2015

DO URBAN ENVIRONMENTS INFLUENCE ANTIPREDATOR AND FORAGING BEHAVIOR OF THE LIZARD *ANOLIS CRISTATELLUS*?

Kevin J. Aviles-Rodriguez
University of Rhode Island, kev.aviles.rodz@gmail.com

Recommended Citation

Aviles-Rodriguez, Kevin J., "DO URBAN ENVIRONMENTS INFLUENCE ANTIPREDATOR AND FORAGING BEHAVIOR OF THE LIZARD *ANOLIS CRISTATELLUS*?" (2015). *Open Access Master's Theses.* Paper 544. https://digitalcommons.uri.edu/theses/544

DO URBAN ENVIRONMENTS INFLUENCE ANTIPREDATOR AND FORAGING BEHAVIOR OF THE LIZARD *ANOLIS CRISTATELLUS?*

BY

KEVIN J. AVILES-RODRIGUEZ

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE IN BIOLOGY

IN

BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2015

MASTER OF SCIENCE IN BIOLOGICAL AND ENVIRONMENTAL SCIENCES

THESIS

OF

KEVIN J. AVILES-RODRIGUEZ

APPROVED:

Thesis Committee:

Major Professor: Jason J. Kolbe

Evan Preisser

Scott McWilliams

Nasser H. Zawia
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND
2015

ABSTRACT

As the human population increases, urban areas are expanding and bringing humans and wildlife into close proximity. Disturbance by humans can lead to changes in animal behavior and ecological interactions. Urban areas also provide access to novel, artificial substrates (e.g., cement walls and metal posts), which may influence the behavior of organisms. We studied whether urban habitats and artificial substrates influenced escape and foraging behavior of the Puerto Rican Crested Anole (*Anolis cristatellus*).

We tested whether lizards in urban environments reduced flight initiation distance (i.e., the distance between the observer and the lizard when the lizard begins escape) in response to differences between the natural habitat and whether flight distance differed between urban and natural habitats. We found that flight initiation distance was significantly shorter in urban environments as compared to forest habitats. Flight distance did not differ between habitats. The proportion of escape modes used varied between the habitats. Urban lizards escaped more frequently by squirreling around the perch and reduced the frequency of jumping. Use of larger perches with less vegetation nearby in urban areas was consistent with our results of lizard's squirreling more and jumping less during escape. Our results show differences in lizard flight initiation and escape mode employed between the urban and natural habitats. Habituation to the presence of humans and/or lower predation risk could account for differences in FID. Moreover, habitat differences in urban areas influence the escape mode used by lizards through the increased availability of larger perches and the reduction of perches to which lizards can jump.

We tested differences in latency to feed between urban and forest environments and in the presence or absence of a life-like model of a lizard predator. We found that lizards in the forest habitat foraged more frequently and faster compared to lizards in the urban area. Lizards did not respond to the presence of the model predator in either habitat. Because lizards are visual predators, the lack of movement of our model predator likely reduced the perceived threat to lizards. We also evaluated the effect of conspecific lizards on latency to feed and found that when conspecifics approach the feeding tray, focal lizards reacted less often in the forest habitat. Because the food resources provided was limited, conspecific lizards often exhausted the food resource in our experimental trials, which eliminated the opportunity for focal lizards to feed. Our results show that forest lizards foraged faster and potentially competed more with conspecifics for food resources.

Both studies show clear differences in behavior between lizards in urban and forest habitats. More work is needed to assess whether these differences are due to behavioral flexibility and/or evolutionary adaptation to human-modified environments. Regardless, differences in behavior found in this study suggests that habitat modifications due to human activities, such as urbanization, may be a potent force impacting the ecology and evolutionary trajectory of these populations.

ACKNOWLEDGMENTS

I am thankful to my major professor for his help and contributions to this research. I would also like to thank members of my thesis committee, Evan Preisser and Scott McWilliams, for their time in helping me develop and execute the ideas found here. I would like to thank my lab members, in particular Dr. Oriol Lapiedra and Hanna Wegener for all their help with this work. I am thankful to the University of Puerto Rico for allowing me to use their properties for fieldwork. I would like to thank the staff of the Museum of Zoology at the University of Puerto Rico for providing laboratory space and the bird specimen used for the foraging trials.

PREFACE

This following work is in manuscript format and contains two manuscripts. Both are in preparation for publication. The first manuscript details the effect of urban environments on escape behavior of the lizard *Anolis cristatellus.* This manuscript will be submitted to the journal *Global Change Biology*. The second manuscript details the effect of urban environments on the foraging behavior of the lizard *Anolis cristatellus*. This work will be submitted to the *Journal of Herpetology.*

Table of Contents

LIST OF TABLES

LIST OF FIGURES

MANUSCRIPT-1

In preparation for Global Change Biology

Do urban environments influence escape behavior of the Puerto Rican Crested Anole (*Anolis cristatellus*)?

Kevin Aviles-Rodriguez and Jason J. Kolbe

Department of Biological Sciences, University of Rhode Island, Kingston RI, USA

Corresponding Author:

ABSTRACT

As the human population increases, urban areas are expanding, which often brings humans in close proximity to wildlife. Disturbance by humans can lead to changes in animal behavior and ecological interactions. Urban areas also provide access to novel, artificial substrates (e.g., cement walls and metal posts), which may influence the behavior of organisms. We studied whether urban habitats and artificial substrates influenced escape behavior of the lizard *Anolis cristatellus*. We tested whether lizards in urban environments reduced flight initiation distance (i.e., the distance between the observer and the lizard when the lizard begins escape) and whether they increased flight distance. We found that flight initiation distance was significantly shorter in the urban environment as compared to a forest habitat. Flight distance did not differ between habitats. Urban lizards escaped more frequently by squirreling around the perch and reduced their frequency of jumping. An increase in squirreling at the expense of jumping in urban lizards is consistent with the greater availability of larger diameter substrates and fewer nearby perches in urban habitats. Our results suggest that urban lizards have adjusted their escape response in urban areas, potentially influenced by habituation to the presence of humans and/or lower predation risk.

INTRODUCTION

Humans are changing the global environment in unprecedented ways, including rapid climate change, invasive species introductions, and dramatic land use modifications (Sih et al., 2011). Understanding the consequences of these changes for natural populations is critical for both evaluating current impacts and predicting future ones (Barnosky et al., 2012). A widespread and growing component of global change is urbanization (United Nations, 2011) – the changes in land use associated with high-density human populations. Urbanization results in a mixture of buildings, impervious surfaces (e.g., roads), managed and unmanaged vegetation, and remnant natural areas. Changes in habitat type can eliminate or significantly alter the available habitat for plant and animal populations, resulting in a pattern of fewer species but an increased abundance of those species that can tolerate urban environments (Ramalho & Hobbs, 2012; Rebele, 1994; Shochat et al., 2006). However, human induced change might not always lead to species decline because some species can adjust to the novel conditions (Sih et al., 2011).

Disturbance by humans in close proximity to wildlife can lead to adverse effects on their behavior and ecology (Burger, 2001). Human-induced stresses for urban wildlife include artificial concentrations of food that can lead to transmission of disease and pathogens, human movement and activity, domestic predators (e.g., cats and dogs), pollution, amongst others (Ditchkoff et al., 2006). These stresses can lead to changes in animal behavior, habitat use, and selection pressures, potentially leading to adaptation to urban environments (Shochat et al., 2006; Atwell et al., 2012); for example, urban landscapes can vary in their composition and abundance of predators (Møller and Ibáñez-Alamo, 2012). Numerous studies have documented high predation rates by feral and domestic felines in urban areas on birds, mammals, reptiles, and amphibians (Ditchkoff, et al., 2006, Lepczyk et al, 2003, Loyd et al, 2013). In contrast, Rodewald et al. (2011) found that higher predator activity in urban areas did not increase nest predation. They suggested that anthropogenic food sources subsidized predators and decoupled predator-prey relationships. Human activity can decrease resource use in some animals because they will avoid foraging when humans are nearby (Sol et al., 2013). Alternatively, some individuals may learn to recognize humans to be non-threatening and even rely on the food they provide (Sol el al, 2013). Some individuals may reduce their antipredator response to humans and this habituation (i.e., reduction of antipredator response after repeated non-threatening encounters) can facilitate colonization of human-dominated landscapes (Rodríguez-Prieto et al. 2011).

The ability to successfully avoid a predator greatly impacts future fitness (Lima & Dill, 1990). To survive in the presence of predators, prey must be able to assess risk quickly and adjust antipredatory behavior according to current risk levels (Cooper, 2006a). Escape theory predicts that when a predator approaches, the prey should monitor the predator's approach and flee when the fitness cost of not fleeing, due to predation risk, equals the cost of escaping (Cooper & Whiting, 2007; Ydenberg & Dill 1986). Flight initiation distance (FID) is the distance separating the predator and prey when an escape attempt begins (Cooper & Wilson, 2007). FID increases as predation risk increases and as escape costs decrease (Cooper and Whiting, 2007). Escape costs include loss of both feeding opportunities and engaging in social behavior, such as mating (Cooper, 2006b). Flight distance (FD) is the distance the prey flees before stopping and it can be influenced by the distance to a refuge, the openness of the microhabitat, and the distance at which the predator is detected before immediate escape is required (Cooper 2003; Cooper 2005; Cooper and Whiting 2007). Differences in the intensity of predation can have a direct effect on escape behavior.

When a predator approaches an organism it is subject to two main costs: direct mortality and nonlethal costs related to behavioral changes (e.g., loss of opportunities to feed and mate) while trying to avoid predation (Rodríguez-Prieto & Fernández-Juricic, 2010). Nonlethal costs are known as nonconsumptive effects (i.e. NCE) and they can play an important role in ecosystem dynamics, local prey abundance, physiological stress, and prey habitat shifts (Peckarsky el al, 2008). For example, a meta-analysis of published empirical work of NCE pathways showed that behaviors such as prey activity, feeding rate, and the use of open versus sheltered habitats are most affected by predator cues (Preisser & Bolnick, 2008). Moreover, Møller and Ibáñez-Alamo (2012) found that differences in bird antipredator behavior were significantly related with time since urbanization. Urban birds used more alarm calls and fear screams and relied less on biting and wriggling behaviors.

Urbanization provides an opportunity to compare the behavior of organisms living in distinct habitats, such as remnant forests and disturbed urban sites. Organisms in urban areas likely have higher encounter rates with humans, experience warmer microclimates, encounter a variety of artificial substrates, and interact with different predator communities. Urban habitats often are more open and have a less complex ground layer than natural habitats (Prosser et al., 2006). For example, urban parks and yards typically consist of mature trees that are widely spaced on a mowed lawn. Furthermore, urban habitats include a variety of artificial substrates, such as cement walls, metal fences, and light posts on which lizards perch. Behavioral options can be limited by the performance abilities and the underlying morphological and physiological traits that determine those abilities (Perry et al., 2004). Inability to perform optimally when using artificial substrates could limit some of the behaviors organisms exhibit when using natural perches.

