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## EFFECTS OF HUMAN LAND USE ON PREY AVAILABILITY AND BODY CONDITION IN THE GREEN ANOLE LIZARD, *ANOLIS CAROLINENSIS*

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**Abstract.**—Lizards frequently occur in disturbed habitats, yet the impacts of human activity on lizard biology remain understudied. Here, we examined the effects of land use on the body condition of Green Anole lizards (*Anolis carolinensis*) and the availability of their arthropod prey. Because human activity generally alters abiotic and biotic habitat features, we predicted that areas modified by humans would differ from areas with natural, intact vegetation in arthropod abundance and biomass. In addition, because biological communities in high use areas are often relatively homogenized, we predicted that higher human land use would result in lower prey diversity. Regardless of land use, we also predicted that areas with greater prey availability and diversity would support lizards with higher body condition. We studied anoles in six plots with varying levels of human modification in Palmetto State Park in Gonzales County, Texas. We quantified arthropod abundance, biomass, and diversity in each plot via transects and insect traps. We also determined lizard body condition using mass:length ratios and residuals, fat pad mass, and liver lipid content. We found that, although arthropod abundance did not differ across plots, arthropod biomass was higher in natural than in disturbed plots. Diversity indices showed that the plots varied in their arthropod community diversity, but not in relation to disturbance. Female (but not male) lizard body condition differed across plots, with body condition higher in natural plots than disturbed plots. Together, these results suggest that land use is associated with lizard body condition, but not through a direct relationship with prey availability.

**Key Words.**—body condition; edge effects; Green Anole; insect diversity; Texas

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### INTRODUCTION

As human activity alters previously undisturbed environments, abiotic and biotic features of the landscape are often dramatically changed. In general, human land use has largely negative impacts on the environment (Johnson 2001; Radeloff et al. 2005). These impacts have caused significant losses among reptiles and amphibians as their habitats are degraded and destroyed (Driscoll 2004; Stuart et al. 2004). In habitats disturbed by human land use, we often find declines in species richness and diversity, changes that may affect the fitness of organisms at all levels of the food web. For example, human disturbance frequently causes habitat fragmentation, which changes the composition and function of the landscape, produces isolated areas of the natural habitat, and increases habitat edges (Murcia 1995; McGarigal and Cushman 2002; Fahrig 2003). The impacts of these changes are diverse: some taxa thrive at the intersection of two habitats (e.g., Hunter 1990; Christie et al. 2010), while others remain abundant only in “interior” habitats (e.g., Schlapfer and Thomas 2001; Grez et al. 2004; Reidy et al. 2009). Human disturbance is also associated with the homogenization of floral and faunal communities, reducing the biological diversity of disturbed communities (McKinney 2002; Dormann et al. 2007; Chen and Qiang 2011). Thus, human land use may impact a particular species directly through its own

response to a disturbed habitat, or through the altering the composition of the competitors, predators, and prey with which it interacts.

In this study, we examined the effects of human disturbance on one measure of fitness (body condition) of an insectivorous lizard, the Green Anole (*Anolis carolinensis*), and we determined how habitat modification and lizard body condition were associated with arthropod prey abundance, biomass, and diversity. The Green Anole is a small, arboreal lizard common throughout the southeastern United States, with its native range extending from Texas to the Carolinas (Conant and Collins 1998). Green Anoles are opportunistic insectivores, consuming a wide variety of invertebrates and on occasion, small vertebrates (Losos 2009). They generally forage for their arthropod prey by moving through vegetation and eating any prey that they encounter, although they may also use a sit-and-wait ambush strategy (Jenssen et al. 1995; Nunez et al. 1997). The Green Anole has become a model organism for studying many aspects of ecology, evolution, and behavior (reviewed in Lovern et al. 2004; Losos 2009), although little work has examined how human disturbance impacts Green Anoles. Because the Green Anole is prevalent in natural areas as well as in disturbed habitats and urban areas (e.g., Wade et al. 1983; McMillan and Irschick 2010), the impacts of varied land use on prey availability are ecologically relevant to this species.

The effects of human land use have been relatively well-studied at the landscape scale (see studies above), but less research has focused on these impacts at a smaller, local scale. Depending on the territory size and mobility of an organism, the spatial scale of these effects can vary greatly across taxa (Crooks and Soulé 1999). Further, because human land use can vary dramatically across even a few acres, ecological interactions such as those among predators and their prey may also vary at the local scale (Lima 2002). Here, we tested the hypothesis that Green Anole body condition varies with human land use as a function of arthropod prey availability at the scale of a single state park. Two sets of predictions follow from this hypothesis. First, we predicted that relatively undisturbed habitats will differ from more highly modified habitats in arthropod availability, as measured by arthropod abundance and biomass. As the diet of Green Anoles is predominantly composed of arthropod prey, we predicted that increases in arthropod abundance and biomass will be positively associated with increases in lizard body condition. Second, we predicted that arthropod diversity will be lower in more disturbed habitats. Previous work assessing the diet of *Anolis* lizards has shown that anoles naturally consume a wide variety of arthropods (e.g., Dial and Roughgarden 1995, Reagan 1996); thus, we predict that habitats with higher prey diversity will maintain higher lizard body conditions.

