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Sexual dimorphisms in habitat-specific morphology and behavior in the green anole lizard

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Abstract

Species that occur in variable environments often exhibit morphological and behavioral traits that are specific to local habitats. Because the ability to move effectively is closely associated with structural habitat, locomotor traits may be particularly sensitive to fine-scale habitat differences. *Anolis* lizards provide an excellent opportunity to study the relationship between locomotion and natural perch use in the field, as laboratory studies have demonstrated that lizards that use broader perches develop longer limbs and have higher sprint speeds. We examined *Anolis carolinensis* (the green anole) in three habitats in close proximity. Our goals were to determine whether habitat-specific differences in hindlimb and toe morphologies occurred in a population in which perch size was variable but not manipulated, whether locomotor behaviors were associated with these morphologies, and whether habitat-specific traits differed between the sexes. We found that while juveniles in the three habitats did not differ in limb or toe morphology, adult females using broader perches had relatively longer limbs than females using narrower perches. Females also differed in toe length across habitats, but not in relation to perch diameter. Males, in contrast, exhibited differing growth patterns (allometry) in these traits, and marginal differences in locomotor behavior. Together, these results suggest that sex-specific responses in morphology and behavior, consistent with experimental observations of phenotypic plasticity, provide a mechanism for refining local habitat use.

Introduction

Many species occur in a range of habitats that place differing functional demands on organismal phenotypes. Populations may respond to these varying pressures by evolving local adaptations via natural selection, if populations are at least somewhat genetically isolated, or if selection is strong despite gene flow. Alternatively, individuals with different phenotypes could differentially disperse, such that they match their phenotype to their habitat (e.g. Davis & Stamps, 2004), or they may be competitively excluded from a habitat in which other individuals' phenotypes more closely match the demands of the habitat. Thirdly, phenotypic plasticity – in which an organism's phenotype is a function of the interaction between its genotype and the environment in which it is expressed – may allow individuals to differentially acclimate to the habitats (West-Eberhard, 1989; Scheiner, 1993). Plasticity may be a particularly effective means of phenotypic differentiation among habitats when organisms within the same population are expected to encounter variable habitats.

In many species, males and females differ in their habitat use in ways that place differing demands on the two sexes (reviewed in Butler, Schoener & Losos, 2000), providing the opportunity for sex-specific responses to habitat use. For example, sex differences in microhabitat can result in differences in food availability and predation risk, and thus the locomotor traits that allow a male or female to most effectively capture food or escape from predators may vary. Because phenotypes associated with locomotion may be especially sensitive to local habitat differences, (e.g. Irschick & Garland, 2001), there may be strong demands for local sex differentiation in locomotor behaviors and morphologies.

In species that occur across diverse structural habitats, morphological and behavioral traits associated with locomotion often covary in a way that maximizes performance in each environment (Bolnick *et al.*, 2003; Stoehr, 2010). Alternatively, variation in one phenotype may influence the extent of variation in associated phenotypes. In particular, behavior is an important means through which animals interact with their environment, and individuals may dampen the effects of macrohabitat variation by using a subset of available microhabitats (e.g. Huey, Hertz & Sinervo, 2003; Johnson *et al.*, 2006; Duckworth, 2009). Or, animals may occur in different structural habitats, but alter the behaviors they use to maneuver in