Anolis lizards, or anoles, are a useful study system because their escape behavior, performance abilities, and habitat use have been extensively studied in natural habitats (reviewed in Losos, 2009). Although some anoles rely on crypsis to avoid predators (Losos 2009), most species actively flee from predators using a combination of three escape modes: squirreling (i.e., rapid movement to the opposite side of a cylindrical substrate, such as a trunk or branch), jumping, and sprinting (Regalado 1998). Anole performance is influenced by the structural habitat on which lizards perch (Irschick and Losos, 1999; Irschick, et al., 2005; Mattingly and Jayne, 2004). For many anole species, sprint speed declines with both decreasing perch diameter (Losos & Sinervo 1989; Losos & Irschick, 1996) and increasing perch compliance or flexibility (Foster el al, in press). Sprinting lizards must reduce their speed on narrow diameter and flexible surfaces to reduce the chance of slipping or falling. In contrast, perch diameter has less of an effect on jumping ability in anoles (Losos & Irschick, 1996).

As a consequence of performance ability mediated by the substrate, lizards should employ different escape strategies on different substrates. For example, narrow perches might not fully conceal lizards, which should decrease the use of squirreling. Similarly, lizards should escape more often by jumping when perch diameters decrease and sprinting is compromised. However, recent studies have shown that narrow perches are often more compliant (i.e. flexible), which can reduce jumping performance (Gilman et al., 2012; Gilman & Irschick 2013). Laboratory studies of jumping performance of the green anole as a function of perch compliance showed that narrower and more compliant perches reduce jumping distance and take off speed. Furthermore, compliant perches often lead to lizards being struck by their perch after takeoff, which negatively impacts their flight and landing (Gilman et al., 2012). In the field, Gilman and Irschick (2013) found that jumping ability was impaired by perch complexity. Furthermore, narrower perches often occur in clusters, such that the availability of nearby perches might be higher (Rodriguez-Robles et al., 2005; Losos & Irschick, 1996), and Gilman & Irschick (2013) found that jumping ability was impaired on thin narrow perches and isolated perches.

Losos (1990) showed that much of the variation in performance (i.e., running, jumping, and clinging ability) in *Anolis* is explained by body size. He noted that locomotor performance is also related to limb proportions where longer-limbed lizards can achieve higher maximal sprint speeds. Similarly, longer-limbed individuals are superior jumpers (Toro et al., 2004). Microhabitat influences performance such that broad surfaces favor sprinting and narrower perches favor jumping as long as the perch compliance is low (Gilman et al, 2012). Given these interactions among performance, morphology, and habitat use for different types of locomotion, we expect lizards to adjust their escape behavior to fit their current location. For example, lizards should increase their FID if they occupy a habitat in which their performance is reduced or employ a trajectory that minimizes encounters with substrates that would reduce performance (Foster et al, in press). Moreover, lizards should avoiding using escape modes which result in poor performance, such as sprinting on narrow perches.

In this study, we evaluate how urban environments influence the escape behavior of the Puerto Rican Crested Anole, *Anolis cristatellus.* First, we ask whether escape behavior differs between natural forest and urban habitats. For this question, we compare lizards occupying the same substrate (i.e., tree trunks) in each habitat. Second, because lizards in urban habitats use artificial substrates in addition to natural vegetation, we compare escape behavior among three types of substrate that are common in urban areas - cement walls, metal poles, and tree trunks. We hypothesize that lizards in urban environments will reduce their flight initiation distance (i.e., distance between the observer and the lizard when the lizard begins escape) as a response to habituation to human activity near their perches. We also expect escape mode to vary based on the characteristics of the substrates used by lizards. For example, we predict that lizards will rely more on sprinting rather than jumping when using broad diameter perches, such as cement walls and large trees, both of which are characteristic of urban habitats. This is because *A. cristatellus* sprints faster on broad diameter substrates compared to narrow ones (Losos and Irschick, 1996). We also predict that the decrease in structural habitat complexity associated with urban environments will reduce jumping opportunities because of the lack of available vegetation on which to land.

METHODS

We conducted this study in May and June 2014 at two sites in the San Juan metropolitan area in Puerto Rico. The "urban site" (18°24'12.8"N 66°02'33.0"W) was the faculty-housing complex at the University of Puerto Rico, Rio Piedras. This site was "park-like" with large open areas dominated by mowed lawns and widely spaced large diameter trees. Most green space was within 10 m of sidewalks and houses. This site was characterized by frequent movement of humans, both on foot and by car, and the presence of domestic cats. The "natural forest site" (hereafter "forest site"; 18°23'02.7"N 66°02'32.8"W) was a secondary forest in an urban park, the Bosque del Nuevo Milenio. This site was characterized by a dense overstory cover, dense trees of various sizes, and leaf litter covering most of the ground. No domestic animals or humans were observed in the forest during field studies. In contrast, both cats and ground lizards (*Ameiva exsul)* were observed in the urban site. Lizards were sampled at least 10 m from the forest edge.

Studies have shown that lizards respond to human-simulated predators, supporting the validity of using human researchers as surrogate predators (Cooper, 2006a). In pilot trials, we found no difference in flight initiation distance between a novel threat (i.e., an umbrella) and a human (ANOVA: $F_{1,74}=0.224$, $P<0.64$). Our protocol consisted of one researcher (KAR) wearing the same color clothing for all trials and approaching lizards at a constant walking speed with an outstretched hand (Cooper, 2009). Following Cooper (2005), we measured flight initiation distance (FID) as the distance between the observer and the lizard when the lizard initiates escape, and flight distance (FD) as the continuous escape movement of a lizard until it first stops. We videotaped trials to aid in assessing the flight trajectory of lizards. Lizard escape mode was scored as squirreling (i.e., moving around the perch and breaking the line of sight), jumping, or sprinting (see Regalado 1998). To estimate lizard body temperatures at the time of escape, we used a copper model of a lizard fitted with a thermal couple (Hertz 1992) placed at the exact location of the focal lizard immediately after it fled from its perch. We measured the escape response of lizards perched on tree trunks at both the forest and urban sites. In addition to trees at the urban site, we also evaluated escape responses of lizards perched on metal posts and cement walls. Metal posts consisted primarily of posts supporting chain-link fences, but also included light posts. Cement walls consisted of the exterior walls of apartment buildings or small houses. We characterized perch use by measuring the height and diameter in cm of the initial perch occupied by a lizard as well as the number of perches within 0.5 m (termed "nearby perches").

STATISTICAL ANALYSES

We tested for mean differences in perch height, perch diameter, and the number of nearby perches for lizards occupying each substrate type (i.e., forest trees, urban trees, metal posts, and cement walls) using analysis of variance (ANOVA). We used a non-parametric rank transformation to normalize FID and FD values. We used ANOVA to test for differences in FID and FD among substrate types and Tukey’s Honestly Significant Difference (HSD) *post hoc* test to determine which substrates differed significantly when the ANOVA was significant. We used linear regressions to test for difference in FID and FD with estimated lizard body temperatures. We used contingency tables to compare proportional use of different escape modes when lizards used different substrates, assessing overall and pairwise significance with chi-square tests. We used multinomial logistic regression to determine if the probability of using different escape modes differed with increasing substrate diameter, number of nearby perches or temperature. Cement walls were not included in analyses using diameter because no appropriate diameter could be measured on these broad, flat surfaces. Separate analyses were conducted for forest and urban sites.

RESULTS

Lizards at urban sites used substrates with broader diameters than the natural site (ANOVA: $F_{3,206}=17.00$, $P<0.001$, Table 1). At the urban site, lizards used trees that were four times broader than forest trees, metal posts used by lizards were twice as broad as forest trees, and even though diameters were not measured for cement walls, these substrates were also substantially broader than forest trees. Lizards perched on cement walls and metal posts had fewer perches nearby (ANOVA: $F_{3,214}=7.80$, $P<0.001$, Table 1), areas immediately adjacent to lizards perched on cement walls had 75% fewer nearby perches than trees in both the forest and urban areas. Lizards occupying different substrates did not differ in their perch height (ANOVA: $F_{3,235}=0.89$, $P=0.45$, Table 1). Model temperatures of forest lizards were lower than urban lizards (i.e. mean of 31.35°C and 32.44°C, respectfully) using both natural and artificial perches (ANOVA: $F_{3,205}=39.78$, $P<0.001$, Table 1), model temperature were highest for lizards using metal posts, and lizards using cement walls and urban trees showed similar temperatures.

We assessed the escape response of 126 lizards from the urban site and 112 from the forest site. We found a significant difference in flight initiation distance between habitats (ANOVA: $F_{3,235}=5.96$, $P<0.01$). Flight initiation distance was significantly greater for lizards perched on trees in the forest compared to those perched on trees and metal posts at the urban site (Tukey's HSD test: $P<0.05$; Fig. 1).

We found no difference in flight initiation distance among substrates in the urban habitat (Tukey’s HSD test: all P>0.5), although lizards on cement walls tended to have longer and more variable FIDs. Lizards on cement walls used either the middle of the wall or the edge, and those on the middle had significantly greater FID (ANOVA: $F_{1,27}=5.34$, P=0.03). Our results are limited by our sample size of lizards on this substrate, but show potential increase in FID when lizards are in the middle of a cement wall. Lizard flight distances did not differ among the four substrate types (ANOVA: $F_{3,195}=0.837$, P=0.48). Temperature did not influence either FID or FD (FID: $R^2= -0.003$, P=0.63; FD: $R^2= -0.005$, P=0.73).

We found a relationship between the escape mode used by lizards and the substrate they perched on ($X^2=18.20$, P<0.01, df=6; see Table 2 for pairwise comparisons). Lizards on all substrates at the urban site tended to squirrel around the perch more and jump less compared to lizards on trees at the forest site. Lizards never jumped when on cement walls at the urban site.