### MATERIALS AND METHODS

**Study sites and plots.**—We studied Green Anole prey availability and body condition at Palmetto State Park in Gonzales, Texas, USA (N 29°35.34', W 97°35.07') during summer 2010. Palmetto State Park is a 1.09 km<sup>2</sup> park that averages about 90,000 visitors per year, with about 33,000 who camp in the park using tents or recreational vehicles (RVs). We studied anoles and their prey in six approximately 1000 m<sup>2</sup> plots across the park (Fig. 1), chosen to represent the range of human activity across the park, from protected natural palmetto swamp to heavily used campsite areas. All plots were located in a central area of the habitat they were chosen to represent, were within 1 km of each other, and were embedded in a matrix of continuous forest.

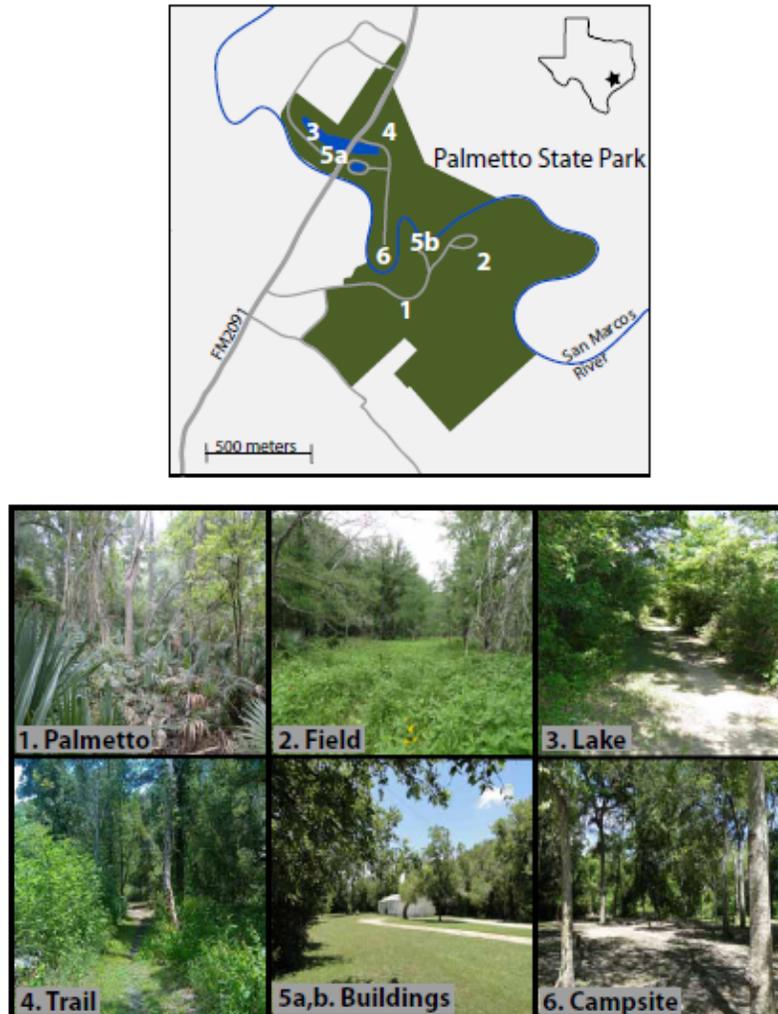
The two plots in the most natural, least-disturbed habitats were studied most intensively, as they were also the focus of other simultaneous studies. The Palmetto plot was characterized by dense stands of Dwarf Palmettos (*Sabal minor*) and extensive canopy cover from trees such as Burr Oak (*Quercus macrocarpa*), Lacey Oak (*Quercus laceyi*), Cedar Elm (*Ulmus crassifolia*), Green Ash (*Fraxinus pennsylvanica*), and Box Elder (*Acer negundo*). This plot, which represented the protected palmetto forest for which the state park was named, was situated in the middle of a natural forest

matrix with no habitat edges in the plot. The Field plot was a narrow field consisting of tall grasses surrounded by a moderately dense forest of primarily Live Oak (*Quercus virginiana*), Cedar Elm, and small clusters of Dwarf Palmettos. The intersection of the open field and the forest resulted in a natural habitat edge on each side of this plot.

The Lake and Trail plots were in areas along trails, and were thus moderately impacted by human activity. The Lake plot was a third intensively studied plot and was located along a park-maintained trail situated adjacent to Oxbow Lake. This plot featured very dense understory, small trees and vines [e.g., Alabama Supplejack (*Berchemia scandens*), Mustang Grape (*Vitis candicans*), and the invasive Trumpet-creeper (*Bignonia radicans*)], and a continuous canopy across the trail. This closed canopy allowed lizards to utilize habitat on both sides of the trail, although the trail that bisected the plot and the lake on the northwest side of the plot created forest edges in the plot. The Trail plot consisted of a wider trail segment surrounded by a moderately dense forest (similar to the Lake plot), but had almost no canopy cover across the trail. As in the Lake plot, the trail created distinct edges throughout the plot. The trail in this plot was also more heavily used by park visitors than the trail segment in the Lake plot, and was closer to bathrooms, the parking lot, and campsites.

The Building and Campsite plots were the most heavily disturbed by human activity. The Building plot was composed of two smaller sites: the grounds surrounding the park's Refectory (constructed by the Civilian Conservation Corps in 1933) and Little Hill Baptist Church (a small church immediately adjacent to the park). Both were buildings in the middle of a forested area, surrounded by large (200–400 m<sup>2</sup>) mowed-grass lawns. The lawns ended abruptly at the edge of the forest. The Campsite plot had a cleared central area (approximately 400 m<sup>2</sup>) with tall grass, surrounded by forest similar in composition to the Palmetto plot. The edge structure of the campsite was similar to that of the building sites.

