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## Prey availability affects territory size, but not territorial display behavior, in green anole lizards



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### ABSTRACT

The availability of food resources can affect the size and shape of territories, as well as the behaviors used to defend territories, in a variety of animal taxa. However, individuals within a population may respond differently to variation in food availability if the benefits of territoriality vary among those individuals. For example, benefits to territoriality may differ for animals of differing sizes, because larger individuals may require greater territory size to acquire required resources, or territorial behavior may differ between the sexes if males and females defend different resources in their territories. In this study, we tested whether arthropod abundance and biomass were associated with natural variation in territory size and defense in insectivorous green anole lizards, *Anolis carolinensis*. Our results showed that both male and female lizards had smaller territories in a habitat with greater prey biomass than lizards in habitats with less available prey, but the rates of aggressive behaviors used to defend territories did not differ among these habitats. Further, we did not find a relationship between body size and territory size, and the sexes did not differ in their relationships between food availability and territory size or behavioral defense. Together, these results suggest that differences in food availability influenced male and female territorial strategies similarly, and that territory size may be more strongly associated with variation in food resources than social display behavior. Thus, anole investment in the behavioral defense of a territory may not vary with territory quality.

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### 1. Introduction

In environments where resources are limited, many animals defend territories to protect access to food, water, refuges, or mating opportunities (Stamps, 1994; Maher and Lott, 2000). Populations may vary in the extent of territorial defense as a function of population density or sex ratios, predation pressure, or the distribution of resources (Stamps, 1994). Food availability, in particular, is often a critical factor in territoriality, as the availability of high quality food drives individual growth and reproductive success (e.g., Stamps and Tanaka, 1981; Reznick, 1985). The size and shape of territories, and the behaviors used to defend them, are

influenced by the abundance and spatial distribution of food resources in a wide variety of taxa including mammals, birds, fish, amphibians, and reptiles (Jarman, 1974; Maher and Lott, 2000; Adams, 2001; Golabek et al., 2012).

Food availability may differentially affect territorial behavior among individuals. For example, larger animals require more food resources than smaller animals, and so larger animals generally defend larger territories than smaller animals, a pattern found both within and among species (Schoener and Schoener, 1982; Woodward et al., 2005). Fluctuations in food supply may therefore affect territory size and defense differently in large and small animals. Secondly, differences in the costs and benefits of territorial defense between the sexes may influence the response of males and females to varying food supply. In many species, males defend territories to gain access to females, while female territories are often maintained for access to food or other resources (Jarman, 1974; Stamps, 1983). In such a case, food supply could influence female territory size and defense directly, while male territorial behavior may be more indirectly influenced by food supply to the extent that it alters the distribution of potential female mates. In addition to these factors, the food-value theory states that

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individual animals should defend the smallest territory necessary to gain access to the required food resources (Stenger, 1958). This theory predicts that in habitats with higher quality and/or more abundant food resources, animals will defend smaller territories, a relationship that has been confirmed across diverse taxa (Simon, 1975; Adams, 2001; Marshall and Cooper, 2004; Streby et al., 2013).

In this study, we examined the relationships between prey availability and territorial defense in a natural population of the green anole lizard, *Anolis carolinensis*. Green anoles are medium-sized, sexually-dimorphic lizards; the average snout-vent length for males is 55–65 mm, and 45–55 mm for females (Jenssen et al., 1995). These lizards are generalist insectivores that consume arthropod prey encountered on their arboreal perches, on the ground, and in the air by both active and sit-and-wait foraging strategies (Jenssen et al., 1995). This species has been a model system in many studies of physiology and behavior (reviewed in Lovern et al., 2004; Losos, 2009), and its territorial behavior has been described in detail (e.g., Schoener and Schoener, 1982; DeCourcy and Jenssen 1994; Nunez et al., 1997; Jenssen et al., 2000, 2001). In brief, adult green anoles of both sexes are territorial, competing for resources with other members of their sex. Both males and females defend territories using visual displays, including head bobs and pushups, extension of the throat fan (i.e., dewlap), raising a dorsal crest, and developing a black spot behind the eyes. Males also use dewlap extensions and pushup displays to court potential mates. Green anoles have a polygynous mating system, in which male territories (which are larger and more vigorously defended than female territories [Nunez et al., 1997]) generally overlap multiple female territories. Females are thought to mate with the males that they regularly encounter in their territories, as there is little evidence for female choice in this species or lizards in general (reviewed in Tokarz, 1995).