Multinomial logistic regression results revealed that lizards in the forest site favored jumping when on the smallest diameter perches (Forest: $X^2 = 30.0$, df = 2, P < 0.01; Fig. 4). The probability of jumping decreased to nearly zero when perch diameters increased to about 10 cm, but relatively few lizards used perch diameters larger than this at the forest site. As perch diameter increased, the probabilities of squirreling increased while sprinting decreased, but only 20% of lizards in the forest used perch diameters greater than 10 cm (Fig. 4). Lizards at the urban site also favored jumping from small diameter perches and the probability of jumping decreased to zero for perch diameters of 20 cm and greater (Urban: $X^2 = 21.9$, df = 2, P

< 0.01; Fig. 4). However, lizards at the urban site used perches with diameters greater than 20 cm more frequently than forest lizards (Fig. 4). In contrast to the forest site, lizards at the urban site maintained a 0.25 probability of sprinting across the range of perch diameters occupied. The broader perch diameters used at the urban site likely facilitated both sprinting and squirreling compared to the forest site where the probability of sprinting decreased to zero at perches larger than about 20 cm. In contrast to the difference between the forest and urban sites in the effect of perch diameter on the probability of using different escape modes, the number of nearby perches had a similar effect in each habitat. As the number of nearby perches increased, the probability that lizards would escape by jumping increased steadily in both habitats (Forest: $X^2 = 6.3$, df = 2, P = 0.04, Urban: $X^2 = 16.2$, df = 2, $P < 0.01$; Fig. 5). The lack of perches surrounding cement walls likely contributed to the reluctance of lizards to jump from this substrate. The probability of different escape modes did not vary significantly with increasing temperature at either site (Forest: $X^2 = 0.40$, df = 2, P = 0.82; Urban: $X^2 = 0.53$, df = 2, P = 0.77; Fig. 6).

DISCUSSION

In this study, we found that urban lizards have shorter flight initiation distances and favor the use of squirreling compared to lizards from the natural forest. Differences in the structural habitat between the forest and urban sites likely influence the escape mode used by lizards, providing evidence that habitat modifications associated with urbanization can affect escape behavior.

Other studies have reported greater FID in forest habitat as opposed to more open and urban like habitats (Grolle et al., 2014; Irschick et al. 2005). Irschick et al. (2005) showed that anoles had greater FID in a habitat that was relatively undisturbed by people and had complex vegetation where anoles were using narrower diameter perches. Grolle et al. (2014) showed that fence lizards had significantly shorter FID at sites with nearly constant foot traffic near lizards. Similarly, our results show urban lizards had shorter FID, consistent with the idea that these lizards are habituated to human activity at this site, but differences in the structural habitat may also contribute to differences in escape behavior.

Habitat structure is a critical factor that may hinder the efficiency of tasks such as prey and predator detection and social interactions (Rodrígues-Robles et al, 2005). A recent study in aquatic invertebrates showed that the impact of habitat structure on prey mortality can vary with regards to prey and predator microhabitat use (Klecka & Boukal, 2014). Their results show that in some cases vegetation provides perches for predators which increases prey mortality leading to an anti-refuge effect (Klecka & Boukal, 2014). Two studies have shown higher injuries in structurally complex forest habitat using lizard clay models (Shepard 2007; McMillian & Irschick 2010). Moreover, McMillian and Irschick (2010) showed clay models in the forest habitat had more avian-like injuries and their urban habitat models had conspecific lizard injuries. Grolle et al. (2005) found a higher abundance of birds in a more structurally complex rural habitat, making it difficult to tease whether increased predator attacks are due to increased abundance of potential predators or decreased visibility of approaching predators. Rodríguez-Robles et al. (2005) suggested the yellow-chinned anoles (*Anolis gundlachi*) use wider, less cluttered perches because of the greater detectability of approaching predators and potential increase in locomotor performance. Lower vegetation complexity in the urban habitat could allow lizards to detect approaching predators at a greater distance. Future work of urban escape behavior should address potential differences in FID when lizards detect an incoming threat from relatively close (i.e., less than 3 m distance) and far distances (i.e., more than 5 m).

Our study evaluated cement walls as a substrate where lizard locomotion was potentially reduced. Lizards on cement walls showed a trend towards greater flight initiation distance as compared to lizards on other substrates at the urban site. Cooper (2006b) suggested that vertical perches might provide greater safety because they are taller, allowing escape above the reach of terrestrial predators and possibly because they permit more rapid climbing. However, there is a trade-off between acceleration and stability in vertical climbing (Higham et al., 2011; Clemente et al., 2013). Highman et al. (2011) showed that when lizards accelerate their center of mass moves away from the surface, which can lead to slips and falls when sprinting vertically. Studies have shown that variability in surface substrates can affect sprint performance (Tulli et al., 2012) and cement walls potentially impact the ability of lizards to run at maximal speed, particularly when these substrates are also smooth. Because maximum acceleration is vital for escaping predators (Higham et al., 2011; Walker et al., 2005), lizards on cement walls may increase their flight initiation distance to compensate for performance limitations of this substrate. Further work is needed to fully characterize how sprinting on cement walls might constrain escape speed, if lizards can modulate their speed to escape without slipping or falling, and how the location of the lizard on this substrate (e.g. middle of the wall versus the corner of a building) influences the escape mode used. For example, higher FID for lizards on the middle of the wall could be a function of decreased escape speed. Potentially lizards perched on the corner of a building can overcome this constrained by relying on squirreling and using the adjoining wall to hide from incoming predators.

Habituation may be an important component of organisms' success in urban environments. Repeated exposure to low-risk predators should lead to decreased flight initiation distances, minimizing costly escapes and maximizing time for foraging and reproduction (Groelle et al. 2014). However, if organisms habituate to a predator that is inconsistent in its predatory behavior, it could face lethal consequences (Rodríguez-Prieto et al. 2010). It is likely that urban lizards have habituated to the presence of humans and have reduced their FID. Black iguanas with higher encounter rates with humans showed decreased FID (Burger & Gochfeld, 1990). However, higher encounter rates with people do not always lead to lower FID. Blumstein (2013) showed that birds do not always habituate by quantifying human encounter rates on trails and fire roads in the Santa Monica Mountains. This study found that only four out of fourteen species of chaparral birds showed differences in FID as a consequence of high human impact. An alternative hypothesis is that longer FID is a response to greater predation risk (Cooper, 2006). McMillan and Irschick (2010) found that forest lizards faced greater predation pressure compared to urban lizards. It is possible that urban lizards encounter fewer predators and decrease their FID as a consequence. We did not assess the composition or abundance of predators at our sites. However, a recent study found higher caudal autonomy in four urban sites in Puerto Rico, one of which was the urban site used for this study (Tyler et al, submitted). Either predation risk is higher in urban environments leading to more encounters with predators or predators are more inefficient leading to lizard escape by autotomizing their tails (Tyler et al, submitted). With increased predation risk, urban lizards should exhibit longer FID to avoid incoming predators. On the other hand, if predators are more inefficient at capturing prey, then FID should decrease. More work is needed to assess the effect of habituation and predation risk, or a combination of these factors as a potential explanation for differences in FID between sites in our study.

Other factors, besides habituation, could account for shorter flight initiation distances at our urban site. Flight initiation could be influenced by air temperature, recent feeding history, reproductive status, predator-approach path and tail loss (Prosser et al., 2006). Some studies suggest that lizards with cooler body temperatures initiate flight sooner (Rand, 1964; Smith 1967). However, our results did not support a relationship between model-lizard temperature and flight initiation distance or flight distance. When lizards escape they should minimize the probability of being located by the predator later (Martin & Lopez, 1995). In some cases, it might be beneficial to remain vigilant and allow predators to come closer because flight movement can attract the attention of predators (Burger & Gochfeld, 1990; Martín & Lopéz, 2000). Lizards can decrease their detectability by squirreling around the perch, which interrupts the predatory sequence and introduces uncertainty as to the location of the prey (Regalado, 1998).

Escape tactics in *Anolis* lizards vary with habitat structure and morphology (Losos & Irschick, 1996). Lizards at our urban site showed a reduced use of jumping and this shift in escape mode is likely influenced by differences in perch diameter and number of nearby perches between habitats. Lizards should jump from smaller diameters because jumping ability is not constrained on these smaller perches and the ability to run is maximized on wider substrates (Losos & Irschick, 1996). Consistent with these ideas we found a higher proportion of jumping in the forest habitat where lizards used smaller diameter perches. Other factors can also affect jumping performance, which could in turn influence when and how this escape tactic is used. Gilman & Irschick (2013) showed that lizards prefer to jump from less compliant (i.e., flexible) substrates. They also found that compliance decreases with increasing perch diameter for trunks and branches. Based on compliance alone, lizards should jump more from wider trunks and/or cement walls because these are more rigid substrates. However, for optimal jumping lizards must take off at angles between 39° and 42° (Toro et al., 2003), wider diameter perches and walls might constrain the ability of lizards maneuver into a position to jump at this take off angle. Furthermore, the lack of nearby vegetation constrains where lizards can jump to, these factors likely both contribute to the lack of use of this escape mode on cement walls. In our study, no lizard jumped from cement walls where few nearby perches existed (Table 2). A previous study of Green Anoles in nature found that lizards used diameters ranging from 0.2 to 5 cm for jumping (Gilman & Irschick 2013). Gilman & Irschick (2013) showed that for branches and trunks compliance was relatively low at perch diameters greater than 1.30 cm. Our lizard jumped from narrow perches, the narrowest being 1 cm, presumably at this point perches were rigid enough that jumping ability was not reduced. Performance studies are needed to fully understand how jumping from rigid, vertical perches, such as cement walls, affects jumping ability.

We show that urban habitats can lead to differences in escape behavior (Ditckoff et al., 2006), which is mediated by modifications of the structural habitat in urban areas. These changes in behavior and potential performance effects of urban substrates may have fitness consequences. Marnocha et al (2011) found that lizards from human-modified habitats were larger in body size and had longer hindlimbs compared to natural forest lizards. Moreover, they found that lizards in human-modified habitats used broader diameter perches, which performance studies show favor longer-limbed lizards (Losos and Sinervo 1989; Irschick and Losos, 1999). Changes in behavior found in this study suggest habitat modifications due to human activities, such as urbanization, may be a potent force impacting the ecology and evolutionary trajectory of these populations.

REFERENCES:

Atwell JW, Cardoso GC, Whittaker DJ, Campbell-Nelson S, Robertson KW, Ketterson ED (2012) Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral ecology*, **23**, 960–969.

Barnosky AD, Hadly EA, Bascompte J et al. (2012) Approaching a state shift in Earth's biosphere. *Nature*, **486**, 52–8.

Blumstein DT (2013) Attention, habituation, and antipredator behavior: implicaitons for urban birds. In: *Avian urban ecology: Behavioural and physiological adaptations* (eds Gil D, Brumm H), pp. 41–53. Oxford University Press, Oxford.

Burger J (2001) The behavioral response of basking Northern water (*Nerodia sipedon*) and Eastern garter (*Thamnophis sirtalis*) snakes to pedestrians in a New Jersey park. *Urban Ecosystems*, **5**, 119–129.