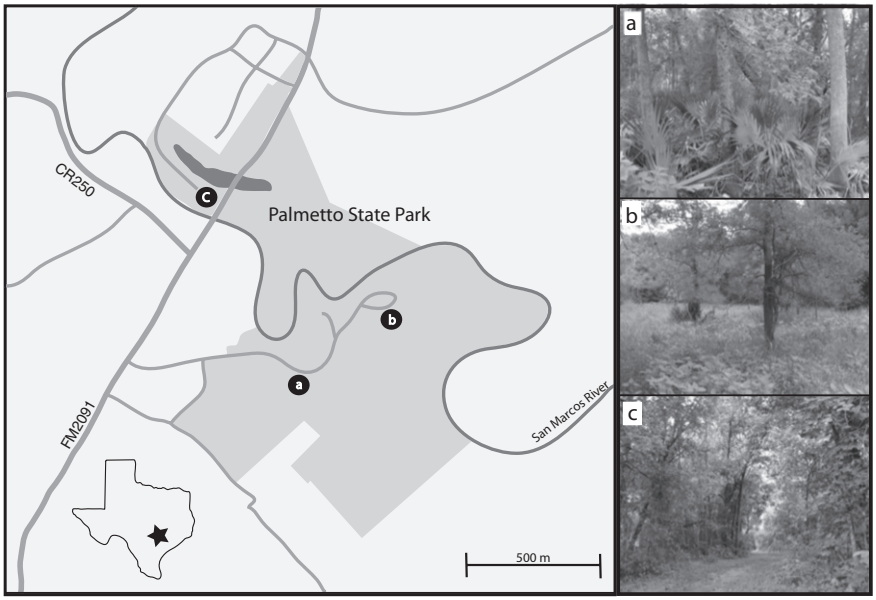

Figure 1 Study plots within Palmetto State Park, Gonzales, Texas. The star on the small map of Texas (bottom left) indicates the location of the park within the state.

these habitats, allowing similar morphologies to be successful in varying environments. Therefore, observations of both locomotor behaviors and morphologies are necessary to interpret habitat-level sex differences in locomotion within wild populations.

In this study, we examined locomotor-associated traits within a single population of *Anolis* lizards in different natural habitats. *Anolis* lizards (anoles) exhibit strong correlations among habitat, limb length and locomotor behavior, as species occupying broader perches tend to have longer limbs and higher sprint speeds than those using narrow perches (Losos, 1990; Irschick & Losos, 1999). These macroevolutionary patterns of limb length divergence are often attributed to natural selection and likely underlie the adaptive radiation of this genus into different parts of the arboreal habitat (reviewed in Losos, 2009).

Phenotypic plasticity has also been observed in *Anolis* and is predicted to improve locomotor performance in particular microhabitats. Experimental manipulations have consistently shown that anoles raised on broad perches develop relatively longer limbs than those raised on narrow perches. Male Cuban brown anoles *Anolis sagrei* exhibited differences in hindlimb length in experimental field populations on islands with differing vegetation (although whether these differences were plastic or genetic was not determined; Losos, Warheit & Schoener, 1997), and in laboratory experiments both sexes exhibited hindlimb plasticity as a function of perch diameter (Losos *et al*., 2000, 2001). The green anole *Anolis carolinensis* has also shown hindlimb plasticity, with laboratory-reared females showing a much greater response to perch diameter than males (Kolbe & Losos, 2005). While intraspecific differences in limb morphology appear to mirror interspecific relationships across the genus, the differences between species that specialize on dramatically different perch diameters is far greater than experimentally induced plastic differences within a species (Losos *et al*., 2000).

We studied green anoles in three habitats in close proximity that varied substantially in the diameters of available perches (Fig. 1; Results) to determine whether locomotor morphology and behavior differed among habitats in a natural population. Thus, we build on previous results from experimental studies to determine the effects of differential habitat use on multiple phenotypes – a uniquely integrative perspective not yet explored in this system. We examined the relative lengths of the hindlimb and fourth toe separately, because these structures perform different functions. Longer limbs are generally correlated with faster sprint speeds, while shorter limbs are associated with greater maneuverability on narrow perches (Losos & Sinervo, 1989; Irschick & Losos, 1998). Toe morphology is associated with clinging ability (Zani, 2000) as adhesive lamellae (i.e. subdivisions of the toepad) increase clinging performance (Irschick *et al*., 1996), and anoles on narrow perches tend to wrap the entire length of their toes around them (Losos *et al*., 2000). We tested the hypotheses that habitat-specific differences in limb and toe morphologies would occur in a natural population, such that lizards using broader perches would have relatively longer limbs and toes, that locomotor behaviors would be associated with these morphologies, and that if habitat use differed between males and females, limb and toe morphologies and locomotor behaviors would correspondingly differ between the sexes.