**Measures of prey availability and diversity.**—We used two methods to measure arthropods to quantify their abundance, biomass, and diversity in each plot. Following Dial and Roughgarden (1995), we used transects to census a wide range of arthropods and sticky glue traps to census flying insects. The transect data provided us with descriptive information on general arthropod availability in the plots, while the replicated data from the sticky traps provided data for statistical analyses comparing the plots. For both survey methods, we did not collect data during inclement weather (i.e., rain). We collected data from all transect and sticky traps between 23 June and 13 July 2010, with approximately equal intervals between dates of data



**FIGURE 1.** A map of Palmetto State Park, Gonzales, Texas, USA showing the locations of the plots to study the Green Anole Lizard (*Anolis carolinensis*), along with representative photos of the plots. (Photographed by Michele A. Johnson).

collection in each plot.

We measured arthropod availability within a 2 x 30 m transect in each plot by choosing an arbitrary starting point within the plot and identifying a haphazard direction to follow for 30 m. We used this approach to choose a starting point rather than a formal randomization system because using random points and directions in the plot may not have resulted in a 30 m long transect that was completely inside the study areas. We looked for insects and other arthropods along stems and branches, on all surfaces of leaves, in the leaf litter on the ground, and in the air. Within the entire transect area (60 m<sup>2</sup>), we identified each observed arthropod to order (or, for spiders, to class Arachnida) and estimated its body length to the nearest mm. We performed transect surveys between 1300 and 1600 for each study plot. To survey primarily flying insects, we used

Catchmaster® sticky traps (AP&G Co., Inc., Brooklyn, California, USA) commonly used for catching rodents, which were 12.7 x 17.8 cm (5 x 7 in) cardboard rectangles coated on one side with a glue-like material. For four or five nonconsecutive days, we set five traps in each plot for 10 h (approximately 0800–1800, the general period of anole activity). In each plot, we set the traps haphazardly at various locations and heights (from ground level to approximately 4 m) to represent the range of available anole microhabitats. We attempted to maintain a consistent distribution of trap heights and types of locations across the plots. For each arthropod captured on a trap, we recorded its order and measured its body length using digital calipers.

To determine insect biomass from the body length data from both transects and sticky traps, we used the formula  $W = 0.035 * L^{2.62}$ , where W is biomass in mg

and L is body length in mm (Rogers et al. 1976). This equation provides reasonable biomass estimates across diverse insect taxa (Rogers et al. 1976; Robertson et al. 2011). We also used transect and trap data to estimate arthropod abundance (i.e., the total number of arthropods) by order for each plot.

Additionally, we calculated the relative diversity of the arthropod community in each of the plots using three indices of community diversity. We calculated the Shannon-Weaver Index of diversity ( $H'$ , also known as the Shannon-Wiener Index; Shannon 1948; Shannon and Weaver 1949), a measure of both the number of taxa (richness) and how many members of each taxon are present in a given habitat (evenness). We also determined Simpson's D (a measure of evenness; Simpson 1949) for both transect and sticky trap data, and we calculated the percentage in each plot of the five most abundant orders (following Sponseller et al. 2001) in transect data. This latter measure was not calculated for sticky trap data, as traps rarely captured arthropods from more than five orders.

**Lizard body condition.**—In each of the six study plots, we attempted to capture all observed lizards by hand or noose in overlapping two week periods between 24 May and 28 June 2010. For each lizard captured, we recorded its sex and measured its snout-vent length (SVL) using a ruler, and mass using a Pesola spring scale. In the three most intensively studied plots (Palmetto, Field, and Lake), we also marked each lizard by sewing a unique bead tag into its tail muscle (Fisher and Muth 1989). In late July, we re-sampled the study plots to capture lizards for tissue collection. We euthanized these lizards in the lab and immediately dissected them to harvest liver and fat pad tissues, which we flash froze and stored at  $-80^{\circ}\text{C}$  (Table 1).

Because there is currently no consensus on the most appropriate index of animal body condition (Vervust et al. 2008; Peig and Green 2010), we examined body condition using four methods. First, we calculated the mass/SVL ratio, or body mass index (BMI), of each lizard captured in the six plots across the summer. This is the simplest, standard measure of body condition in reptiles (e.g., van Berkum et al. 1989; van Marken Lichtenbelt et al. 1993; Goodman 2008). Second, we calculated the residual of the relationship between mass and SVL using linear regression, a measure robust to differences in body size (Jakob et al. 1996), using a separate regression analysis for each sex.

The third method we used to determine body condition was to measure fat accumulation in abdominal fat pads. Fat bodies contain the most labile lipids; therefore accumulation and utilization of lipids is most likely to occur in the fat pads, a mechanism confirmed in many reptilian taxa (Derickson 1976; Warner et al. 2008; Counihan et al. 2009). Using lizards captured in late

