located within the same general area as the body size variation study described above (i.e., southwest Broward County).

Only male brown anoles were used in this experiment to avoid any potential differences in anti-predator behavior between the sexes and also to better represent the full size range attained by brown anoles (i.e., female brown anoles are smaller than males). Male brown anoles were tethered to a telescopic fishing pole via a 10-cm long piece of dental floss and held in a 5-gallon bucket prior to being presented to curly-

tailed lizards. Each anole was used on the same day of capture and for only a single trial.

We identified focal adult curly-tailed lizards from a distance of at least 3 m. Once a focal curly-tailed lizard was observed, we expanded the telescopic fishing pole with tethered anole so that the distance between the observer and the anole was 3 m. The anole was then placed ~1 m from the curly-tailed lizard and the pole was laid flat on the ground. Trials began when the anole reached the ground and were terminated when either the curly-tailed lizard approached to within 20 cm of the anole or 3 minutes had elapsed. Trials were only conducted between the hours of 1000-1600 when curly-tailed lizards are most active (Lapiedra et al. 2017). Following each trial, focal curly-tailed lizards were captured, measured (mass and SVL), and temporarily marked to prevent repeated trials with the same individual.

Statistical Analysis

We performed a survival analysis to test for differences in the latency of curly-tailed lizards to attack differently sized brown anoles. We used the semi-parametric Cox proportional hazards model available in the R package “survival” (Therneau & Lumley, 2015), which is ideal for handling right-censored data such as these. We included the body size of brown anoles and curly-tailed lizards as well as their interaction as factors in the model. The interaction term was not significant and was removed from the model. The remaining models were compared using chi-square difference tests and when not significantly different, we chose the model with the least number of parameters as the best model.

Common Garden Experiment

Experimental Design and Husbandry

We utilized a common garden experimental design to determine whether body size differences among urban sites with and without curly-tailed lizards are genetically based. A total of 60 females were collected from habitats containing high curly-tailed lizard abundance and habitats containing no curly-tailed lizards (abundances determined from previous VES and confirmed on day of capture), each replicated three times (i.e., three sites per habitat with 10 females per site). The body size distributions of females in the common garden experiment matched the site-specific size distributions determined from the body size variation study described previously. We measured mass and SVL of each female before transporting them to the University of Rhode Island. Each female was housed individually in a 13 x 7.5 x 8 in (length x width x height) terrarium provided with a single perch, artificial plants, and a plastic container filled with moist, ground coconut husk for egg laying. Full spectrum lighting was set on a 14:10 hr light:dark cycle, and each cage was misted daily to provide drinking water. Temperatures in the room ranged from 88°F during the day to 75°F at night. Females were fed five appropriately sized crickets every third day and we searched containers for eggs just prior to feeding. We collected eggs continuously from June 3, 2017 until August 14, 2017.

We measured the mass (0.0001g), length and width (0.1 mm) of each egg before half-burying them in glass containers filled with moistened vermiculate (1:1 water:vermiculite by weight), which we then sealed with plastic wrap to prevent

evaporation. Eggs were incubated at 28°C until hatching. Each hatchling was sexed using the presence/absence of post-anal scales and dorsal patterning, measured for SVL to the nearest 0.5 mm and mass to the nearest 0.01 g within 24 hours of hatching and placed into a 11 x 6.75 x 6.5 in terrarium with two perches, artificial plants and a small container filled with moistened coconut husk to maintain humidity. We housed hatchlings in pairs that were from the same habitat (i.e., with or without predators) and within 1 week of age to minimize any dominance effects within cages. Mortality over the course of the experiment required that we re-pair single hatchlings using these criteria. Lighting, misting and feeding schedules for hatchlings were the same as those for adult females. We randomized cage positions every two weeks to eliminate potential positional effects. Hatchlings below six weeks of age were fed five 0.5-week old crickets every third day. We then provided five one-week old crickets for hatchlings between six and 14 weeks of age. Lastly, we increased the amount of one-week old crickets from five to eight for hatchlings over 14 weeks of age. We measured the mass and SVL of each hatchling prior to feeding every two weeks for up to 18 weeks.

Statistical Analysis

We log-transformed body size for analysis using linear mixed-effect models with habitat type, age, egg mass, egg order, and mother SVL as fixed effects. We also included the interaction between habitat type and age to test for differences in growth rate between habitats. Survival rates of hatchlings did not differ between habitats for either males (coef: 0.1215, exp(coef): 1.1292, se(coef): 0.2147, $z=0.566$, $p=0.572$) or

females (coef: -0.03299, exp(coef): 0.96755, se(coef): 0.19718, $z = -0.167$, $p = 0.867$) and thus all individuals (i.e., both survivors and non-survivors) were included in the analysis. We used a nested random effect structure (random intercept) with hatchling ID nested within mother, which was nested within site. Due to the sexual dimorphism observed in this species, we modeled male and female body size separately.