Materials and methods

Study sites

We examined the morphology and behavior of *A. carolinensis* in Palmetto State Park in Gonzales, Texas in summer 2010. We studied lizards in three *c*. 1000-m^2 plots, chosen to maximize differences in available perch size. The 'Palmetto' plot (Fig. 1a) was characterized by broad perches, including dense dwarf palmettos *Sabal minor* and medium-sized trees such as

burr oak *Quercus macrocarpa*, lacey oak *Quercus laceyi*, cedar elm *Ulmus crassifolia*, green ash *Fraxinus pennsylvanica* and box elder *Acer negundo*. The 'Field' plot (Fig. 1b) consisted primarily of a field of tall grasses with clusters of dwarf palmettos and medium-sized trees. The 'Lake' plot (Fig. 1c) was located along a park-maintained trail beside a small lake and contained smaller trees and vines, such as Alabama supplejack *Berchemia scandens*, trumpet-creeper *Bignonia radicans* and mustang grape *Vitis candicans*. All plots were within 1 km of each other and were embedded in a matrix of continuous forest, although the Lake plot was separated from the others by a two-lane paved park road, lined on both sides by primarily oak and elm forest, with a grassy underpass connecting the habitat on both sides of the road.

To quantify differences in perch availability among plots, we measured the diameter of available perches along a transect within each plot. For each transect, we chose an arbitrary starting point within the plot and followed a haphazardly chosen direction for 60 m. Preliminary data suggested that 1.5 m was the average perch height of anoles in these plots. Therefore, we measured all perches that occurred within 1 m to the right or left of the linear transect, at a height of 1.5 m, at intervals of 1 m (our subsequent measures of 159 anoles at Palmetto State Park confirmed that their average perch height was 1.4 m). We compared the diameters in each plot using analysis of variance (ANOVA).

Field data collection – adults

In each plot, we attempted to capture as many adult lizards as possible by hand or noose. Immediately following capture, we sexed each individual and measured snout–vent length (SVL) to the nearest millimeter and lengths of the hindlimb and fourth toe to the nearest 0.1 mm. Although previous studies of anole morphology have defined the hindlimb as the length of the limb from the insertion of the limb to the distal tip of the claw on the fourth (longest) toe (e.g. Losos *et al.*, 2000; Kolbe & Losos, 2005), we measured the hindlimb and toe separately. We measured hindlimb length as the distance from the body wall to the termination of the lower leg at the foot, and the fourth toe as the distance from the tip of metatarsal IV not including the claw, to the point of insertion of the toe at the footpad. Both measures were taken on the lizard's right side unless it was injured, in which case the left limb was used. At the time of capture, we gave each lizard a permanent, unique tag using three colored beads sewn into the tail muscle (Fisher & Muth, 1989). We then released each lizard at its capture location.

We identified adults as those with SVL >45 mm, the approximate size at which green anoles reach sexual maturity (Lovern, Holmes & Wade, 2004; Irschick *et al.*, 2006). In total, we caught 23 adult males and 35 adult females in the Palmetto plot, 23 males and 29 females in the Field plot, and 24 males and 36 females in the Lake plot. Of the 170 adults we measured, we collected subsequent behavioral data on 91. We collected 40–45 h of behavioral data in each plot (total = 127 h) through 5–60 min (average = 34 min) focal observations. During each observation, we remained at least 10 m away from the lizard, minimizing our own movements, and observed the lizard through binoculars. We recorded all locomotor behaviors, identifying each movement as a run, crawl or jump. To assess differences in locomotor behavior between the plots, we calculated the total locomotor rate (the sum of all locomotor movements/time) and the proportions of each type of movement (runs, crawls and jumps) from the total number of all movements for each individual (e.g. # runs/# movements). If a lizard was observed in more than one period, we calculated its average for each behavioral measure across observations.

At the initial capture, and upon each sighting of a marked lizard, we measured the diameter of the perch where it was first observed. During observations, we also measured the diameter of the perch used by each lizard *c*. every 20 min. For each individual, we calculated an average perch diameter.

Field data collection – juveniles

To determine whether differences among plots in adult morphologies were associated with juvenile morphologies, we also compared juveniles in the three plots. We identified juveniles as lizards with SVL <45 mm, as below this size green anoles are not sexually mature (Lovern *et al.*, 2004; Irschick *et al.*, 2006). In late July, we captured 45 juveniles (nine in Palmetto, 12 in Field and 24 in Lake), with an average SVL of 28.6 mm (range 23–44 mm). We measured morphological traits (sex, SVL, hindlimb and fourth toe lengths) as described earlier. To assure that each individual was only measured once, each lizard was given a toe clipping unique within its plot and released at the site of capture.