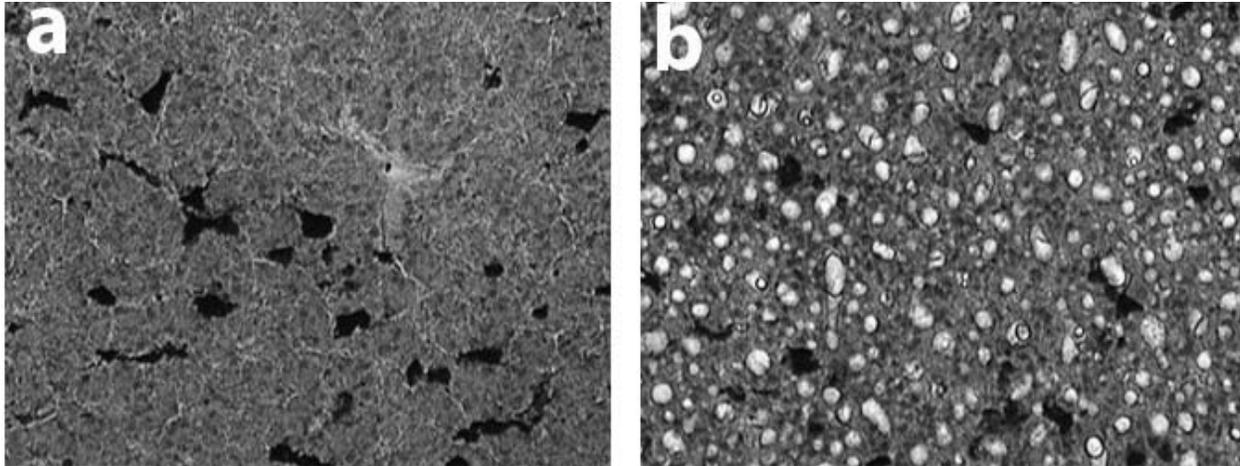
**TABLE 1.** Sample sizes for body condition analyses (body mass index and tissue-based measures of condition) of the Green Anole Lizard (*Anolis carolinensis*) at Palmetto State Park, Gonzales, Texas, USA.

Plot	Sample Sizes: Body Mass Index		Sample Sizes: Tissue Collection	
	(June-July)		(Late July)	
	Males	Females	Males	Females
Palmetto	20	30	9	5
Field	18	21	9	0
Lake	23	37	4	14
Trail	10	4	3	0
Building	8	3	0	0
Campsite	5	2	1	0

July, we quantified an index of lipid storage as fat pad mass (determined immediately after euthanasia) divided by live body mass (Goldberg 1972).

Finally, we determined the concentration of lipids stored in the liver, as levels in these lipids have been shown to fluctuate as a function of the amount and quality of food an animal consumes (lizards: Gist 1972; birds, mammals, and reptiles: McCue 2010). Because lipids accumulate in the liver in globules, they can be observed and measured using a microscope. We sectioned each frozen liver at  $20\ \mu\text{m}$  using a cryostat and stained the sections for microscopy using hemotoxylin and eosin. To determine lipid content in these sections, we photographed one section of each liver under 100X magnification (Fig. 2). In Photoshop (Adobe Systems, San Jose, California, USA), we used the threshold tool to change all pixels in the image to black and white, isolating the lipid areas as white. We then determined the proportion of white pixels in each image, thus determining the percentage of the liver composed of stored lipids.

**Statistical analyses.**—To determine whether there were differences in arthropod abundance and biomass among the six plots, we used insect trap data to perform a one-way analysis of variance (ANOVA) for each of these variables. We then used one-way ANOVA to compare arthropod abundance and biomass from trap data among three categories of plot disturbance, pooling the two relatively natural plots (Palmetto and Field), the two moderately disturbed plots (Lake and Trail), and the two highly disturbed plots (Campsite and Buildings). We also used one-way ANOVA separately for each sex to determine whether measures of lizard body condition differed among the three primary study plots (Palmetto, Field, and Lake), and across the three disturbance levels. We used Tukey's post-hoc tests for all pair-wise comparisons following significant ANOVA results. All analyses were performed in SPSS (IBM Corporation, Armonk, New York, USA), with  $\alpha = 0.05$ .



**FIGURE 2.** Liver samples stained with hemotoxylin and eosin from a) a wild-caught Green Anole Lizard (*Anolis carolinensis*) with no fat globules, and b) a laboratory-housed Green Anole fed *ad libitum*, with extensive fat globules throughout the liver. The scale is the same for both pictures. (Photographed by Tara K. Whittle).

## RESULTS

Analysis of insect trap data showed that the six plots differed in both arthropod abundance ( $F_{5,21} = 5.48$ ,  $P = 0.002$ ) and biomass ( $F_{5,21} = 2.91$ ,  $P = 0.038$ ). Comparing the natural, moderately disturbed, and highly disturbed plots showed that the plots with differing levels of human modification differed in arthropod biomass ( $F_{2,24} = 5.42$ ,  $P = 0.011$ ), with post hoc tests showing that the two most disturbed plots had greater arthropod biomass than the two natural plots. The categories of plots also differed in arthropod abundance ( $F_{2,24} = 5.74$ ,  $P = 0.009$ ), with post hoc tests showing that the most disturbed plots had greater arthropod abundance than the two moderately disturbed (but not the natural) plots (Table 2).

Measures of arthropod community diversity using the Shannon-Weaver index with primarily flying insects (insect trap data) showed lower overall diversity than the same measures of transect data, which included all of the arthropods we could see (both flying and crawling), but the opposite pattern was revealed using Simpson's D, as evenness was on average greater in the transect data (Table 2). Comparing across the plots, the relatively natural Field plot contained the highest evenness (Simpson's D), but the lowest diversity as measured by the Shannon-Weaver index. In contrast, the Trail plot, a plot with moderately high human activity, had the highest Shannon-Weaver index but the lowest Simpson's D. The two most disturbed plots, Building and Campsite, had moderate values for both of these diversity indices (Table 2).

Across all plots, the most common arthropod orders captured by the insect traps were Lepidoptera, Diptera, and Hymenoptera, while the most common orders on the transects were Lepidoptera, Orthoptera, Odonata,

Hemiptera, and Diptera (Appendix). The percentage of arthropods in each plot among the most abundant five orders showed that each plot's arthropod community was more than 86% composed from these orders. The undisturbed Palmetto plot had the lowest percentages, indicating the highest contribution of "rare" orders, and the undisturbed Field and highly disturbed Campsite plots had the highest percentages (Table 2).