Previous field studies that have tested the relationship between lizard food supply and territorial defense have experimentally manipulated available food resources. In a manipulation of food in the tropical anole *Anolis (Norops) humilis*, home range size for either sex did not change in response to the addition of food, although growth and reproduction were increased (Guyer, 1988a, b). In addition, in *Oligosoma grande*, the grand skink, the addition of food resources resulted in an increase in male home range size, but did not affect female home ranges (Eifler and Eifler, 1999). However, the relationships between territorial strategies and food availability in natural, unmanipulated populations have received much less attention.

Here, we examined natural prey availability and territorial behavior in an unmanipulated green anole population in three habitats that varied in prey availability. We predicted that territories of both sexes would be smaller in habitats with greater food availability; in those habitats a smaller territory would provide sufficient food for females, and males could defend smaller territories that would overlap the same number of females. We also

predicted that males and females would have differing responses in their behavioral defense of the territories. If females are primarily defending food resources, their investment in behavioral defense should be greater when food resources are more limited. If males are primarily defending access to females, an altered food supply may not directly influence their social display behavior. Finally, we predicted that larger lizards would defend larger territories than smaller lizards, and that the relationship between body size and territory size would differ in habitats with differing food availability.

## 2. Methods and materials

### 2.1. Field study sites

We studied arthropod availability and green anole territory size and behavior in Palmetto State Park in Gonzales, Texas (N 29° 35.22', W 097° 34.92') in late May – early July 2010. To determine whether territorial strategies differed among anoles in habitats with varying arthropod availability, we established a ~1000 m<sup>2</sup> study plot in each of three distinct habitats, with all plots within 1 km of one another. The first plot, the “Palmetto” plot, was characterized by a thick stand of dwarf palmetto (*Sabal minor*) and extensive canopy cover provided by primarily oak, elm and ash trees. The second plot, “Field,” was a field of tall grasses with little canopy cover, interspersed with clusters of live oak, cedar elm trees and dwarf palmetto. Thirdly, the “Lake” plot was positioned along a rarely used park trail beside Oxbow Lake. The understory in this plot was composed of small trees and vines and was dense in comparison to the other two plots. A continuous canopy allowed lizards to use habitat on both sides of the trail. (See Dill et al. (2013) and Battles et al. (2013) for more detailed descriptions of these study plots.) Although the plots differed in vegetation type, they supported similar densities of green anoles (Table 1). Measures of arthropod abundance and biomass and observations of lizard behavior (described below) occurred in the three plots in overlapping periods during the study.

### 2.2. Arthropod abundance and biomass

Anoles are generalist, opportunistic insectivores known to consume beetles, ants, flies, orthopterans, lepidopterans (including caterpillars), hemipterans, homopterans, termites, spiders, earthworms, millipedes, centipedes, snails, and on occasion even seeds and nectar (reviewed in Losos, 2009). Thus, we measured all arthropods encountered in our surveys as potential green anole prey. We used two methods to quantify arthropod abundance and biomass in each plot (following Dial and Roughgarden, 1995). In the first, we sampled primarily flying insects with Catchmaster<sup>®</sup> traps, 5 in x 7 in cardboard rectangles coated on one side with a glue-like material. On each of five nonconsecutive days during our lizard

**Table 1**  
Estimates of male (M) and female (F) lizard densities, arthropod abundance, and arthropod biomass in the three study plots.

Plot	Sex	Lizards/m <sup>2</sup>	Sticky Traps <sup>a</sup>		Transects <sup>b</sup>	
			Abundance	Biomass (mg)	Abundance	Biomass (mg)
Lake	F	0.0331	4.07 (0.27)	48.48 (13.85)	7.47 (2.08)	193.10 (69.47)
1120 m <sup>2</sup>	M	0.0206				
Field	F	0.0141	7.81 (0.94)	18.85 (8.73)	12.03 (2.61)	154.96 (38.06)
1492 m <sup>2</sup>	M	0.0121				
Palmetto	F	0.0285	8.74 (0.99)	27.68 (6.63)	7.63 (6.29)	91.74 (35.02)
1053 m <sup>2</sup>	M	0.0190				

<sup>a</sup> Sticky trap data are average number (abundance) of arthropods per trap per day, and average mg of arthropod biomass per trap per day. Measures of SE are in parentheses.