Statistical analyses

We determined that there were no differences between male and female juveniles in SVL (using ANOVA) or relative limb morphologies [using analysis of covariance (ANCOVA) with SVL as the covariate; see Results section]. Therefore, we pooled juveniles of both sexes in subsequent analyses. Because adult males, adult females and juveniles exhibited different relationships between body size and limb morphologies (ANCOVA; Supporting Information Table S1), for each group we conducted a separate ANCOVA, with SVL as the covariate, to determine whether relative hindlimb or toe length differed among habitats. Each ANCOVA (for males, females and juveniles) included an interaction term between plot and SVL, which tested for differences in slope among the plots. A difference in slope indicated that the relative rate of limb growth differed among the plots (Sanger *et al.*, 2012). When this interaction term was not statistically significant, we repeated the ANCOVA without the interaction term in a test for differences in intercept among plots. We followed significant ANCOVAs with main effects tests to determine differences among the three plots. In separate analyses for each demographic, we compared SVL and perch diameter among the three plots using ANOVA, with significant analyses followed by Tukey's honestly significant difference (HSD) post hoc tests. When significant differences in relative hindlimb and toe lengths were seen across plots for adult lizards of a sex, we

performed an ANCOVA with relative limb morphologies using only juveniles of that sex. We compared locomotor behaviors (i.e. rate of total movements and proportions of runs, crawls and jumps) in adult lizards across the three plots using separate ANOVAs for each sex.

Results

Adult and juvenile morphology

Across the three habitats, adult green anoles exhibited sex-specific differences in morphology, although lizards of either sex did not differ in body size among the plots (males: $F_{2,67} = 0.75$, $P = 0.80$; females: $F_{2,97} = 2.42$, $P = 0.09$). Across the plots, males differed in the slopes of hindlimb and fourth toe length regressions, showing differences in the scaling of these traits among plots (Table 1a; Fig. 2a, d). However, females differed in the intercepts (but not slopes) of both morphologies across the plots (Table 1b; Fig. 2b, e). In particular, females from the Lake plot had shorter relative hindlimbs than females in both the Field ($P < 0.001$) and Palmetto plots ($P = 0.002$), and females in the Field plot had shorter relative fourth toes than females in Palmetto ($P = 0.001$) and Lake ($P = 0.049$).

In contrast, juveniles showed no differences in relative morphologies across sexes or plots. Combining data from all plots, juveniles did not differ in SVL ($F_{1,42} = 0.86$, $P = 0.358$) or relative limb and toe morphologies (Table 2a). Further, juvenile morphologies did not differ among plots in slope or intercept (Table 1c, Fig. 2c, f). Because adult females and males differed in relative limb morphologies across the plots, we examined whether each sex of juveniles exhibited similar differences. Neither juvenile males (Table 2b) nor females (Table 2c) showed differences among plots in these traits.

Perch use and locomotor behavior

Perch availability at a height of 1.5 m differed significantly across the plots ($F_{2,238} = 4.44$, $P = 0.013$), such that the Lake plot provided narrower perches than Field, and the available perches in Palmetto did not statistically differ from those in the other plots (Fig. 3). In each plot, adult lizards generally used broader perches on average than those randomly available in the habitat (Fig. 3).

Adult perch diameters differed among the plots (males: $F_{2,71} = 4.07$, $P = 0.021$; females: $F_{2,99} = 3.77$, $P = 0.027$), with male and female lizards in the Lake plot using narrower perches than those in the Palmetto plot, but perch diameter in Field did not differ from the other plots (Fig. 3). However, juveniles in the three plots did not differ in perch diameter ($F_{2,53} = 0.5$, $P = 0.64$; Fig. 3), although juveniles used narrower perches than adults ($F_{2,226} = 4.37$, $P = 0.038$).

For males, the relative proportion of crawls differed marginally across the plots ($F_{2,43} = 2.92$, $P = 0.065$), with males in Field performing more crawls than males in Palmetto. Males did not differ in the proportions of jumps or runs, or in total movement rates. Females did not differ across plots in any measure of locomotor behavior (all $F_{2,42} < 1.8$, all $P > 0.2$). Overall, males performed more frequent locomotor movements than females ($F_{1,89} = 28.4$, $P < 0.001$).