We captured and calculated BMI (mass/SVL) and the residual index for 181 lizards in the park (Table 1). Neither sex differed in SVL across the six plots (males:  $F_{5,78} = 1.37$ ,  $P = 0.25$ ; females:  $F_{5,91} = 1.73$ ,  $P = 0.14$ ). Males also did not differ across the six plots in BMI ( $F_{5,78} = 1.28$ ,  $P = 0.28$ ) or the residual index ( $F_{5,78} = 1.05$ ,  $P = 0.40$ ). Because the sample sizes for females in the Trail, Building, and Campsite plots were so small (Table 1), we compared female BMI only among Palmetto, Field, and Lake plots. We found that female BMI differed across these three plots ( $F_{2,85} = 11.1$ ,  $P < 0.001$ ) with post hoc tests showing that BMI was lower in the Lake plot than Palmetto and Field. The residual index showed the same pattern ( $F_{2,85} = 7.64$ ,  $P = 0.001$ ). Of these three plots, Lake plot had the lowest arthropod abundance, yet the highest arthropod biomass (Table 2).

In a comparison of the BMI of all males and females pooling data from the highly disturbed, moderately disturbed, and natural plots, females had the highest BMI in the natural plots ( $F_{2,94} = 12.2$ ,  $P < 0.001$ ), with the average female BMI in the two categories of disturbed plots 0.074 and the average BMI in the natural plots 0.083. The residual index was also highest in the natural plots ( $F_{2,94} = 7.93$ ,  $P = 0.001$ ). Males did not differ in BMI among the plot types ( $F_{2,81} = 0.44$ ,  $P = 0.65$ ), with the male average BMI across plots 0.084, and they did not differ in the residual index ( $F_{2,81} = 1.29$ ,  $P = 0.28$ ). Comparisons of the two other measures of body

**TABLE 2.** Measures of arthropod abundance, biomass, and community diversity across six plots at Palmetto State Park, Gonzales, Texas, using two methods of arthropod data collection (transects: total per m<sup>2</sup>; traps: average per trap per day). Diversity indices include the Shannon-Weaver diversity index (H'), and Simpson's diversity index (D). The transect data include the percentage of the five most abundant orders (% 5 MAO) in each plot.

Plot	Disturbance Level	Abundance	Biomass (mg)	Shannon-Weaver H'	Simpson's D	% 5 MAO
Transects						
Palmetto	Natural	3.5	58.5	1.91	0.17	86.1
Field	Natural	12.4	125.5	1.25	0.44	94.9
Lake	moderately disturbed	5.8	176.6	1.44	0.37	90.2
Trail	moderately disturbed	6.7	314.4	1.74	0.24	89.3
Building	highly disturbed	6.6	191.2	1.63	0.29	90.4
Campsite	highly disturbed	13.9	174.4	1.56	0.28	94.5
Traps						
Palmetto	natural	8.8	28.4	0.68	0.68	---
Field	natural	7.7	17.3	0.55	0.77	---
Lake	moderately disturbed	4.1	50.5	0.94	0.43	---
Trail	moderately disturbed	4.2	34.2	1.06	0.40	---
Building	highly disturbed	4.8	67.5	0.81	0.52	---
Campsite	highly disturbed	13.6	99.1	0.86	0.57	---

condition showed no differences among the plots for either sex. Neither mass of abdominal fat pads (males:  $F_{2,21} = 0.63$ ,  $P = 0.55$ ; females:  $F_{1,17} = 0.76$ ,  $P = 0.40$ ) nor liver lipid content (male:  $F_{2,21} = 1.34$ ,  $P = 0.29$ ; female:  $F_{1,17} = 1.03$ ,  $P = 0.33$ ) differed among the plots.

### DISCUSSION

Together, the results of this study indicate that both lizard body condition and arthropod availability differ across habitats, even within a small geographic area. At this local scale, human habitat modification differed considerably across our study plots, with some habitats (i.e., palmetto swamp) being carefully protected from disturbance, while others (i.e., areas where buildings were constructed or cleared for campsites) are relatively heavily used by humans, and the observed differences in the conditions of lizards and their prey may be (but is not necessarily) associated with the varying degrees of modification. However, the hypothesis that lizard body condition would vary with habitat use as a function of variation in arthropod prey received mixed support from our results.

**Arthropod abundance and biomass and lizard condition.**—We first predicted that natural and disturbed habitats would differ in arthropod prey abundance and biomass. Using both transect and sticky trap data, we found that while the six plots differed in arthropod

abundance, these differences did not align with human disturbance level. However, we found that the most disturbed plots supported higher arthropod biomass than the natural plots, a difference that may result from the more extensive habitat edges in the disturbed plots. Previous research has suggested that arboreal invertebrates are more common in areas with more edges because their predators were less abundant in those areas (e.g., Christie et al. 2010). We did not directly measure the relationship between habitat edges and arthropod biomass or lizard abundance in this study, but our qualitative observations allow us to speculate on these relationships. First, there appeared to be fewer anoles in the most disturbed areas in our study plots. Yet, we did not attempt to systematically census the populations in our six plots, and so we cannot directly assess this pattern. Alternatively, this difference in biomass across plots may be due to altered abiotic factors at habitat edges (Murcia 1995) providing a habitat more suitable for a few higher biomass arthropods such as Lepidoptera and Odonata, which were far more common in the most disturbed, more open plots (i.e., Lake, Building, and Campsite). In contrast, the low biomass, high abundance orders such as Diptera and Hymenoptera were common in all plots (Appendix 2).