<sup>b</sup> Transect data are average number (abundance) of arthropods per m<sup>2</sup>, and average mg of arthropod biomass per m<sup>2</sup>. Measures of SE are in parentheses.

behavioral observations (see below), we placed five of these “sticky traps” in each of the study plots. The traps were haphazardly placed on vegetation at various heights and locations within each plot to sample a wide range of microhabitats, and traps were left undisturbed for 10 h (from approximately 08:00 to 18:00, the general period of anole activity). We then identified each insect collected on a trap to taxonomic order and measured its body length in mm with digital calipers. This method of sampling allowed for comparisons among plots using statistical analysis, because replicated traps were sampled for each study plot.

The second method we used to measure arthropod availability was to identify all arthropods observed in two 2 m × 30 m transects in each plot. This method allowed us to sample both flying and crawling arthropods. To establish the location of each transect, we arbitrarily determined a starting point within a plot and then followed a direction approximately toward the plot's center for 30 m, identifying each arthropod within 1 m of each side of the central transect line. Within the transect area (60 m<sup>2</sup>), we searched for arthropods along the ground, in the leaf litter, perched on vegetation, and flying in the air. We identified each arthropod to order and used digital calipers to estimate its body length in mm using its perch immediately prior to our disturbance as a size reference (for example, if a moth was found on a leaf but fled because of our disturbance, we used calipers to measure the spot on the leaf where the moth had been to obtain a reasonable approximation of its length). For each plot, we measured arthropods along one transect in the morning (08:00–11:00) of one day and another transect in the afternoon (13:00–16:00) of a different day to gain a representative sample of the arthropods in the plot, and we combined data from both transects per plot. In contrast to the sticky trap method, this approach provided more complete, qualitative descriptions of the arthropod availability in the plots, but these descriptive data could not be statistically analyzed.

For both transect and sticky trap data, we estimated arthropod biomass using the equation  $W = 0.035 * L^{2.62}$ , where  $W$  is arthropod biomass in mg and  $L$  is body length in mm (Rogers et al. 1976). This method accurately estimates biomass for a wide diversity of arthropods (Rogers et al. 1976; Johnson and Strong, 2000; Robertson et al., 2011).

### 2.3. Lizard behavioral observations

We captured almost all anoles in each of the three plots by hand or noose. Each captured lizard was sexed, measured for snout-to-vent length (SVL) with a ruler and massed with a Pesola spring scale. We marked each lizard with a unique tag that consisted of three beads sewn into the dorsal tail muscle (Fisher and Muth, 1989) to allow us to identify the lizards for subsequent observational data collection. We released each anole at its site of capture.

After a minimum of 24 h post-capture, we conducted focal observations on marked lizards. We located undisturbed lizards by walking slowly through the plots, and we observed their behavior using binoculars from a minimum distance of 10 m. Observations lasted from 5 to 60 min (average = 34 min), and we conducted no more than 3 h of observation per lizard, for an average of 2.6 observation periods and 86 min of observation per lizard. No observations were performed during inclement weather (i.e., rain). We recorded all behaviors performed by the focal lizard during the observation period, particularly focusing on the number of pushups and dewlap displays and the total time duration of display performance (following Johnson et al., 2010). The target of an individual anole display is often difficult to determine, as high population densities cause most displays to have multiple potential targets, and some displays are assertion displays to declare the presence of a territory owner to any (unseen) lizards who may be nearby

(Losos, 2009). Therefore, we used all social displays in our analysis of territorial defense. If lizards were observed in more than one focal observation period, we calculated an average for each behavioral measure for use in statistical analyses.

### 2.4. Estimating territory size

Because green anoles behaviorally defend all of their home ranges (confirmed by the behavioral observations performed in this study and reviewed in Losos, 2009), we follow the convention established among anole biologists to use all of a lizard's occupied space as an estimate of its territory size (e.g., Schoener and Schoener, 1982; Jenssen and Nunez, 1998; Johnson et al., 2010). We recorded location data for each marked lizard by measuring the distance and compass angle from the lizard's location to predetermined reference points within the plot and converting these data to Cartesian coordinates. We recorded these data upon each initial sighting of a lizard and, if the lizard moved among perches during focal observations, at up to three locations during each observation.