Table 1 Comparisons of relative hindlimb and toe morphologies across green anoles in three habitats

	Slopes			Intercepts		
	d.f.	F	*P*	d.f.	F	*P*
(a) Adult males						
Hindlimb length	2, 64	4.67	0.013*			
Toe length	2, 64	3.53	0.035*			
(b) Adult females						
Hindlimb length	2, 94	0.81	0.449	2, 96	9.53	<0.001*
Toe length	2, 91	0.01	0.963	2, 93	6.34	0.003*
(c) Juveniles						
Hindlimb length	2, 39	0.43	0.653	2, 41	0.63	0.539
Toe length	2, 39	0.23	0.174	2, 41	0.12	0.885

Adult males differed in slope for both hindlimb and toe, and adult females differed in intercept for both traits. Juveniles did not differ between the habitats. Significant *P*-values are indicated with asterisks. d.f., degrees of freedom.

Discussion

In this study, adult *A. carolinensis* lizards exhibited sexually dimorphic local habitat differentiation in locomotor morphologies, and to a lesser extent, behavior. Juvenile lizards, however, appeared to be morphologically similar across habitats, suggesting that the adult differences may have arisen through the differential growth of limb elements that occurred when individuals were exposed to different perches.

Habitat-specific differentiation in morphology and behavior

Consistent with previous laboratory studies, females exhibited longer legs in plots with broader perches (Palmetto and Field) than the plot with narrower perches (Lake). The ecological relevance of this relationship is clear; lizards with longer limbs have higher sprinting speeds on broad perches, while lizards with shorter limbs are more adept in using narrow perches (e.g. Losos & Sinervo, 1989; Losos, 1990; Losos & Irschick, 1996). However, adult females did not differ in patterns of hindlimb growth across plots, suggesting that modification of long bone length likely occurred through subtle changes in relative growth rates, with effects lasting into adulthood (Sanger *et al.*, 2012). In contrast, males differed in hindlimb growth patterns among plots. Variation in the slope of the morphological traits in adult males suggests that the underlying mechanics of long bone growth are modified in the different habitats.

Toe length exhibited a similar sexual dimorphism, with adult males showing allometric growth, and adult females showing similar growth across habitats. Further, lizards of both sexes from Palmetto exhibited longer toes than those from Field (Fig. 2). These plots did not differ in perch diameters used by lizards, suggesting that toe length may be linked