We also predicted that arthropod availability should be positively associated with lizard body condition. Although we found differences in female (but not male) BMI and residual indices across the plots, our data did

not support this prediction. Using the three most intensively studied areas, comparing the two natural to one disturbed plot showed that female lizards had higher BMI and residual indices in natural plots. However, the disturbed plot (Lake) had higher available arthropod biomass, and generally lower arthropod abundance, than the natural plots. One possible explanation for this pattern might be that the disturbed Lake plot in fact provides a higher quality habitat for anoles (with its greater availability of prey biomass) than the natural plots, attracting a larger number of competitors, and resulting in more competition for prey than in the natural plots. Consistent with this, we captured the largest number of lizards in the Lake plot, suggesting that they were likely most abundant in that plot. Another possibility is that all arthropod prey are not equally valuable to Green Anoles, and that the natural habitats provide a higher proportion of palatable or nutritious prey than the disturbed plot, and therefore support a higher body condition for female anoles. Thus, while human habitat modification does appear to be associated with female lizard body condition, it does not seem to do so through a direct relationship with arthropod abundance or biomass.

The lack of positive relationship between prey biomass and lizard body condition in either sex may result if not all arthropods are accessible prey to the lizards. The size and shape of the skull of the lizard, and in particular its jaw, can constrain the ability of a lizard to consume a particularly large or tough prey item (reviewed in Montuelle et al. 2012). However, if these factors limit prey consumption in anoles, females should be constrained more than males, as male Green Anoles have larger jaws and greater bite force than females (Herrel et al. 2007). Further, because each individual female's BMI and residual index would vary with her reproductive status, it is perhaps even more striking that females differed in body condition across the plots. Female anoles lay one-egg clutches approximately every 1–4 weeks throughout the summer breeding season (Andrews and Rand 1974), and the condition of a female would presumably be maximized just before parturition, and minimized just after. Higher female condition in the natural plots can then indicate that females in those plots produce eggs at a higher rate, produce larger eggs, have greater mass in non-reproductive tissues, or some combination of these factors.

The two measures of body condition directly associated with lipid accumulation did not reveal any variation among plots. This is likely because few lizards of either sex exhibited fat pads, and the livers of these lizards had almost no fat accumulation. Dessauer (1955) noted that stored lipid levels in Green Anoles are highest in September and October, and much lower throughout the rest of the year. However, the season in which body condition may be most important for fitness is early

spring, when these lizards begin to enter breeding conditions. Therefore, it is possible that lipid storage in fat pads or livers may differ among our plots at other critical times of the year, but this could not be tested in the current study.

**Arthropod diversity and lizard condition.**—Because human land use often homogenizes biotic communities (Dormann et al. 2007; Chen and Qiang 2011), we predicted that the most highly modified plots would exhibit lower arthropod diversity than natural plots. The three measures of community diversity used here (Shannon-Weaver, Simpson's D, and percentage of the five most abundant orders) suggest that the plots differed in arthropod diversity, but did not reveal an association between arthropod diversity and human disturbance. For most of these measures, the two natural plots (Palmetto and Field) actually had the highest and lowest diversity indices, with the disturbed plots exhibiting relatively moderate values. Thus, the differences in human activity represented across these six plots do not explain differences in arthropod diversity in the plots.

Interestingly, the Shannon-Weaver and Simpson's D indices show almost exactly opposite results across the six plots in our study, such that plots that have the highest Shannon-Weaver indices have the lowest Simpson's D, and vice versa. This pattern has been reviewed in detail by Nagendra (2002). In brief, these differences in diversity indices occur because the Shannon-Weaver index is more sensitive to the presence of rare taxa, and Simpson's D is more sensitive to the proportion of individuals representing the most dominant taxa (Nagendra 2002; Dogan and Dogan 2006). Our results are consistent with this interpretation, as the Palmetto plot had the highest Shannon-Weaver index using transect data, and the lowest percentage of the five most abundant orders; thus this plot included the most rare arthropod taxa. The important question in this study is which measure provides the most relevant assessment of the diet of Green Anoles; however, this is not an easy question to answer. Because the measures of anole body condition were not associated with any measure of diversity, it remains unclear whether abundance or evenness of rare or dominant taxa has a more direct impact on condition.

In conclusion, this study suggests that varying human land use at a local scale directly impacts lizard body condition, as females in natural plots had higher BMI than those in one of the disturbed plots, but this relationship does not appear to be directly mediated by arthropod abundance, biomass, or diversity. Thus, Green Anoles appear to be sensitive to the decreased quality of human-altered habitats, but it is not clear what factors are the primary causes of this effect. Further, the subjective categories defining levels of human habitat modification in this study may be simplifications of the

actual effects of habitat disturbance on lizards and their prey. Overall, these results suggest the complexity of the impacts of human disturbance on the interacting components of a biological community (Donovan et al. 1997; Richmond et al. 2011), and point to the need for conservation efforts to examine small scale, population level patterns that may result from varied land use.