Burger J, Gochfeld M (1990) Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): Variation as a function of human exposure. *Journal of Comparative Psychology*, **104**, 388–394.

Clemente CJ, Withers PC, Thompson GG, Lloyd D (2013) Lizard tricks: overcoming conflicting requirements of speed versus climbing ability by altering biomechanics of the lizard stride. *The Journal of experimental biology*, **216**, 3854–62.

Cooper WE (2003) Effect of risk on aspects of escape behavior by a lizard *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology*, **109**, 617–626.

Cooper WE (2006a) Dynamic Risk Assessment: Prey Rapidly Adjust Flight Initiation Distance to Changes in Predator Approach Speed. *Ethology*, **112**, 858–864.

Cooper WE (2006b) Risk factors affecting escape behaviour by Puerto Rican Anolis lizards. *Canadian Journal of Zoology*, **84**, 495–504.

Cooper WE (2009) Theory successfully predicts hiding time: New data for the lizard *Sceloporus virgatus* and a review. *Behavioral Ecology*, **20**, 585–592.

Cooper WE, Whiting MJ (2007) Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology*, **113**, 661–672.

Cooper WE, Wilson DS (2007) Beyond Optimal Escape Theory : Microhabitats as Well as Predation Risk Affect Escape and Refuge Use by the Phrynosomatid Lizard *Sceloporus virgatus*. *Behaviour*, **144**, 1235–1254.

Ditchkoff SS, Saalfeld ST, Gibson CJ (2006) Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, **9**, 5–12.

Foster, K. L., Collins, C. E., Higham, T. E., & Garland, T. (in press). Determinants of lizard escape performance: decision, motivation, ability, and opportunity. In W. E. J. Cooper & D. T. Blumstein (Eds.), *Escaping from predators: An integrative view of escape decisions*.

Gilman CA, Bartlett M, Gillis G, Irschick D (2012) Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*). *Journal of Experimental Biology*, **215**, 568–568.

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

Grolle EK, Lopez MC, Gerson MM (2014) Flight initiation distance differs between populations of Western fence lizards (Sceloporus occidentalis) at a rural and an urban site. *Bulletin of the Southern California Academy of Sciences*, **113**, 42–46.

Hertz PE (1992) Evaluating thermal resource partitioning - By sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia*, **90**, 127–136.

Higham TE, Korchari P, Mcbrayer LD (2011) How to climb a tree: Lizards accelerate faster, but pause more, when escaping on vertical surfaces. *Biological Journal of the Linnean Society*, **102**, 83–90.

Irschick DJ, Carlisle E, Elstrott J et al. (2005) A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society*, **85**, 223–234.

Irschick DJ, Herrel A, Vanhooydonck B, Huyghe K, Van Damme R (2005) Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: a cautionary tale for performance-to-fitness studies. *Evolution*, **59**, 1579–1587.

Irschick DJ, Losos JB (1998) A Comparative Analysis of the Ecological Significance of Maximal Locomotor Performance in Caribbean *Anolis* Lizards. *Evolution*, **52**, 219–226.

Irschick DJ, Losos JB (1999) Do Lizards Avoid Habitats in Which Performance Is Submaximal? The Relationship between Sprinting Capabilities and Structural Habitat Use in Caribbean Anoles. *The American Naturalist*, **154**, 293–305.

Drakeley M, Lapiedra O, & Kolbe JJ (Submitted) Predation risk perception, food density and conspecific cues shape foraging decisions in anoles. *Behavioral Ecology*.

Lepczyk CA, Mertig AG, Liu J (2004) Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation*, **115**, 191–201.

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology,* **68**, 619–640.

Losos JB (1990) Ecomorphology, performance capability, and scaling of West Indian Anolis lizards: An evolutionary analysis. *Ecological Monographs*, **60**, 369–388.

Losos, JB (2009). Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. Berkeley, CA: University of California Press.

Losos JB, Sinervo B (1989) The Effects of Morphology and Perch Diameter on Sprint Performance of Anolis Lizards. *Journal of Experimental Biology*, **145**, 23–30.

Losos JB, Irschick DJ (1996) The effect of perch diameter on escape behaviour of *Anolis* lizards: Laboratory predictions and field tests. *Animal Behaviour*, **51**, 593–602.

Loyd KAT, Hernandez SM, Carroll JP, Abernathy KJ, Marshall GJ (2013) Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation*, **160**, 183–189.

Klecka J, Boukal DS (2014) The effect of habitat structure on prey mortality depends on predator and prey microhabitat use. *Oecologia*.

Marnocha E, Pollinger J, Smith TB (2011) Human-induced morphological shifts in an island lizard. *Evolutionary Applications*, **4**, 388–396.

Martin J, López P (1995) Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. *Canadian Journal of Zoology*, **73**, 129–132.

Mattingly WB, Jayne BC (2004) Resource use in arboreal habitats: Structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, **85**, 1111–1124.

Møller AP, Ibáñez-Álamo JD (2012) Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour*, **84**, 341–348.

Peckarsky BL, Abrams PA., Bolnick DI et al. (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator prey interactions. *Ecology*, **89**, 2416–2425.

Perry G, Levering K, Girard I, Garland T (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour*, **67**, 37–47.

Preisser EL, Bolnick DI (2008) The many faces of fear: Comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE*, **3**, 5–8.

Prosser C, Hudson S, Thompson MB (2006) Effects of urbanization on behavior, performance, and morphology of the Garden Skink, *Lampropholis guichenoti*. *Journal of Herpetology*, **40**, 151–159.

Rand AS (1964) Inverse relationship between temperature and shyness in the lizards *Anolis lineatopus*. *Ecology*, **45**, 863–864.

Ramalho CE, Hobbs RJ (2012) Time for a change: Dynamic urban ecology. *Trends in Ecology and Evolution*, **27**, 179–188.

Rebele F (1994) Urban Ecology and Special Features of Urban Ecosystems. *Global Ecology and Biogeography Letters*, **4**, 173–187.

Regalado R (1998) Approach distance and escape behavior of three species of Cuban Anolis (Squamata, Polychrotidae). *Caribbean Journal of Science*, **34**, 211–217.

Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator-prey relationships. *Ecological Applications*, **21**, 936–943.

Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2010) Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology*, **64**, 1937–1945.

Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2010) Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology*, **64**, 1937–1945.

Rodríguez-Robles JA, Leal M, Losos JB (2005) Habitat selection by the Puerto Rican yellow-chinned anole, *Anolis gundlachi*. *Canadian Journal of Zoology*, **83**, 983–988.

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

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, **21**, 186–191.

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Smith DG (1997) Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. *Behavioral Ecology*, **8**, 622–629.

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. *Animal Behaviour*, **85**, 1101–1112.

Toro E, Herrel A, Vanhooydonck B, Irschick DJ (2003) A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. *The Journal of experimental biology*, **206**, 2641–2652.

Tulli MJ, Abdala V, Cruz FB (2012) Effects of different substrates on the sprint performance of lizards. *Journal of Experimental Biology*, **215**, 774–784.

Tyler KR, Winchell KM, Revell LJ (submitted) Tails of the city: Caudal autotomy in the tropical lizard , Anolis cristatellus , in urban and natural areas of Puerto Rico. *Journal of Herpetology*.

United Nations. 2011. World urbanization prospects. The 2011 Revision. New York, NY

Walker JA, Ghalambor CK, Griset OL, McKenney D, Reznick DN (2005) Do faster starts increase the probability of evading predators? *Functional Ecology*, **19**, 808–815.

Ydenberg RC, Dill LM (1986) The Economics of Fleeing form Predators. *Advances in the study of behavior*, **16**, 229–249.

	Perch diameter				Number of Nearby Perches			Perch Height			Temperature		
	N	Mean	SE	Tukey's HSD	Mean	SE	Tukey's HSD	Mean	SE	Tukey's HSD	Mean	SE	Tukey's HSD
Forest tree	97	7.95	1.28	A	2.32	0.16	A	103.94	4.19	A	31.35	0.06	C
Urban tree	71	24.11	2.78	B	2.22	0.31	AB	111.94	4.48	A	32.32	0.08	B
Metal Post	41	15.70	2.64	AB	1.34	0.17	BC	115.83	7.22	A	32.74	0.06	A
Cement Wall	30	NA	NA	NA	0.57	0.12	C	112.60	11.91	A	32.32	0.16	B

Table 1: Mean (± SE) for lizard microhabitat use at the forest and urban sites. Forest site trees are shown in green. Urban site trees and artificial substrates are shown in grey. Letters denote significant differences in means at different substrates based on Tukey's HSD test. Length measurements are in cm and temperature is in Celsius degrees.

	Forest tree	**Urban tree**	**Metal Post**	**Cement Wall**
Forest tree		X^2=8.35	X^2=3.30	X^2=8.32
Urban tree	P=0.015		X^2=4.86	X^2=9.20
Metal Post	P=0.192	P=0.088		X^2=3.08
Cement Wall	P=0.016	P=0.01	P=0.214	

Table 2: Results of pairwise contingency tests for differences in the three escape mode used by lizards when perched on different substrates (n=231). Forest site trees are shown in green, and urban sites in grey. Squirreling (n=117) is the most common escape mode used, followed by sprinting (n=77) and jumping (n=37).

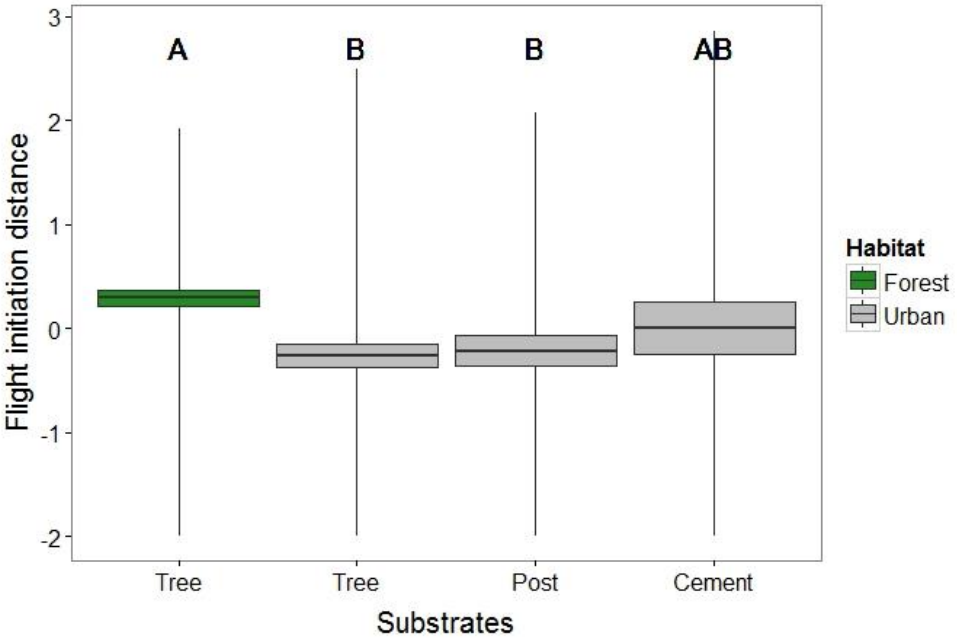

Figure 1: Mean (± SE) flight initiation distance when lizards were on one of the four substrates types (i.e., forest tree N=97, urban tree N=71, metal post N=41 and cement wall N=30). FID was rank-transformed for normality. Green color represents trees in the forest habitat and grey colors represent substrates in the urban habitat. These boxplots are drawn using the standard error and mean for the box and the whisker show the range. Letters denote significant pairwise comparisons using Tukey's HSD *post hoc* test. Flight initiation was significantly longer in forest trees when compared to most urban substrates.