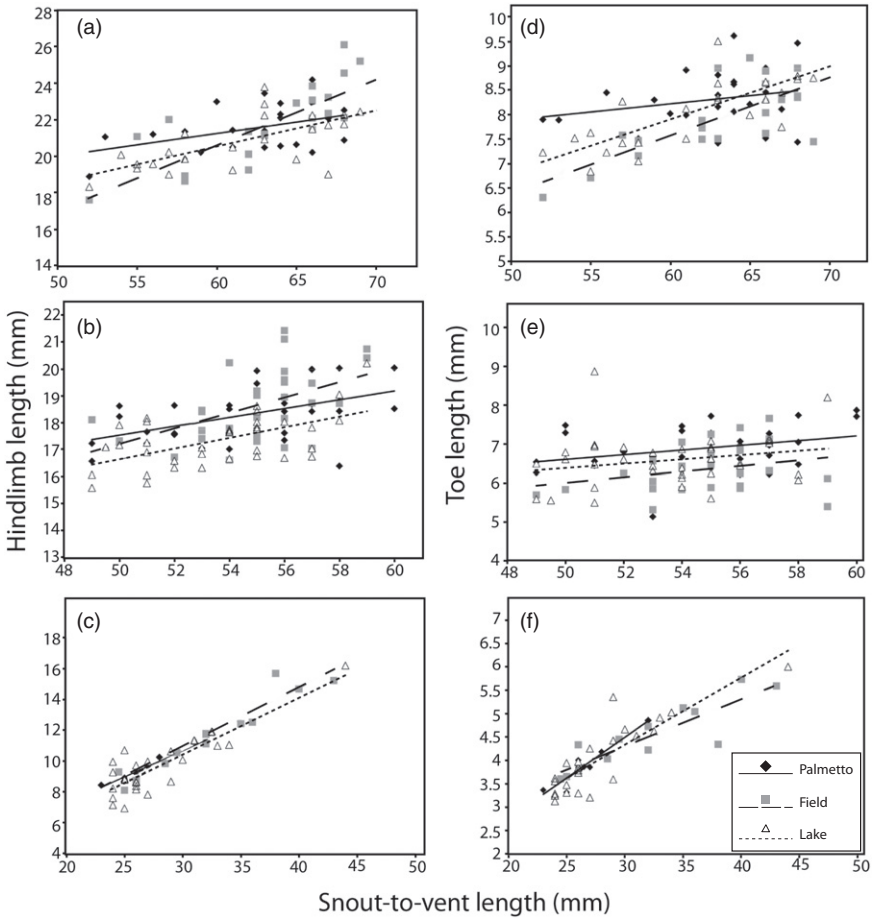

Figure 2 Relative limb morphologies for each sex/age class of green anoles *Anolis carolinensis* in the three study plots. Solid lines show the relationship between snout–vent length and hindlimb or fourth toe length in the Palmetto plot (where lizards used perches of intermediate diameter), dashed lines show relationships in the Field plot (where lizards used the broadest perches), and dotted lines show relationships in the Lake plot (where lizards used the narrowest perches). (a) Males in the three plots differ in the slope of relative hindlimb length. (b) Females in the three plots differ in the intercept of relative hindlimb length. (c) Juveniles do not differ in relative hindlimb length among the plots. (d) Males in the three plots differ in the slope of relative toe length. (e) Females in the three plots differ in the intercept of relative hindlimb length. (f) Juveniles do not differ in the relative toe length among the plots.

Table 2 Comparisons of relative hindlimb and toe morphologies in juvenile green anoles

	Slopes			Intercepts		
	d.f.	F	*P*	d.f.	F	*P*
(a) Juvenile males versus females						
Hindlimb length	1, 40	1.33	0.255	1, 41	0.63	0.433
Toe length	1, 40	0.23	0.633	1, 41	0.21	0.650
(b) Juvenile males across plots						
Hindlimb length	2, 11	0.25	0.787	2, 13	0.01	0.989
Toe length	2, 11	0.39	0.684	2, 13	0.56	0.585
(c) Juvenile females across plots						
Hindlimb length	2, 21	0.01	0.992	2, 23	0.88	0.428
Toe length	2, 21	1.00	0.383	2, 23	0.06	0.938

Male and female juveniles did not differ from each other in slope or intercept for the morphologies, and neither sex differed across the plots. d.f., degrees of freedom.

to a habitat characteristic not examined here. One possibility is perch substrate, as *A. carolinensis* using smooth perches, such as the dwarf palmetto plants common in the Palmetto plot, may need toepads with larger surface areas to maintain sufficient adhesion for locomotion (Irschick *et al.*, 1996; Zani, 2000), while anoles using primarily rough substrates may need less toepad surface area for locomotion. Although we did not measure toepad area, and we are aware of no studies that test for a relationship between these measures in anoles, it seems likely that longer toes could be associated with larger toepads.

The observed variation in adult morphology across habitats may be the result of habitat-specific natural selection (e.g. Kolbe *et al.*, 2012), phenotype-habitat matching via dispersal or intraspecific competitive exclusion, or phenotypic plasticity. We believe these data are most consistent with plasticity for three reasons. First, because the three habitats were separated by less than 1 km, it is extremely unlikely that the lizards in these habitats have evolved genetically based differences in the allometric limb growth (e.g. Sanger *et al.*, 2012). Second, genetically based differences in lizard limb morphologies across habitats can be evident even at hatching (Langkilde, 2009; Sanger *et al.*, 2012), but we saw no differences in juvenile morphology across habitats. Third, it is unlikely that dispersal to a habitat that matches a juvenile's morphology, or intraspe-

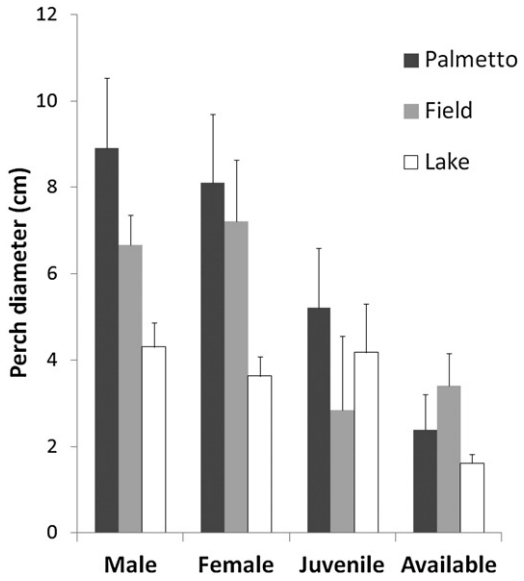

Figure 3 Average perch diameters for each age/sex class, and for available perches, in the three study plots, + 1SE (standard error). Adult male and female perches were narrower in the Lake than Palmetto plots, while juvenile perches did not differ in size among the plots. Lizards generally used broader perches than those randomly available in each plot.