Results

Predator abundance was the only significant predictor of anole body size for both males and females among the 38 urban sites (Table 1). Specifically, body size increased with increasing predator abundance (Figure 1). For males, body temperature was also significantly related to body size such that larger individuals had higher temperatures, but there was no relationship between body temperature and female body size (Table 1). We observed a significant negative correlation between body size variation (i.e., the coefficient of variation for SVL) and predator abundance for males (cor=-0.329, $p = 0.043$). This relationship was also negative for females, but not significant (cor=-0.102, $p = 0.542$). The correlation between brown anole perch heights (in the afternoon) and predator abundance was positive, but not significant across all 38 sites for males (cor=0.066, $p = 0.697$) and females (cor=0.136, $p = 0.415$). These correlation coefficients increased when considering only those sites with non-zero predator abundance, but they were still non-significant (males: cor=0.317, $p = 0.200$; females: cor=0.389, $p = 0.100$).

In the tethered intruder survival analysis, anole SVL was found to be the only significant predictor of latency to attack (coef: -0.054, exp(coeff): 0.948, se(coeff):

0.027, $z = -1.959$, $p = 0.050$). Larger brown anoles were attacked less often and at longer latencies compared to smaller individuals (Figure 2).

For the common garden experiment, we found significant effects of age and egg mass on both male and female hatchling body sizes (Table 2). Body size increased with age and egg mass (Figure 3). For males, we also found a significant interaction between habitat and age indicating faster growth rates in anoles from habitats with predators compared to anoles from habitats without predators. In contrast, no differences in female growth rate were observed between sites with and without curly-tailed lizard predators (Figure 4).

Discussion

In this study, we utilized urbanization-induced variation in multiple abiotic and biotic factors to simultaneously test their relative effects in shaping body size variation of urban brown anoles. Across 38 sites, brown anole body size in both males and females was positively related to predator abundance. To further assess the role of curly-tailed lizard predation on brown anole body size, we also demonstrate that larger anole body size confers reduced attack rates by predators, suggesting that being larger might offer a survival advantage when confronted with this predator. Lastly, male body size differences between habitats with and without predators are, at least in part, determined by genetic differences in growth rate. Overall, these results suggest that predators may be important agents of natural selection on brown anole body size in urban environments.

Both ecological and evolutionary mechanisms have been considered to drive patterns in body size variation of anoles. First, a recent study in the Bahamas found that in the field, male body size of brown anoles was explained by the availability of arthropod biomass (Bonneaud et al., 2016). In the lab, male hatchlings reared under high food availabilities had faster growth and attained larger maximum body sizes compared to males raised under a low food treatment. While genetic differences between populations were not assessed in this study, these results provide support for the role of food in determining brown anole body size. Second, changes in male brown anole body size have been attributed to variation in population density, with larger size favored in those populations with the highest density (Calsbeek & Cox, 2010). For food availability, we found no relationship between arthropod biomass and body size for either male or female brown anoles in southeast Florida, despite using similar methods compared to Bonneaud et al. (2016). Theoretically, the relationship between food availability and body size could be obscured if arthropod abundances exceed that which would promote maximum anole growth. Therefore, this discrepancy may potentially be explained by food saturation in urban habitats. Arthropod biomass in our urban sites was on average over 12 times greater than the site with the highest biomass in the study by Bonneaud et al. (2016). Moreover, other studies have also found that some groups of arthropods can reach exceedingly high abundances in urban areas (Shochat et al., 2004; Bang & Faeth, 2011; Philpott et al., 2015). For competition, we did not observe any relationship between body size and conspecific abundance suggesting that, at least in our system, predator-induced selection may be relatively more important compared to that generated by intraspecific competition.

Predators have also been shown to alter body size distributions and body size selection in brown anoles. The experimental introduction of curly-tailed lizards to naturally occurring populations of brown anoles in the Bahamas revealed selection for larger body size in females, but not males (Losos et al., 2004). In a different study in the same island system, curly-tailed lizard introductions resulted in narrower brown anole body size distributions such that smaller lizards were less common on islands with predators (Schoener et al., 2002). We also found reductions in brown anole body size variation in habitats where predators occurred, which was driven by a reduction in the number of smaller individuals. However, our results suggest that predatory curly-tailed lizards similarly influence both male and female body size. While it is uncertain why predator-induced selection was found only for female body size in the Bahamas, this does provide evidence that predatory curly-tailed lizards can indeed generate natural selection on anole body size.