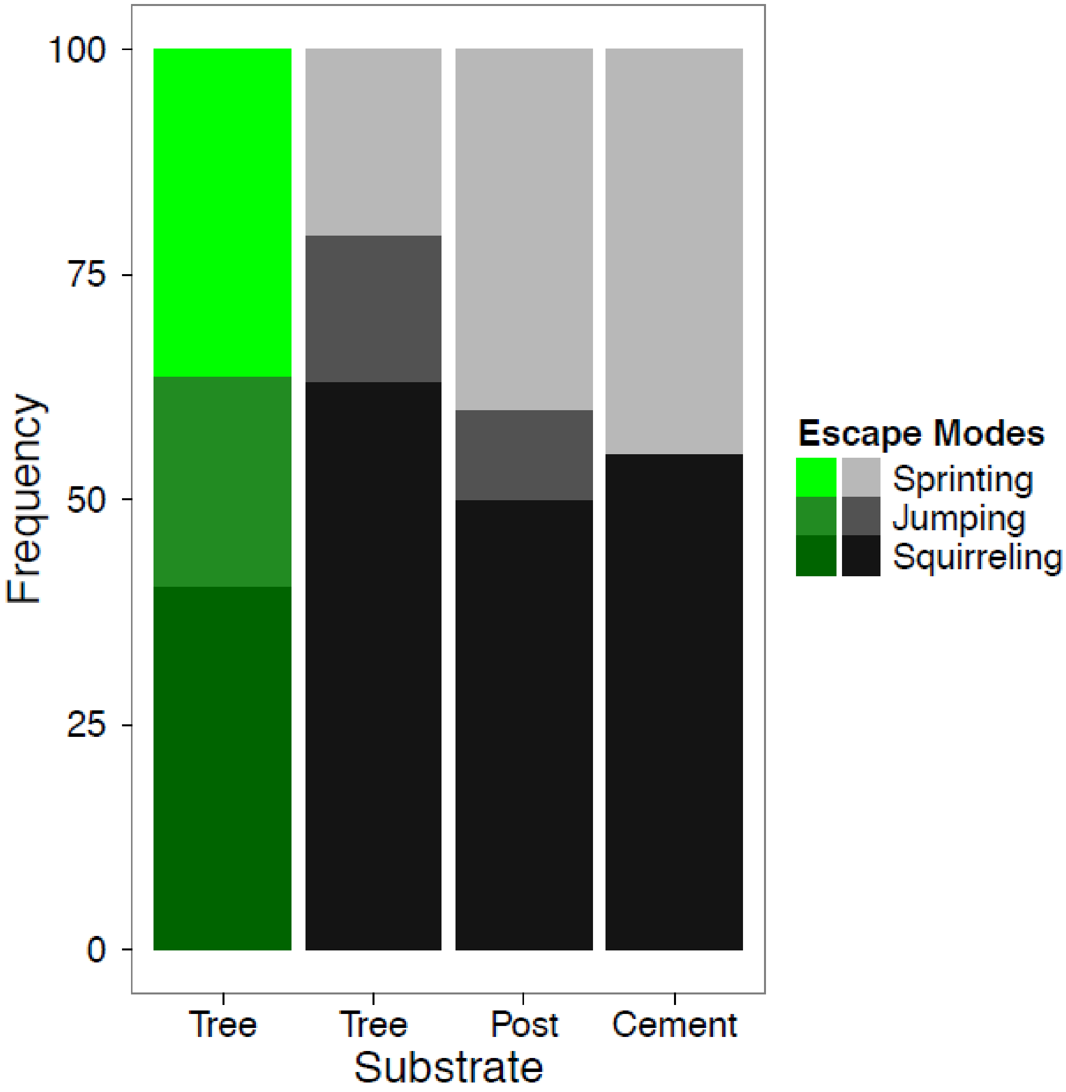

Figure 2: Proportion of escape modes used across different substrate types (i.e., forest tree N=97, urban tree N=71, metal post N=41 and cement wall N=30). Natural site substrate is shown in green and urban site substrates are shown in grey. There was an increase in squirreling around at the expense of jumping in the urban habitat.

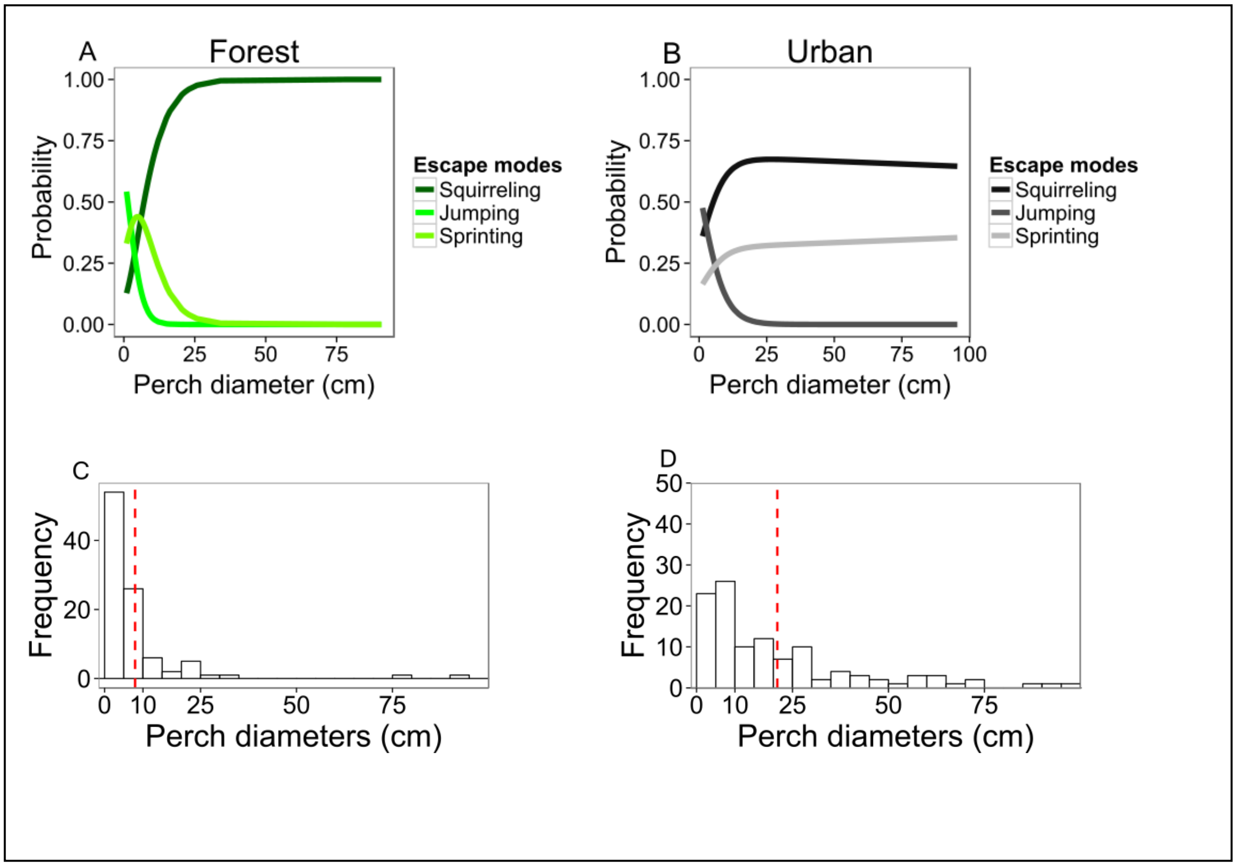

Figure 3: Results from multinomial logistic regressions assessing the probability of using each escape mode with increasing perch diameters for the A) forest site (N=97) and B) urban site (N=112). Histograms show the frequency of perch diameters used by lizards at the C) forest site and D) urban site. The red dashed line shows the mean perch diameter used by lizards at each site.