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### LITERATURE CITED

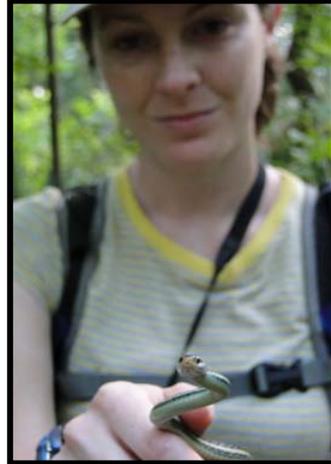
- Andrews, R., and A.S. Rand. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317–1327.
- Chen, G., and S. Qiang. 2011. Human activities are the principle cause of biotic homogenization. *Acta Ecologica Sinica* 31:4107–4116.
- Christie, F.J., G. Cassis, and D.F. Hochuli. 2010. Urbanization affects the trophic structure of arboreal arthropod communities. *Urban Ecosystems* 13:169–180.
- Conant, R., and J.T. Collins. 1998. Reptiles and Amphibians of Eastern/Central North America. 3<sup>rd</sup> Edition. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.
- Counihan, J., P. Zani, B. Fried, and J. Sherma. 2009. Characterization and quantification of the polar lipids in the lizard *Uta stansburiana* by HPTLC-Densitometry. *Journal of Liquid Chromatography and Related Technologies* 32:1289–1298.
- Crooks, K.R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- Derickson, W.K. 1976. Lipid storage and utilization in reptiles. *Integrative and Comparative Biology* 16:711–723.
- Dessauer, H.C. 1955. Seasonal changes in the gross organ composition of the lizard, *Anolis carolinensis*. *Journal of Experimental Zoology* 128:1–12.
- Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821–1834.
- Dogan, H.M., and M. Dogan. 2006. A new approach to diversity indices – modeling and mapping plant biodiversity of Nallihan (A3-Ankara/Turkey) forest ecosystem in frame of geographic information systems. *Biology and Conservation* 15:855–878.
- Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- Dormann, C.F., O. Schweiger, I. Augenstein, D. Bailey, R. Billeter, G. de Blust, R. DeFilippi, M. Frenzel, F. Hendrickx, F. Herzog, et al. 2007. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecological Biogeography* 16:774–787.
- Driscoll, D.A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. *Ecological Applications* 14:220–240.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Fisher, M., and A. Muth. 1989. A technique for permanently marking lizards. *Herpetological Review* 20:45–46.
- Gist, D.H. 1972. The effects of starvation and refeeding on carbohydrate and lipid reserves of *Anolis carolinensis*. *Comparative Biochemistry and Physiology Part A: Physiology* 43:771–780.
- Goldberg, S.R. 1972. Seasonal weight and cytological changes in the fat bodies and liver of the iguanid lizard *Sceloporus jarrovi* Cope. *Copeia* 1972:227–232.
- Goodman, R.M. 2008. Latent effects of egg incubation temperature on growth in the lizard *Anolis carolinensis*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 309:525–533.
- Greze, A., T. Zaviero, L. Tischendorf, and L. Fahrig. 2004. A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia* 141:444–451.
- Herrel, A., L.D. McBrayer, and P.M. Larson. 2007. Functional basis for intersexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society* 91:111–119.
- Hunter, M.L., Jr. 1990. Edges. Pp. 101–114 *In* *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Jakob, E.M., S.D. Marshall, and G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77:61–67.
- Jenssen, T.A., N. Greenberg, and K.A. Hovde. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* 9:41–62.
- Johnson, M.P. 2001. Environmental impacts of urban sprawl: a survey of the literature and proposed research agenda. *Environment and Planning A* 33:717–735.

- Lima, S.P. 2002. Putting the predators back in behavioral predator-prey interactions. *Trends in Ecology and Evolution* 17:70–75.
- Losos, J.B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. The University of California Press, Berkeley, California, USA.
- Lovern, M.B., M.M. Holmes, and J. Wade. 2004. The Green Anole (*Anolis carolinensis*): a reptilian model for laboratory studies of reproductive morphology and behavior. *ILAR Journal* 45:54–64.
- McCue, M.D. 2010. Starvation physiology: reviewing the different strategies animals use to survive a common challenge. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology* 156:1–18.
- McGarigal, K., and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12:335–345.
- McKinney, M.L. 2002. Urbanization, biodiversity, and conservation. *BioScience* 52:883–890.
- McMillan, D.M., and D.J. Irschick. 2010. Experimental test of predation and competition pressures on the Green Anole (*Anolis carolinensis*) in varying structural habitats. *Journal of Herpetology* 44:272–278.
- Montuelle, S.J., A. Herrel, P.-A. Libourel, S. Daillie, and V. Bels. 2012. Prey capture in lizards: differences in jaw-neck-forelimb coordination. *Biological Journal of the Linnean Society* 105:607–622.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- Nagendra, H. 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography* 22:175–186.
- Nunez, S.C., T.A. Jenssen, and K. Ersland. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 134:205–223.
- Peig, J., and A.J. Green. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* 24:1323–1332.
- Radeloff, V.C., R.B. Hammer, S.I. Stewart, J.S. Fried, S.S. Holcomb, and J.F. McKeefry. 2005. The wildland-urban interface in the United States. *Ecological Applications* 15:799–805.
- Reagan, D.P. 1996. Anoline lizards. Pp. 321–345 *In* *The Food Web of a Tropical Rain Forest*. Reagan, D.P., and R. Waide (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Reidy, J.L., F.R. Thompson III, and R.G. Peak. 2009. Factors affecting the Golden-cheeked Warbler nest survival in urban and rural landscapes. *Journal of Wildlife Management* 73:407–413.
- Richmond, S., E. Nol, and D. Burke. 2011. Avian nest success, mammalian nest predator abundance, and invertebrate prey availability in a fragmented landscape. *Canadian Journal of Zoology* 89:517–528.
- Robertson, B.A., P.J. Doran, E.R. Loomis, J.R. Robertson, and D.W. Schemske. 2011. Avian use of perennial biomass feedstocks as post-breeding and migratory stopover habitat. *PLoS ONE* 6:1–9.
- Rogers, L.E., W.T. Hinds, and R.L. Buschbom. 1976. A general weight vs. length relationship for insects. *Annals of the Entomological Society of America* 69:387–389.
- Schlaepfer, M.A., and G.A. Thomas. 2001. Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology* 15:1079–1090.
- Shannon, C.E. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27:379–423 and 623–656.
- Shannon, C.E., and W. Weaver. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, Illinois, USA.
- Simpson, E.H. 1949. Measurement of diversity. *Nature* 163:688.
- Sponseller, R.A., E.F. Benfield, and H.M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409–1424.
- Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Van Berkum, F.H., R.B. Huey, J.S. Tsuji, and T. Garland Jr. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Functional Ecology* 3:97–105.
- Van Marken Lichtenbelt, W.D., R.A. Wesselingh, J.T. Vogel, and K.B.M. Albers. 1993. Energy budgets in free-living Green Iguanas in a seasonal environment. *Ecology* 74:1157–1172.
- Vervust, B., S.P. Lailvaux, I. Grbac, and R. Van Damme. 2008. Do morphological condition indices predict locomotor performance? A test using the Wall Lizard *Podarcis sicula*. *Acta Oecologia* 34:244–251.
- Wade, J., A.C. Echternacht, and G.F. McCracken. 1983. Genetic variation and similarity in *Anolis carolinensis* (Sauria: Iguanidae). *Copeia* 1983:523–529.
- Warner, D.A., X. Bonnet, K.A. Hobson, and R. Shine. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology* 77:1242–1249.