Though we did not measure selection in our study, we present multiple lines of evidence that suggest size-selective predation may be a source of natural selection influencing brown anole body size in urban habitats. Several criteria are needed to support evolution by natural selection. First, body size variation must exist for selection to act. We observed the greatest variation in body size (i.e., coefficient of variation for SVL) in sites without predators, and brown anole body size variation decreased with increasing predator abundance. This reduction in body size variation is consistent with the expectation from directional selection favoring larger body size (Endler, 1986). Second, body size must be linked to differences in survival. Our tethered intruder experiment suggests that curly-tailed lizards attack smaller anoles

more rapidly and more often than larger ones, which may lead to larger lizards having a higher probability of survival during predatory confrontations compared to smaller lizards. Additionally, hindlimb length is positively related to body size and sprint speed in many squamate lizards, including *A. sagrei*, meaning that larger lizards are also faster (Losos, 1990; Van Damme & Vanhooydonck, 2001). Thus, even smaller brown anoles (e.g. females) can benefit from being relatively large compared to other individuals through an increased ability to escape from predators. Lastly, some component of body size must be heritable for selection to translate into evolution in the next generation. Our common garden experiment supports that genetic differences in male growth rate contribute to the observed differences in body size between sites with and without predators. This is further supported by other studies demonstrating relatively high heritability estimates ($h^2=0.55$) for body size in brown anoles (Calsbeek & Smith 2007; also see Calsbeek & Bonneaud, 2008). Therefore, we have shown that the relationship between body size variation and predator abundance is consistent with expectations under predator-induced selection, larger brown anoles have a survival benefit when confronted with predatory curly-tailed lizards, and body size is indeed heritable. Yet, to verify that predators are in fact producing selection on brown anole body size, we suggest that future work should use mark-recapture studies to estimate selection gradients on the body size for brown anoles in urban areas.

While increases in body size may include substantial fitness benefits, it is important to also consider the potential costs. For example, the resting metabolic rate of many reptiles scales with body size, which increases the amount of food needed by larger individuals for maintenance (Andrews & Pough, 1985). Such increases in

metabolism likely require higher foraging rates and may lead to greater risk-taking behaviors to fuel higher metabolic demands. However, even if urban environments contain sufficient food, the presence of predatory curly-tailed lizards can reduce food availability through reductions in anole ground use, a potential proxy for foraging activity (Lapiedra et al., 2017). The higher growth rate of males from habitats with predators may also entail costs, specifically in immune function. Trade-offs between growth and immune function have been demonstrated in a variety of taxa including lizards (e.g. chickens: van der Most et al., 2011; insects: Rantala & Roff, 2005; lizards: Uller et al., 2006). Furthermore, the costs of impaired immune function are likely to be exacerbated in urban environments given the positive relationship between parasitism and distance to urban habitats for brown anoles (Perkins et al., 2007).

Urban habitats have been increasingly regarded as hotspots for evolutionary change (Johnson & Munshi-South, 2017). Over the past decade, evidence for genetically based changes between urban and non-urban populations has been growing. For example, male European Blackbirds showed decreased migratory behavior, a genetically determined trait, in urban habitats compared to forest conspecifics (Partecke & Gwinner, 2007). More recent studies have also demonstrated urbanization-induced changes in genetically determined traits such as seed dispersal in plants (Cheptou et al., 2008) and pollution tolerance in killifish (Whitehead et al., 2010). Yet, most of these studies fail to explicitly address the fitness consequences of these changes as well as the specific drivers underlying them (Donihue & Lambert, 2015). Nonetheless, the altered abiotic and biotic conditions in cities are generally

hypothesized to create novel selection pressures that result in phenotypic divergence between urban and natural populations (e.g., Garroway & Sheldon, 2013; Winchell et al., 2016; Brans et al., 2017). While this may indeed be the case, urban habitats are often highly fragmented, which may decrease gene flow among nearby populations and thus impact the ability of urban populations to evolve (Keyghobadi, 2007). Genetic drift can erode genetic variation in such isolated populations and thereby constrain future evolutionary potential (e.g. Epps et al., 2005). However, if sufficient genetic variation exists in a population, these dispersal limitations imposed by habitat fragmentation can facilitate genetic differentiation and thus local adaptation among urban populations. Given the high variability of abiotic and biotic conditions within a given urban area, selective pressures are likely to differ even among neighboring localities. Therefore, reduced dispersal of individuals among these localities can prevent maladapted genotypes from entering a population and spreading deleterious alleles (Boulding & Hay, 2001). In our study, curly-tailed lizards were patchily distributed and urbanization-induced habitat fragmentation is likely facilitating body size evolution by reducing the possibility of genetic mixing between brown anoles from habitats with and without predators. Therefore, in order to better predict the potential for adaptive evolution in urban habitats, it is important to identify the specific factors responsible for phenotypic changes and the geographic scale at which these factors vary.