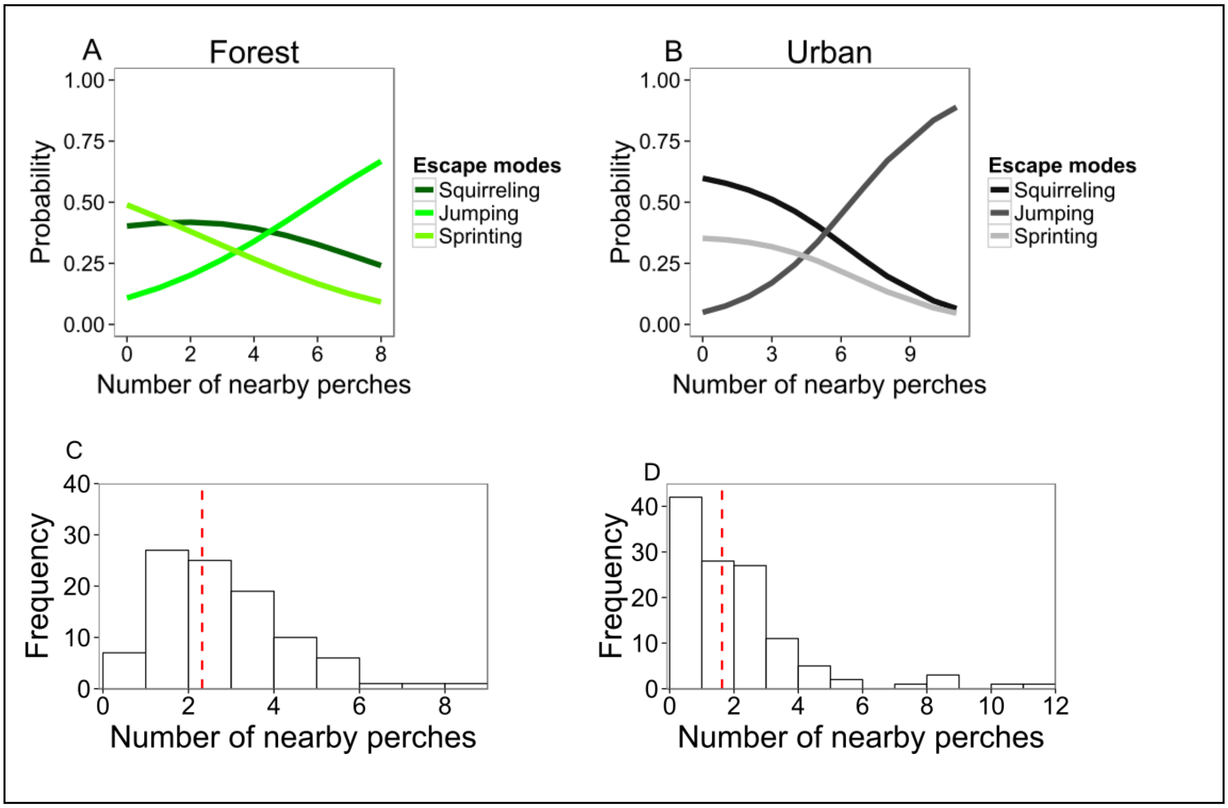

Figure 4: Results from multinomial logistic regressions assessing the probability of using each escape mode with increasing number of nearby perches for the A) forest site (N=97) and B) urban site (N=142). Histograms show the frequency of number of nearby perches at near the lizard at the C) forest site and D) urban site. The red dashed line shows the mean number of nearby perches near the lizards at each site

MANUSCRIPT-2

In preparation for the *Journal of Herpetology*

Do urban environments influence foraging behavior of the Puerto Rican Crested Anole (*Anolis cristatellus*)?

Kevin Aviles-Rodriguez and Jason J. Kolbe

Department of Biological Sciences, University of Rhode Island, Kingston RI, USA

Corresponding Author:

ABSTRACT

Animals increase their chance of survival and reproduction in the wild by successfully responding to the ecological challenges they encounter. A widespread and growing component of global change is urbanization - the changes in land use associated with high-density human populations. In this study, we evaluate how urban environments influence the foraging behavior of the Puerto Rican Crested Anole, *Anolis cristatellus*. We used Kaplan-Meier estimates of the survival function to quantify differences in the latency to feed by habitat type, model predator presence or absence, and conspecific presence or absence near the food tray. Lizards at the forest site responded faster than urban lizards, but lizard responses were not influenced by the presence of the model predator. We found that lizards in the forest site took longer to feed when conspecifics were present. We also found that lizards in the forest fed less often in the presence of conspecifics, because conspecifics often exhausted the food treatment ending the visual cue to forage for our focal lizards. Our results suggest that our urban habitat lizards foraged more slowly, which could be influenced by differences from forest lizards in their motivation to feed or predation risk associated with differences in the structural habitat and predator composition.

INTRODUCTION

Animals increase their chance of survival and reproduction in the wild by successfully responding to the ecological challenges they encounter (Drakeley et al, in review) and modifying behavior as the environment changes is a key response (Sol et al., 2013). For example, animals may avoid or adjust their response to novel enemies, utilize novel resources or habitats, and behaviorally adjust to changing spatiotemporal conditions such as changes in the structural habitat or climate (Sih et al., 2011). Understanding the consequences of changes from a natural habitat to a human-impacted habitat is critical for both evaluating current impacts and predicting future ones (Barnosky et al., 2012).

Changes associated with urban areas have the potential to influence when and how animals forage. For example, urban habitats incur a number of structural changes that often results in a habitat that is a combination of artificial structures, managed vegetation such as open grassy areas and unmanaged vegetation. These changes alter the habitat available for animal populations, often resulting in fewer species overall but increased abundance of urban-tolerate species (Ramalho & Hobbs, 2012; Rebele, 1994; Shochat et al., 2006). Some studies suggest that predatory pressures may be greater in urban habitats, particularly because of domestic or feral cats (Ditchkoff et al., 2006). Loyd et al. (2013) found that 44% of free-roaming cats hunted wildlife, and reptiles were the most common taxa of prey items, including Green Anole lizards. However, a higher density of potential predators may not necessarily translate into higher predation rates because domestic predators mainly rely on food provided by humans (Møller and Ibáñez-Alamo, 2012). Predator-prey relationships may become decoupled when synanthropic predators are subsidized by anthropogenic resources (Rodewald, el al. 2011).

A forager should forage when the benefits of acquiring resources outweigh the risk of predation (Tsurim et al., 2008; Jacob and Brown, 2000). For example, a forager must react accordingly to each opportunity to feed given that failure to avoid a predator is more costly than failure to obtain a meal (Lima and Dill, 1990). However, foraging is also influenced by intrinsic factors, such as physiology, body condition, cognitive ability, sex, ontogeny, variation in animal personality, and extrinsic factors, such as the type or availability of food, structural habitat, and other environmental characteristics (Drakeley et al, in review). Some potential foraging costs include the energetic cost of searching and handling food, the cost of missed feeding opportunities, and the cost of predation (Tsurim et al, 2008). The decision to exploit a potentially risky patch depends on the forager's state of hunger, direct or indirect cues of predation risk, and time since last exposure of a predator (Brown, 1999).

Anolis lizards, or anoles, are a useful system for this study because aspects of their behavior and its relationship to the natural habitat have been studied (Losos, 2009), which aids in predicting how urban habitats might influenced their behavior. Anoles are primarily sit-and-wait predators, hunting by waiting at a single location while scanning the surrounding area for prey (Moermond, 1979). For example, *Anolis cristatellus* spends most of its time in survey posture - head down, forequarters lifted off the substrate, and hindlimbs extended backward up the vertical tree trunk (Losos 2009). Lizards in survey posture are receptive to foraging and they decrease their use of this position when fed to satiation (Stamps 1977; Drakeley et al. in review). Anoles capture prey by employing a rapid approach and quick strike.

Anole habitat use can influence foraging behavior (Moermond, 1979) and predation risk (Stamps, 1983). Moermond (1979) showed that more open habitats favor sit-and-wait foraging strategies because cluttered habitats require that anoles move more to search for prey. Stamps (1983) found that predation risk differed between patches and at different life stages, where juveniles moved to more open areas and later as adults returned to shaded areas. She suggested that juveniles shifted to open areas as a consequence of predation risk by congeners in the shaded areas. As adults they returned to shaded areas potentially because larger body size reduced predation risk. The presence of conspecifics can be an important social cue to determine territory quality (Stamps 1987). Stamps (1988) showed that juvenile *Anolis aeneus* preferred to settle in territories occupied by conspecifics. This study proposes that conspecific presence could be a social cue providing information about resource availability and potentially serve as predator defense because of increased detection of predators in a group.

In this study, we evaluate how urban environments influence the foraging behavior of the Puerto Rican Crested Anole, *Anolis cristatellus*. Following Drakeley et al. (in review), we present lizards with a standardized foraging opportunity to test for differences in the foraging decision-making process in urban and natural habitats. First, we ask whether foraging behavior differs between natural forest and urban habitats. For this question, we compare the latency to feed of lizards perched on trees in both environments. We hypothesize that lizards in the urban habitat will have a greater latency to feed due to the presence of cats, dogs, ground lizards and other ground dwelling predators. Second, we ask if the presence of a life-like model predator influences the latency to feed. We hypothesize that lizards at both habitats should increase their latency to feed with the presence of the model predator because the presence of a known predator should increase their wariness. Third, we ask whether the presence of conspecific lizards influences the latency to feed. We hypothesize that the presence of a conspecific should decrease the latency to feed in both habitats either due to the increased risk of missing a foraging opportunity or because approaching conspecifics indicate safety from potential predators.

METHODS

We conducted this study in July 2014 at two sites in the San Juan metropolitan area in Puerto Rico. The "urban site" (18°24'12.8"N; 66°02'33.0"W) was the faculty-housing complex at the University of Puerto Rico, Rio Piedras. This site was "park-like" with large open areas dominated by mowed lawns and large diameter trees. Most green space was within 10 m of sidewalks and houses. This site was characterized by frequent movement of humans, both on foot and by car, and the presence of domestic cats. The "natural forest site" (hereafter "forest site"; 18°23'02.7"N, 66°02'32.8"W) was a secondary forest in an urban park, the Bosque del Nuevo Milenio. This site was characterized by a dense overstory cover, dense trees of various sizes, and leaf litter covering most of the ground. No domestic animals or humans were observed in the forest during field studies. Lizards were sampled at least 10 m from the forest edge.

We sampled adult male *Anolis cristatellus* perched on trees with their heads down in survey posture. Sampled lizards were selected at least 5m from a previously sampled individual, and the habitats were sampled from a distinct starting point to avoid sampling the same individual twice. Lizards in survey posture are likely scanning their home range for feeding opportunities (Stamps 1977; Drakeley et al. in review). We placed a rectangular cardboard tray (dimensions = 14 x 20 x 5 cm) approximately 1 m away from the perch and directly in front of the focal lizard. Drakeley et al. (in review) showed that lizards respond fastest when two mealworms are presented as a food reward as compared to five or ten mealworms. We selected this number of mealworms because it elicited the fastest response time in their study. The tray was covered with a retractable lid that concealed the mealworms until the trial began. We used a two-minute habituation period prior to starting trials. The observer crouched at a distance greater than 3 m from the tray and remained still during trials. Our response variable was the latency to feed for the focal lizard, which we measured from video recordings as the time from the start of the trial to the acquisition of the first mealworm. Trials were continued until either both mealworms were consumed or 20 minutes elapsed. Lizards that did not respond were assigned the maximum time of 20 minutes for their latency to feed, which underestimates their actual value assuming a lizard would eventually feed in the tray. Our treatments included urban and natural habitats, the presence or absence of a model predator (i.e., a stuffed pearly-eyed thrasher, *Margarops fuscatus*), and the presence of conspecifics. We selected a pearly-eyed thrasher because this species is a documented predator of anoles (Stephen & Roughgarden, 1983) and present at our study sites. Pearly-eyed thrashers were seen at both our forest and urban sites; however, thrashers were mostly found along edges in the forest. The model predator was placed 30 cm behind the tray. Conspecifics were not manipulated, but allowed to approach the tray freely during trials.