We used the *adehabitat* package in R (Calenge, 2006) to calculate 95% minimum convex polygons (MCP; Rose, 1982) and 95% adaptive kernels (AK; Worton, 1989). We used these two measures of territory size because, while MCP is the most commonly reported method used to measure territories in lizards, AK is reported to be less sensitive to the number of data points included (Powell, 2000). Because both measures of territory size can be influenced by the number of sightings of an animal, we followed the protocol described by Smith (1995) to determine the minimum number of sightings required to accurately estimate MCP and AK (Abell, 1997; Morrison et al., 2002; Qi et al., 2012). In brief, beginning with all lizards for which we had four or more sightings, we used linear regression to determine the relationship between the square root-transformed territory sizes and the number of sightings, and repeated this analysis with increasing minimum numbers of sightings until the relationship became nonsignificant. In subsequent analyses, we then only used data from lizards that had more sightings than this minimum.

### 2.5. Statistical analyses

We calculated the total arthropod abundance and biomass from each sticky trap and compared these measures among plots using one-way ANOVAs, followed by Tukey's HSD post hoc tests. We calculated lizard density in each plot by dividing the total number of lizards captured in a plot by the MCP of all available territory data points in that plot (including all lizards in each plot, not only those with five or more sightings), calculated using *adehabitat* in R (Calenge, 2006). We also calculated a measure of body condition by using the residuals from a regression of mass and SVL (Jakob et al., 1996), and we used a series of one-way ANOVAs, separately for each sex, to determine if lizards differed among plots in mass, SVL, or body condition.

Because we were interested in the interaction of territory size and territorial behavior, we only used data from lizards that had a minimum of five (for AK) or six (for MCP) territory sightings in our analyses comparing territory size and behavior among plots, as these were the minimum numbers of sightings required to calculate territory size (see above). Considering the two sexes separately, we used regression analyses to determine whether estimates of territory size were associated with two measures of body size (SVL and mass). We also used ANCOVAs with SVL or mass as the covariate to determine if plots differed in territory size as a function of body size. With separate Kruskal-Wallis tests for each sex, we compared the rates of dewlap extensions and pushup displays, the

percent of time each lizard spent displaying, and MCP and AK territory sizes, with pairwise Mann-Whitney U tests following significant results.

### 3. Results

#### 3.1. Arthropod abundance and biomass

In sticky traps, we captured arthropods from class Arachnida and orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera, and Orthoptera. Using these replicated sticky traps, we found that the abundance of flying arthropods differed among plots ( $F_{2,12} = 6.9$ ,  $P = 0.01$ ,  $\eta_p^2 = 0.54$ ), such that the Lake plot had a lower abundance of arthropods than the Field or Palmetto plots (Table 1). However, arthropod biomass did not significantly differ across the plots ( $F_{2,12} = 2.0$ ,  $P = 0.18$ ,  $\eta_p^2 = 0.25$ ; Table 1). Because the Lake plot sticky traps had a lower abundance but similar overall biomass compared to the other plots (Fig. 1a), this indicates that the Lake plot had a greater number of large flying arthropods.