Predation is considered a fundamental mechanism driving the structure of natural communities (Shochat et al., 2006). However, the role of predators in urban systems is currently under debate (Fischer et al., 2012). This is due to conflicting

reports of increased predator abundance in urban habitats, but also decreased anti-predator behavior and mortality in urban prey populations. We propose that these contradictory findings may be the result of underlying evolutionary mechanisms. Urbanization has facilitated the establishment and spread of predatory curly-tailed lizards in southern Florida (Smith et al., 2004), supporting the argument for higher predator abundances in urban habitats. Furthermore, the fact that curly-tailed lizards attacked brown anoles in over half of our tethered intruder trials suggests that these higher predator numbers may translate into higher predation pressure. But if predator-induced selection towards larger brown anole body size is sustained, this could result in lower brown anole mortality as populations adapt while predators remain in high abundance. Furthermore, we found no support for alternative hypotheses for body size variation except for predation, highlighting its importance relative to other biotic and abiotic factors in structuring urban animal communities in our system. To fully understand the ecological and evolutionary consequences of urbanization on animal communities, future research should focus on predation and species interactions in general given the lack of information regarding their importance in urban habitats.

Table 1 Results of the linear mixed effect models for male and female SVL. Site was included as a random effect. SVL was squared before fitting each model to improve normality of the residuals.

Variable	Value	Std. Error	DF	T-Statistic	P
Males					
Intercept	2123.233	415.089	560	5.115	0
Body Temperature	31.506	12.069	560	2.610	0.009
<i>A. sagrei</i> Abundance	439.527	1529.483	34	0.287	0.776
<i>L. carinatus</i> Abundance	20831.648	8998.844	34	2.315	0.027
Food Availability	3275.911	3526.924	34	0.929	0.360
Females					
Intercept	2009.928	183.632	558	10.945	0
Body Temperature	-4.450	5.263	558	-0.846	0.398
<i>A. sagrei</i> Abundance	1033.586	757.992	34	1.364	0.182
<i>L. carinatus</i> Abundance	11286.512	4457.508	34	2.532	0.016
Food Availability	2375.751	1745.266	34	1.361	0.182

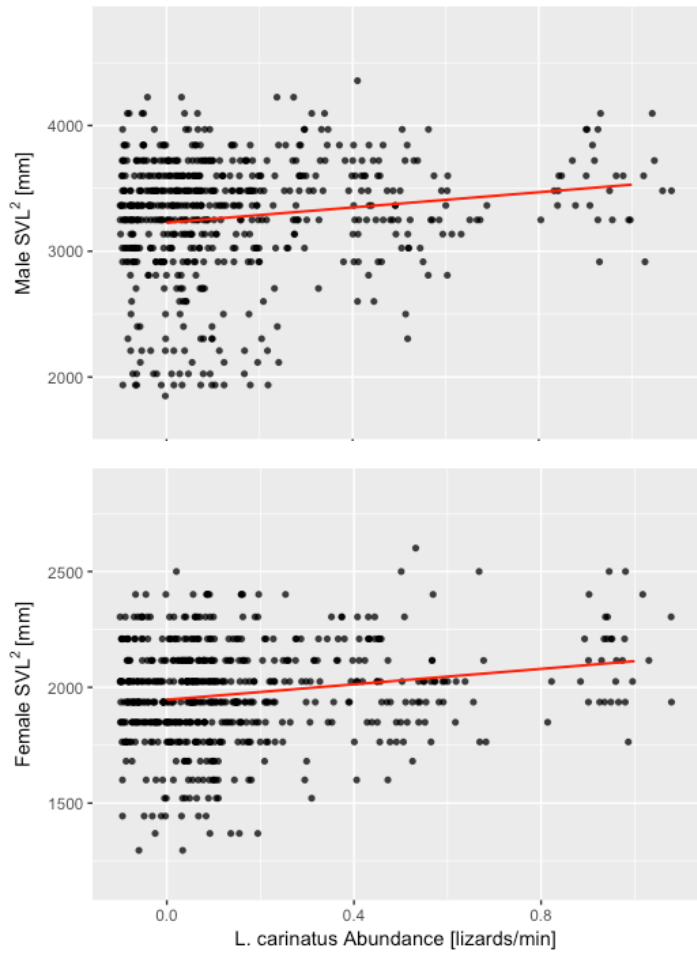


Figure 1 Relationships between SVL and *L. carinatus* abundance for male (top) and female (bottom) brown anoles. Each point represents a single individual and SVL values were squared to improve normality