We captured 20 male lizards from each site to assess their stomach contents after the conclusion of our foraging trials, from 8-16 August 2015. Lizards were captured using a noose on a fishing pole between 1300-1430 hrs. We processed lizards in less than two hours to prevent further digestion of their stomach contents. Lizards were weighed, snout-vent length (SVL) measured, and euthanized using a solution of 10% Tricaine-S (MS 222) (Conroy et al. 2009). Stomach contents were dissected from each lizard and then dried and weighed.

STATISTICAL ANALYSIS

We used Kaplan-Meier estimates of the survival function (Bland & Altman, 1998) to quantify differences in the latency to feed by habitat type, model predator presence or absence, and conspecific presence or absence near the food tray. We used Cox proportional-hazards regressions to test for differences between the treatments. We also used analysis of variance (ANOVA) to test for mean differences in the latency to feed between sites, presence or absence of a model predator, whether or not a conspecific lizard approached the food tray, and interactions among these factors. By using the survival analyses and ANOVAs as described above, we can evaluate the latency to feed for lizards that responded in foraging trials (i.e., actually fed on mealworms) as well as compare the mean latency to feed among treatments including both respondents and non-respondents. We used Tukey's Honestly Significant Difference (HSD) *post hoc* test to determine which treatments were significantly different when the ANOVA was significant. Our methods underestimate feeding times for lizards that did not respond during the 20-minute observation time. In 25 out of 102 trials, a conspecific lizard reached the food tray before the focal lizard, and in 20 of these cases the conspecific exhausted the food resource before the focal lizard responded.

We used ANOVA to test for a difference between habitats in dry stomach content. We used analysis of covariance (ANCOVA) to test for a difference in mass of dry stomach contents between lizards from forest and urban habitats using SVL of the same lizards as covariate.

RESULTS

We conducted a total of 102 foraging trials at our urban (n=52) and forest (n=50) sites with trials being equally split between those with and without the model predator at each site. Lizards at the natural site responded more frequently to the food tray than urban lizards (Cox proportional-hazards regressions: DF=2, P=0.004; Fig. 1). However, lizard responses were not influenced by the presence of the model predator (Cox proportional-hazards regressions: DF=2, P=0.93; Fig. 1). In the forest, when a conspecific was present, focal lizards had greater latency to feed and reacted less to the mealworms (Cox proportional-hazards regressions: DF=2, P=0.93; Fig. 2). In the urban habitat, lizards tended to have a shorter latency to feed when a conspecific approached.

We also used ANOVA to evaluate these results. The main effect of habitat was highly significant (Table 1), but habitat was also significant in an interaction with conspecifics alone as well as with conspecifics and model predators (Table 1). We found that lizards in the forest habitat had lower latency to feed, and the presence of conspecifics increased the latency to feed in the forest habitat. Tukey's HSD tests show that lizards fed faster in the forest irrespective of the presence of the model predator when conspecifics were absent (Fig. 3). In the urban site, lizards had shorter latency to feed when the model predator was absent and conspecifics were present, however, these conditions were only met in only a few instances (N=5).

We found no significant difference in the weight of lizard stomach contents between sites (ANOVA: $F_{1,38}=0.74$, $P>0.40$), suggesting that lizards did not consistently differ in their motivational state (i.e., the amount of food in their stomachs). However, these lizards were captured one month after conducting the foraging trials and therefore may not represent state of the lizards during the foraging trials. We also found hatchling lizards in the stomach of lizards at both sites (Forest: N=3; Urban: N=1). Hatchling weight was not included in these results because it is a resource that is not available throughout the summer. Lizards at the urban site weighed more at a given SVL than forest lizards (ANCOVA: $F_{1,37}=12.29$, $P<0.01$; Table 2), suggesting that lizards in the urban site are in better body condition than lizards from the forest site.

DISCUSSION

In this study, we found that urban lizards were less willing to exploit foraging opportunities and had greater latencies to feed compared to forest lizards. The presence of a model predator known to predate anoles near the foraging tray did not influence the decision of lizards to forage. We also found that the presence of conspecifics influenced the latency to feed in different ways in each habitat. Forest lizards took longer to feed, whereas urban lizards tended to forage faster when conspecifics were present. Differences in foraging behavior between forest and urban sites could be due to a number of factors, including differences in predator composition or abundance, the motivational state of lizards to forage, and differences in the structural habitat.

Anoles rely on visual cues of movement to detect potential predators (Fleishman 1988, Leal 1999), which likely accounts for the poor response to our static model predator (i.e., the pearly-eyed thrasher). Leal (1999) showed that *Anolis* lizards display antipredator pursuit deterrent signals when exposed to a model predator (i.e., the Puerto Rican racer snake, *Borikenophis portoricensis*) moving toward it. Movement is certainly a crucial indicator of a potential predation threat for *A. cristatellus*. When exposed to the model snake, lizards remained still for at least 120 sec before moving towards the predator (Leal, 1999). It is possible that lizards in our trials were able to discern our model as non-threatening because it did not move during the 120-sec habituation period. Future work should incorporate movement of the predator during the trial or conceal the model predator during the habituation period.

Predation risk in urban habitats is inconsistent. For example, Lepczyk et al. (2003) suggested that subsidies provided by humans could result in greater densities of cats leading to greater predatory effects than natural predators. However, because predators are subsidized by anthropogenic food sources, predation risk can decrease because prey-predator interactions can become decoupled (Rodewald, et al, 2011). Tsurim et al. (2008) suggested that urban birds were less vigilant foragers compared to rural birds as a consequence of more intense competition for food and reduced predation risk. Their study made general predictions for predation risk based on the time or effort birds allotted to foraging as a function of predator abundance. In such cases, predator abundance might not directly relate to predator encounter rates or successful predation. Direct measures of encounter rates between domestic predators and lizards are needed to determine whether urban lizards experience higher or lower predation risk and how this influences their foraging decisions.

Differences in motivation could account for differences in foraging behavior (Drakeley et al, in review; Sol et al, 2013). We did not directly assess variation in motivation for lizards in each habitat. However, by sampling only lizards in survey posture, we expect these lizards to be receptive to foraging (Stamps, 1977). Furthermore, stomach content analyses did not reveal any differences between forest and urban lizards. Orros & Fellowes (2012) showed that anthropogenic subsidization of prey can increase prey abundance (e.g., colonies of aphids). Other studies, comparing prey abundance through sticky traps have shown no differences between human-modified and natural habitats (Battles et al., 2013). It is possible that urban lizards might exploit alternative foraging opportunities, such as exploiting artificial light at night to feed (Perry et al., 2008). To control for differences in motivation to feed, future work could manipulate the motivational state of lizards by feeding them prior to foraging trials.

Habitat complexity might play an important role in how lizards assess risk when foraging. In the forest, termite mounds and dead wood may be important for supporting food resources and fallen logs and leaf litter may provide essential cover and microhabitats (Scott el al., 2006). Complex habitats might decrease the risk of foraging by decreasing the ability of potential predators to detect a foraging lizard (Gall and Fernández-Juricic, 2009). Gonzáles-Bernal et al. (2011) showed that cane toads foraged more effectively when the background provided greater visual contrast of prey items. Cryptic colors and patterns interfere with the predators' ability to detect prey (Shepard, 2007). A study on *Anolis gundlachi* showed that habitat selection was non-random and that broad, woody surfaces were preferred because of their potential to minimize conspicuousness and increase the ability of lizards to scan a larger portion of their territory (Rodríguez-Robles el al., 2005). Vegetation may allow lizards to forage while providing protection from predators, with denser habitats providing more protection than open habitats. Lizards can shift their foraging and escape behavior relative to the amount of cover available (Martín & Lopéz, 1995; Smith & Ballinger 2001). For example, Martín and Lopéz (1995) found that when cover was available lizards had shorter flight distance. We propose that the large difference in structural habitat complexity between urban and forest habitats likely influences predation-risk perception. This hypothesis could be tested by manipulating perch availability in urban and forest environments. We predict that lizards will respond more frequently and faster when perches are available between their initial perch and the foraging opportunity.

Urban habitats can lead to divergence in behavior, morphology, and genetic characteristics of populations (Ditckhoff et al., 2006). Changes in the composition of predators and prey in urban habitat can impact when and how these organisms feed. Changes in foraging behavior, particularly as a consequence of novel interactions with domestic predators, might represent strong selective forces for urban animals. As future studies continue to address the ecological implications of urbanization, they should address how foraging decisions are influenced by both changes in the structural habitat and the presence of domestic predators.

REFERENCES

Barnosky AD, Hadly EA, Bascompte J et al. (2012) Approaching a state shift in Earth's biosphere. *Nature*, **486**, 52–8.

Battles AC, Whittle TK, Stehle CM, Johnson MA (2013) Effects of human land use on prey availability and body condition in the green anole, *Anolis carolinensis*. *Herpetological Conservation and Biology,* **8**, 16–26.

Bland JM, Altman DG (1998) Survival probabilities (the Kaplan-Meier method). *BMJ (Clinical research ed.),* **317**, 1572.

Brown JS (1999) Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*, **1**, 49–71.

Ditchkoff SS, Saalfeld ST, Gibson CJ (2006) Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, **9**, 5–12.

Gall MD, Fernández-Juricic E (2009) Effects of Physical and Visual Access to Prey on Patch Selection and Food Search Effort in a Sit-and-Wait Predator, the Black Phoebe. *The Condor*, **111**, 150–158.

González-Bernal E, Brown GP, Cabrera-Guzmán E, Shine R (2011) Foraging tactics of an ambush predator: The effects of substrate attributes on prey availability and predator feeding success. *Behavioral Ecology and Sociobiology*, **65**, 1367–1375.

Fleishman LJ (1988) Sensory influences on physical design of a visual display. *Animal Behaviour*, **36**, 1420–1424.

Drakeley M, Lapiedra, O, & Kolbe JJ. Submitted. Predation risk perception, food density and conspecific cues shape foraging decisions in anoles. *Behavioral Ecology*.

Leal M (1999) Honest signalling during prey-predator interactions in the lizard Anolis cristatellus. *Animal Behaviour,* **58**, 521–526.

Lepczyk CA, Mertig AG, Liu J (2004) Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation,* **115**, 191–201.

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Losos, JB (2009). Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. Berkeley, CA: University of California Press.

Loyd KAT, Hernandez SM, Carroll JP, Abernathy KJ, Marshall GJ (2013) Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation*, **160**, 183–189.

Jacob J, Brown JS (2000) Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos*, **91**, 131–138.

Martin J, López P (1995) Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. *Canadian Journal of Zoology*, **73**, 129–132.

Møller AP, Ibáñez-Álamo JD (2012) Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour*, **84**, 341–348.

Moermond TC (1979) The Influence of Habitat Structure On *Anolis* Foraging Behavior. *Behaviour*, **70**, 147–167.