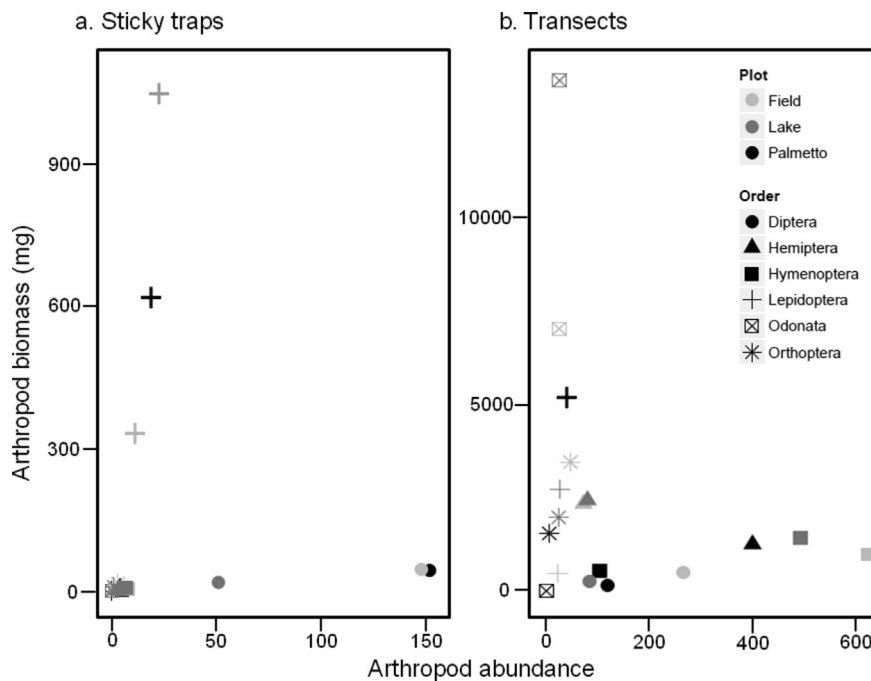
Arthropods identified in the transects included all groups captured in the sticky traps, as well as class Chilopoda and orders Blattodea, Ephemeroptera, Odonata, Mantodea, and Phasmatodea (Supplementary Table 1). With data from the two transects in each plot combined, plotting abundance versus biomass for the six most common orders (Fig. 1b) showed that the Lake plot had the highest prey biomass of the three plots, a pattern likely due to the high biomass of Odonata in the Lake plot. Combined with data from the sticky traps (Fig. 1a), these results show that together Odonata and Lepidoptera were among the highest biomass orders across the plots, while Diptera and Hymenoptera were generally the highest abundance orders across plots. All together, these data indicate that the Lake plot had the highest biomass of available prey and the lowest abundance of those prey, as compared to the Palmetto and Field plots (Table 1).

#### 3.2. Lizard territory size and behavior

We captured a total of 149 lizards: 50 in the Palmetto plot (20 males, 30 females), 39 in the Field plot (18 males, 21 females), and 60 in the Lake plot (23 males, 37 females). The densities of lizards in each plot were similar, although the Lake and Palmetto plots appears to have had a slightly higher population density than the Field plot (Table 1). Overall, males were significantly heavier in mass ( $F_{1,147} = 44.4$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.96$ ) and larger in SVL ( $F_{1,147} = 164.6$ ,  $P < 0.001$ ,  $\eta_p^2 = 1.00$ ) than females. Males across the three plots did not differ in either measure of body size (both  $P > 0.8$ ,  $\eta_p^2 < 0.01$ ). Females across the three plots differed in mass, such that females in the Lake plot were of lower mass than females in the other plots ( $F_{2,85} = 10.7$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.19$ ), but they did not differ in SVL across plots (SVL:  $F_{2,85} = 2.2$ ,  $P = 0.119$ ,  $\eta_p^2 = 0.06$ ). Body condition differed among plots for females, but not males (females:  $F_{2,85} = 9.15$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.15$ ; males:  $F_{2,58} = 1.52$ ,  $P = 0.227$ ,  $\eta_p^2 = 0.04$ ), such that the Lake females had a lower body condition than females from the other two plots (as expected from the measures of mass and SVL reported above).

In our measures of territory size, the relationship between MCP and number of sightings became nonsignificant at six sightings ( $R^2 = 0.066$ ,  $F_{1,40} = 2.83$ ,  $P = 0.10$ ) and the relationship for AK became nonsignificant at five sightings ( $R^2 = 0.002$ ,  $F_{1,52} = 0.11$ ,  $P = 0.74$ ). Thus, in subsequent statistical analyses, we only used data from lizards that had at least six (for MCP) or five (for AK) sightings.