## Herpetological Conservation and Biology



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# Battles et al.—Effects of Land Use on the Green Anole Lizard.

## Appendix 1. Arthropod abundance and biomass from insect trap and transect data.

Table A1. Average arthropod abundance by plot, per trap per day.

	Palmetto	Field	Lake	Trail	Building	Campsite
Arachnida	0.25	0.09	0.18	0.16	0.06	0.22
Coleoptera	0.33	0.04	0.05	0.05	0	0
Diptera	7.00	6.43	2.32	2.37	2.92	7.72
Ephemeroptera	0	0	0	0	0.06	0
Hemiptera	0.17	0.04	0.14	0.05	0	0.39
Hymenoptera	0.21	0.35	0.32	0.42	0.24	3.33
Isopoda	0.08	0.13	0	0	0	0.06
Lepidoptera	0.71	0.43	1.05	0.89	1.42	1.61
Odonata	0	0	0	0	0	0.06
Orthoptera	0	0.13	0.05	0.16	0.06	0.17

Table A2. Average arthropod biomass (mg) by plot, per trap per day.

	Palmetto	Field	Lake	Trail	Building	Campsite
Arachnida	0.12	0.01	0.05	0.05	0.001	0.29
Coleoptera	0.11	0.002	0.04	0.04	0	0
Diptera	1.79	1.95	0.81	0.70	5.12	3.86
Ephemeroptera	0	0	0	0	0.13	0
Hemiptera	0.29	0.01	0.03	0.004	0	0.26
Hymenoptera	0.06	0.16	0.29	0.08	1.08	0.76
Isopoda	0.02	0.04	0	0	0	0.04
Lepidoptera	25.96	14.16	48.89	33.19	63.29	80.36
Odonata	0	0	0	0	0	10.63
Orthoptera	0	0.68	0.40	0.13	0.04	2.96

Table A3. Average arthropod abundance by plot, per m<sup>2</sup> of transects.

	Palmetto	Field	Lake	Trail	Building	Campsite
Arachnida	0.63	1.20	0.92	0.77	0.83	0.58
Blattodea	0.12	0.02	0	0	0.02	0.02
Coleoptera	0.03	0.10	0.02	0.22	0.19	1.12
Diptera	0.77	2.03	0.45	0.67	0.90	2.07
Ephemeroptera	0	0.02	0	0	0	0.02
Isopoda	0.50	0.23	0.17	0.05	0.43	0.12
Hemiptera	0.28	0.38	0.28	1.10	0.52	3.25
Hymenoptera	0.82	7.82	3.33	2.87	3.15	6.12
Lepidoptera	0.27	0.17	0.20	0.23	0.18	0.17
Odonata	0	0.10	0.18	0.17	0.23	0.22
Orthoptera	0.05	0.33	0.25	0.60	0.12	0.23
Phasmidia	0.02	0	0	0.05	0	0

Table A4. Average arthropod biomass (mg) by plot, per m<sup>2</sup> of transects.

	Palmetto	Field	Lake	Trail	Building	Campsite
Arachnida	3.31	25.57	2.66	1.80	2.47	4.86
Blattodea	4.75	1.49	0	0	0.14	0.04
Coleoptera	0.71	0.18	0.06	0.13	0.19	9.68
Diptera	1.20	5.09	3.30	1.02	1.22	8.65
Ephemeroptera	0	0.14	0	0	0	0.10
Isopoda	4.62	1.85	0.73	0.77	3.35	0.62
Hemiptera	8.25	15.57	26.70	3.54	4.64	38.82
Hymenoptera	7.03	14.11	7.67	70.40	10.19	4.61
Lepidoptera	24.05	6.18	14.75	5.81	12.92	10.33
Odonata	0	19.63	107.36	65.74	141.93	76.54
Orthoptera	4.48	35.69	13.32	105.62	14.13	20.17
Phasmidia	0.14	0	0	59.55	0	0