Orros ME, Fellowes MDE (2012) Supplementary feeding of wild birds indirectly affects the local abundance of arthropod prey. *Basic and Applied Ecology*, **13**, 286–293.

Perry, G., Buchanan, B. W., Fisher, R. N., Salmon, M., & Wise, S. E. (2008). Effects of artificial night lighting on amphibians and reptiles in urban environments. In J. C. Mitchell, R. E. Jung Brown, & B. Bartholomew (Eds.), *Urban Herpetology* (illustrate., Vol. 239, pp. 239–256). Society for the study of amphibians and reptiles.

Ramalho CE, Hobbs RJ (2012) Time for a change: Dynamic urban ecology. *Trends in Ecology and Evolution*, **27**, 179–188.

Rebele F (1994) Urban Ecology and Special Features of Urban Ecosystems. *Global Ecology and Biogeography Letters*, **4**, 173–187.

Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator-prey relationships. *Ecological Applications*, **21**, 936–943.

Rodríguez-Robles JA, Leal M, Losos JB (2005) Habitat selection by the Puerto Rican yellow-chinned anole, Anolis gundlachi. *Canadian Journal of Zoology*, **83**, 983–988.

Scott DM, Brown D, Mahood S, Denton B, Silburn A, Rakotondraparany F (2006) The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation*, **127**, 72–87.

Shepard DB (2007) Habitat But Not Body Shape Affects Predator Attack Frequency on Lizard Models in the Brazilian Cerrado. *Herpetologica*, **63**, 193–202.

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, **21**, 186–191.

Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. *BioScience*, **60**, 199–208.

Smith GR, Ballinger RE (2001) The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemporary Herpetology*, 1–23.

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. *Animal Behaviour*, **85**, 1101–1112.

Stamps JA (1977) The Function of the Survey Posture in *Anolis* Lizards. *Copeia*, **4**, 756–758.

Stamps JA (1983) The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behavioral Ecology and Sociobiology*, **12**, 19–33.

Stamps JA (1987) Conspecifics as cues to territory quality: A preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *The American naturalist*, **129**, 629–642.

Stamps JA (1988) Conspecifics attraction and aggregation in territorial species. *The American Naturalist*, **131**, 329–347.

Stephen AC, Roughgarden J (1983) Foraging by Passerine birds and *Anolis* lizards on St. Eustatius (Neth. Antilles): implications for interclass competition, and predation. *Oecologia*, **56**, 313–317.

Tsurim I, Abramsky Z, Kotler BP (2008) Foraging behavior of urban birds: are human commensals less sensitive to predation risk than their nonurban counterparts? *The Condor*, **110**, 772–776.

	Habitat	Conspecific	Model predator	Habitat X Conspecific	Habitat X Model predator	Conspecific X Model predator	Habit X Conspecific X Model predator
Latency to feed	$F_{1,94}$=12.05 **P< 0.001**	$F_{1,94}$=0.99 P=0.32	$F_{1,94}$=0.20 P=0.66	$F_{1,94}$=8.63 **P< 0.004**	$F_{1,94}$=0.47 P=0.49	$F_{1,94}$=1.14 P=0.29	$F_{1,91}$=5.50 **P=0.02**

Table. 1: Results of a three-way ANOVA testing for a difference in the latency to feed of focal lizards with the main effects of habitat (forest and urban), model predator (present or absent), and conspecific (present or absent).

Habitat	**Mean mass (g)**	**SE mass (g)**	**Mean SVL (cm)**	**SE SVL (cm)**
Forest	8.63	0.30	6.54	0.045
Urban	10.12	0.31	6.85	0.066

Table 2: Differences in body conditions of lizards from our urban and natural sites (n=20 for each site) shown in mass and snout vent length of male *A.* Green, color denotes lizards sampled from the forest habitat and grey from the urban.

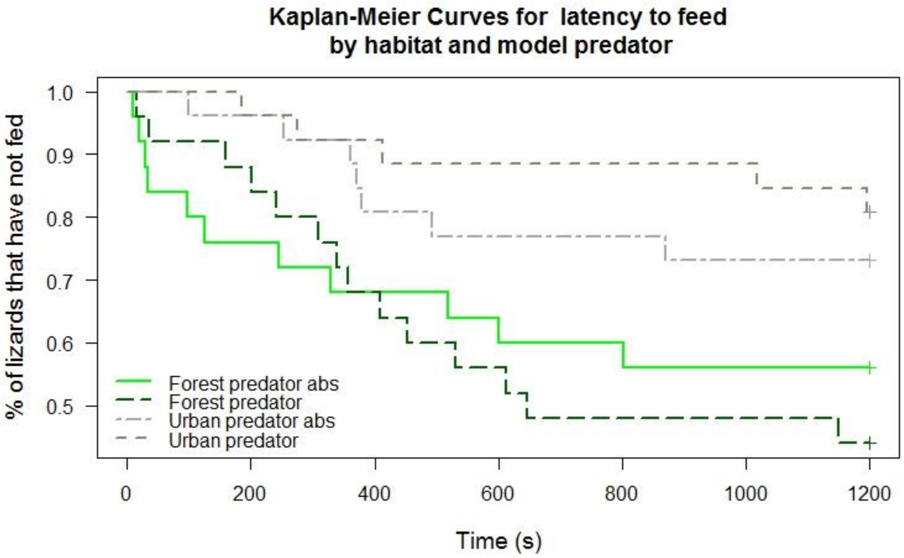

Figure 1: Kaplan-Meier curves for the latency to feed with and without the model predator. Green lines represent the forest habitat and grey lines the urban habitat (N= 25 for each treatment). Darker colors denote treatments with the presence of the model predator.

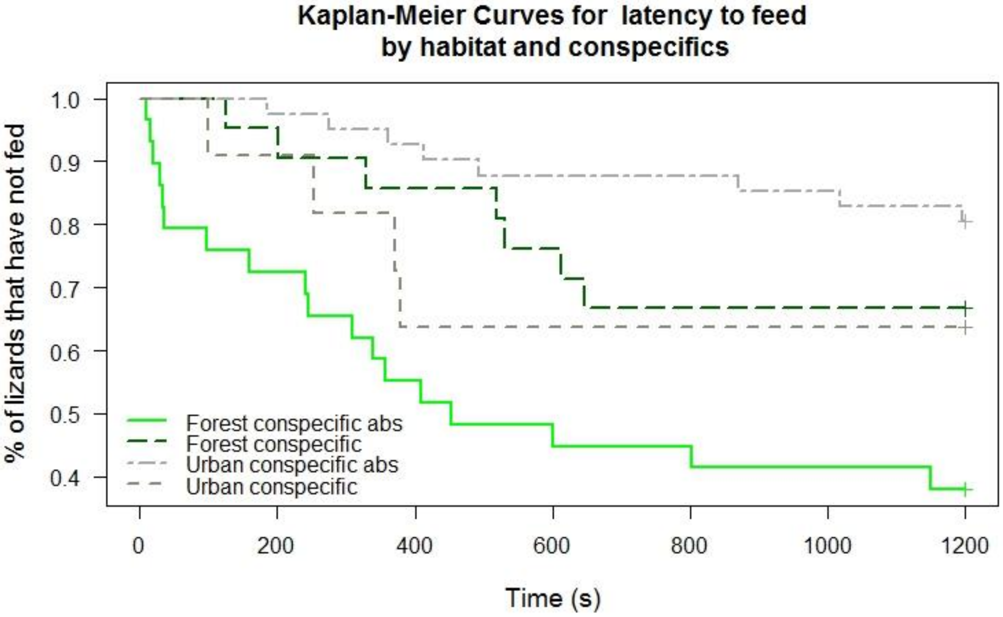

Figure 2: Kaplan-Meier curves for the latency to feed with and without the presence of a conspecific (i.e. forest w/o N= 29, forest w/ N=21, urban w/o N=41, urban w/ N=11). Green lines represent the forest habitat and grey lines the urban habitat. Darker colors denote treatments with the presence of the model predator.

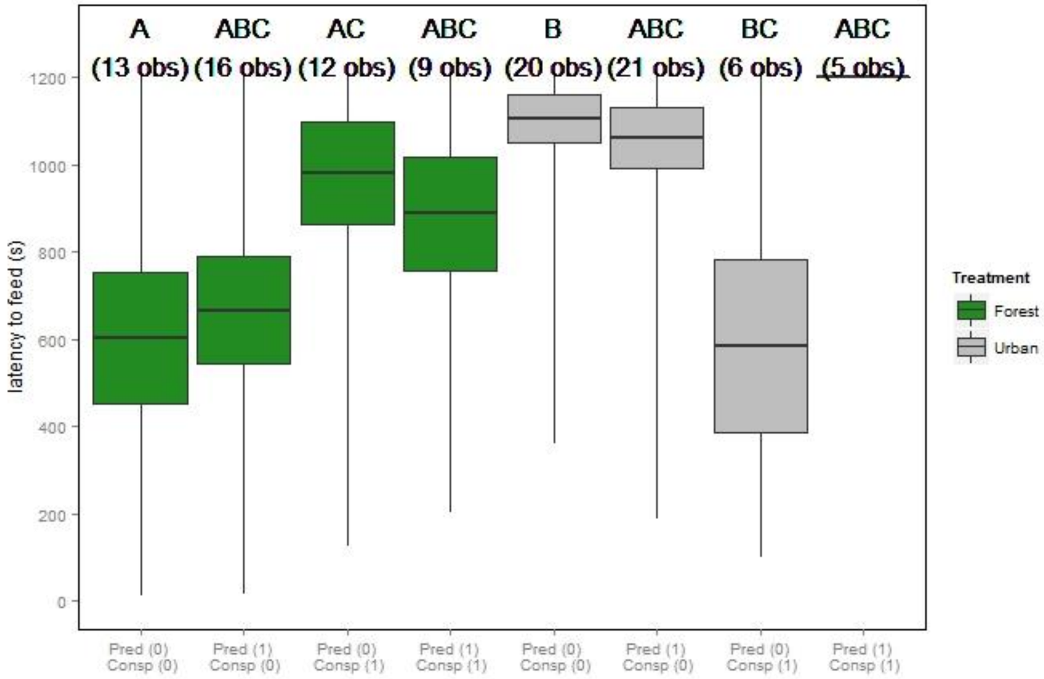

Fig. 3: Mean (± SE) of latency to feed of focal lizards by habitat, model predator presence, and conspecific presence. Green represents the forest habitat and grey represents the urban habitat. Boxplots show the mean, standard error and the whisker show the range. Letters denote significant differences based on Tukey's HSD *post hoc* test.