MCP and AK provided qualitatively similar results, and so only results from the MCP analysis are described here. With lizards from all plots pooled, territory size was not significantly associated with lizard SVL or mass for either sex (females: SVL:  $R^2 = 0.05$ ,  $F_{1,21} = 1.06$ ,  $P = 0.31$ , mass:  $R^2 = 0.26$ ,  $F_{1,21} = 1.52$ ,  $P = 0.23$ ; males: SVL:  $R^2 = 0.02$ ,  $F_{1,29} = 0.52$ ,  $P = 0.48$ , mass:  $R^2 = 0.30$ ,  $F_{1,29} = 2.82$ ,  $P = 0.10$ ). Further, comparisons of territory size among plots using ANCOVA did not reveal SVL or mass to be a significant covariate



**Fig. 1.** Abundance and biomass of the six most common arthropod orders in the three study plots. Each of these orders is used as food by *Anolis* lizard species (Dial and Roughgarden, 1995). Light gray symbols represent data from the Field plot, dark gray symbols represent the Lake plot, and black symbols represent the Palmetto plot. Symbol shape corresponds to arthropod order. a) Total arthropods sampled on sticky traps. b) Total arthropods across two transects (total area = 120 m<sup>2</sup>).

with territory size for either sex (all  $P > 0.1$ ), indicating that the relationship between body size and territory size did not differ in plots with differing food availability.

However, territory size differed markedly among the plots, such that lizard territories of both sexes were consistently smaller in the Lake plot than in the Palmetto plot, the two plots with the most similar lizard densities (Table 1). Male territories differed across plots ( $\chi^2(2, n = 23) = 9.0, P = 0.011$ ), such that Lake males had smaller territories than Palmetto males ( $U = 9.0, Z = -2.60, P = 0.008$ ) and Field males ( $U = 12.0, Z = -2.31, P = 0.021$ ). Palmetto and Field male territories did not differ from one another ( $U = 26.0, Z = -1.28, P = 0.222$ ). Female territory size also differed across plots ( $\chi^2(2, n = 16) = 7.47, P = 0.024$ ), following the same pattern as males. Lake females had smaller territories than both Palmetto females ( $U = 2.0, Z = -2.27, P = 0.024$ ) and Field females ( $U = 4.0, Z = -2.19, P = 0.030$ ), but Palmetto and Field females did not differ from one another ( $U = 8.0, Z = -0.49, P = 0.730$ ). Summary data for territory measures by sex and plot are presented in Supplementary Table 2.

Of those lizards with five or more territory sightings (number of lizards = 54; Palmetto = 16, Field = 20, Lake = 18), we performed 103.7 h of behavioral observations. Males performed higher rates of dewlap extensions ( $F_{1,52} = 70.6, P < 0.001, \eta_p^2 = 0.58$ ) and pushups ( $F_{1,52} = 61.3, P < 0.001, \eta_p^2 = 0.54$ ) than females, and males spent a larger percent of time displaying ( $F_{1,52} = 47.6, P < 0.001, \eta_p^2 = 0.48$ ). We found no behavioral differences (in percent of time displaying, dewlap extension rate, or pushup rate) among the plots for adults of either sex (all  $P > 0.25, \eta_p^2 < 0.035$ ). Summary data for behavioral measures by sex and plot are presented in Supplementary Table 2.

In sum, the relationships among prey availability, lizard territory size, and territorial defense behaviors are summarized in Table 2.

#### 4. Discussion

In a natural population of green anole lizards, we found that male and female lizards in a habitat with greater available prey biomass (Lake) had smaller territories than lizards in habitats with less prey biomass (Field and Palmetto). However, in contrast to our predictions, we did not find a relationship between body size and territory size, and there were no differences between males and females in their relationships between food availability and territory size, or food availability and behavior (Table 2).

One pattern that clearly emerges from our arthropod data is that the lizard prey that provide the greatest biomass, and are therefore potentially the most valuable food items, are also those that occur more rarely in all three habitats (Fig. 1). For example, although Diptera (flies) and Hymenoptera (in our study sites, primarily ants) were quite common, they contributed relatively little to the available arthropod biomass across our plots, while a few large dragonflies (Odonata) and butterflies and moths (Lepidoptera) provided most of the available biomass. While some animals are gape-limited in their prey consumption (e.g., Forsman, 1996), green anoles are known to eat prey from all of these arthropod groups (Losos, 2009), and indeed, we observed the lizards in our study consuming such prey. Yet, the largest prey items may not have been functionally available to the smaller green anoles in our study. Thus,

it is possible that the largest prey in our study sites were more readily available to male anoles than females, as males are substantially larger than females. This possibility has some support in this study, as the mass and body condition of females (but not males) is lower in the Lake plot where the main prey consisted of larger arthropods.