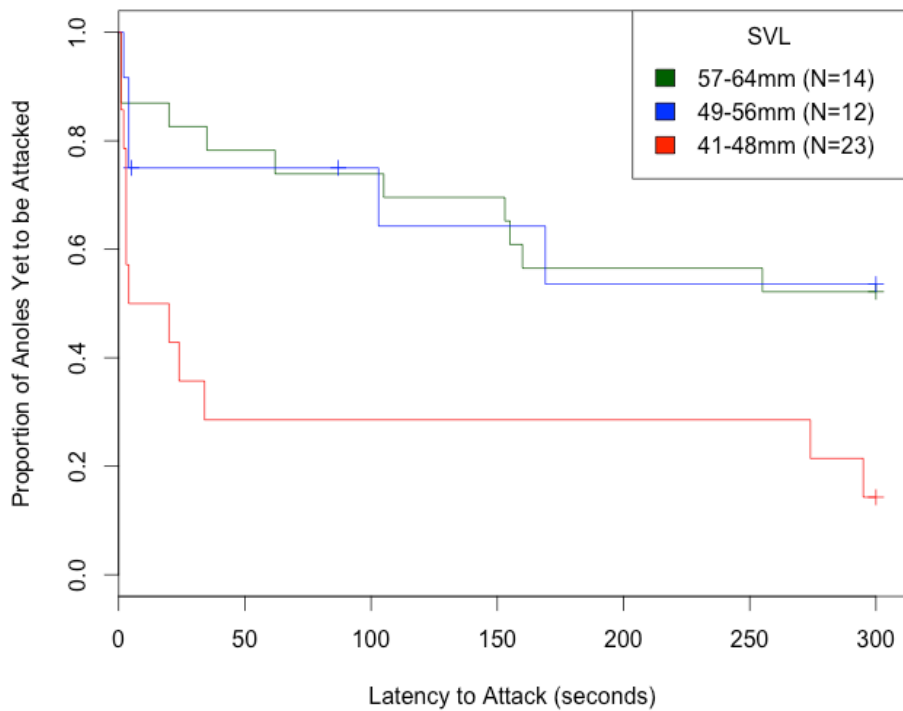


Figure 2 Survival analysis comparing latency of *L. carinatus* individuals to attack male brown anoles of varying SVL. To better visualize this relationship, brown anole SVLs were binned into large (green), intermediate (blue) and small (red) sizes.

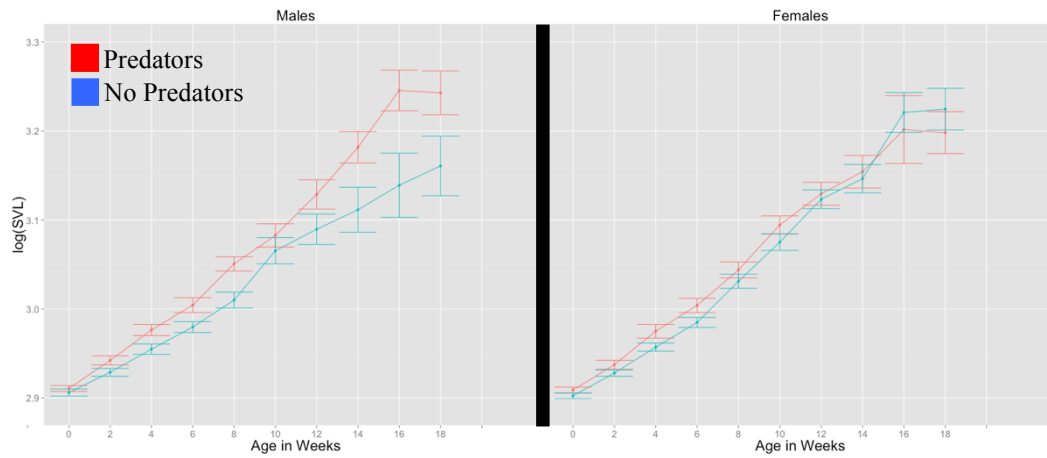


Figure 3 Growth rate of male (left) and female (right) brown anole hatchlings whose mothers were from habitats with (red) and without (blue) predators.

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