As we predicted, territory size was smaller for both males and females in the habitat with the greatest prey availability, as measured by prey biomass. This is consistent with a wealth of previous studies considering a diversity of animal taxa. For example, Herfindal et al. (2005) found that lynx (*Lynx lynx*) home ranges were negatively correlated to prey density, and Zabel et al. (1995) demonstrated that northern spotted owls (*Strix occidentalis caurina*) maintained smaller home ranges in areas with greater prey quality. The negative association between prey availability and territory size reported here, while similar between the sexes, may result from different mechanisms in the two sexes. Female anoles are thought to defend territories primarily to gain access to arthropod prey, and the constant size of their territories across seasons is considered to be determined by their metabolic needs (Andrews, 1971; Jenssen et al., 1998). The size of male territories, on the other hand, is likely more strongly influenced by the arrangement of female territories than the availability of food; in the breeding season, male anole territories are as much as 15× larger than they are during the nonbreeding season (Stamps and Crews, 1976; Lister and Garcia Aguayo 1992), and males arrange their breeding season territories to overlap with as many females as possible (Stamps, 1999; Jenssen et al., 2001). Indeed, males of many species – including mammals (e.g., Komers and Brotherton, 1997; Fisher and Owens, 2000) and other lizards (Haenel et al., 2003) – adjust the size and location of their territories based on the spatial arrangement of female territories. Surprisingly, we did not find differences between the sizes of male and female territories, in contrast to previous studies that have found that male green anoles defend larger territories than females (e.g., Schoener and Schoener, 1982; Nunez et al., 1997), although our measures of territory sizes are within the ranges reported in these studies.

Considering the differences in defended resources between males and females, we predicted that the sexes would differ in their relationships between prey availability and behaviors involved in territorial defense. If males are primarily defending access to females, varying access to prey should not affect their rates of dewlap extensions and pushup displays. Our findings were consistent with this prediction, as males across the three habitats did not differ in behavioral display. Similarly, Donihue et al. (2016) found that populations of the lizard *Podarcis erhardii* did not differ in aggressive behavior across islands that varied in prey availability. However, if the primary resource defended by female territoriality is food, we expected that females would differ among habitats in behavioral defense, with the most frequent territorial displays occurring in the habitats in which prey were most limited. We did not find this predicted behavioral difference among females in this study. This result may be due to the relative infrequency of displays in females in this study – in over 59 h of observation of female behavior, we observed 59% of females displaying, with an average of 0.01 dewlap extensions per min and 0.5 pushups or headbobs per min. For comparison, 100% of males in our study displayed, with an average rate of 1.43 dewlap extensions per min and 12.0 pushups or headbobs per min. While female green anoles have been observed to aggressively defend their territories, particularly against other conspecific females (e.g., Nunez et al., 1997), this is relatively uncommon. Thus, the lack of differences in female aggression between habitats in this study may have been due to the low number of aggressive female interactions observed.

In conclusion, while arthropod prey availability appeared to be

**Table 2**  
Summary of relationships among prey availability, green anole lizard territory size, and territorial defense behaviors.

Plot	Prey Number	Prey Biomass	Territory Size	Territorial Defense
Lake	Lower	Higher	Smaller	No difference
Field	Higher	Lower	Larger	No difference
Palmetto	Higher	Lower	Larger	No difference

negatively associated with territory size in this study of a natural population of green anole lizards, social behaviors seemed relatively insensitive to variation in prey among habitats. Further, our data suggest that male and female anoles may both use similar territorial strategies across habitats with differences in prey availability, although the resources defended may differ between the sexes. Although this experiment did not manipulate food supply or experimentally control for other factors that may influence territoriality (e.g., physical structure of the habitats), together with previous experiments in which prey availability and lizard population structure were manipulated (Guyer, 1988a, b; Eifler and Eifler, 1999), these results suggest a relationship between food supply and territory defense in lizards. Yet, studies of field populations in which food supply and population densities are unmanipulated remain rare, but are needed to determine the generality of these relationships in the complex physical and social environments in which animals live.

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### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.08.008>.

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