cific exclusion from a habitat, are plausible explanations for the habitat differences we observed. While few studies have directly assessed anole dispersal, available data suggest that adult home ranges often overlap substantially with their juvenile home ranges (Andrews & Rand, 1983), and that high site fidelity is exhibited between breeding seasons (Calsbeek, 2009). Further, male anoles disperse significantly more frequently than females (Stamps, 1977; Andrews & Rand, 1983; Johansson, Surget-Groba & Thorpe, 2008; Calsbeek, 2009), so if dispersal for phenotype-matching were to occur in our population, we would expect more habitat-specific differentiation in males than females, when in fact our results showed the opposite pattern. Thus, our results are consistent with the hypothesis that plasticity could potentially be an important factor in habitat differentiation.

An important component of assessing variation in phenotypes is determining the developmental environments with which they are associated (Gilbert & Epel, 2008). We found that *A. carolinensis* juveniles used narrower perches than adults, but across the plots, juveniles did not differ in perch diameter or in relative hindlimb and toe lengths. In contrast, a study of *Sceloporus* lizards found that in genetically differentiated populations, hatchlings differed in relative limb length in patterns consistent with adult limb lengths (Langkilde, 2009), suggesting that the morphological differentiation in adults from the contiguous habitats in our study are the result of different developmental experiences in these habitats.

Behavior can buffer the need for a habitat-specific morphological response, or behavior and morphology may respond to habitat differences in a concerted fashion. In this study, plot differences in locomotor behaviors did not differ in association with hindlimb length for either sex, but the length of the fourth toe may be related to male locomotion. A study of hindlimb kinematics in *A. sagrei* suggested that the orientation of the foot on a narrow perch is more lateral than its medial orientation on a broader perch, causing reduced reaction force on narrow perches (Spezzano Jr & Jayne, 2004). Longer toes may potentially enhance this difference. While overall rates of locomotion did not differ across the plots, males (but not females) in the Field plot (i.e. those with shorter toes) performed a marginally higher proportion of slower, crawling movements than Palmetto males. Perhaps longer toes allow males to move more quickly in their environment (similar to the effects of longer hindlimbs), while shorter toes may constrain the speed of movements on some perches. Alternatively, shorter toes may permit greater precision in locomotion, allowing for slower movements on perches that require greater balance.

Sex-specific habitat differentiation

Our results showed a tighter association between limb length and perch diameter in females than males, consistent with results from previous work in *A. carolinensis* (Kolbe & Losos, 2005). We also found that males and females exhibited marginally different behavioral responses to structural habitat differences. Females exhibited a lower overall rate of locomotion, indicating that they were stationary on a perch for longer than males. This behavioral difference may cause female limb and toe lengths to be more influenced by the characteristics of a particular perch as they develop into adulthood. Consistent with this idea, females differed in intercepts between the plots, indicating that by the time females reach an SVL of 45 mm, they already differ in hindlimb and toe lengths. Males moved approximately twice as often as females, likely because more movement is required to defend their larger territories, and perhaps locomotor behaviors are more plastic in males because they are more ecologically important in that sex. This difference in adult locomotion may cause the differing growth patterns between the sexes, with males showing allometric growth in limb and toe lengths *during* adulthood.

The mechanism that would produce a sex-specific developmental response in limb growth is not clear. Biomechanical studies of endotherms have indicated that the stress on growing bones resulting from increased activity generally causes bones to increase in diameter and/or density, but rarely in length (reviewed in Losos *et al*., 2000). While activity stress during ontogeny may possibly produce longer bones in adult female anoles (but see Rosier & Langkilde, 2012), we found no evidence of differences in locomotor behavior in females across the three habitats. More thorough analyses of long bone growth mechanisms in this population may provide greater insight into the developmental bases of the differences observed in adults.

In conclusion, by considering the interactions of behavior and morphology – which are often studied in isolation – this work suggests that sex-specific responses to local habitat

differences may allow anoles greater refinement in habitat use, even within the same population. To our knowledge, this is one of the few studies that have documented the likely signature of phenotypic plasticity in lizards in a natural setting. Future experimental studies, such as a common garden experiment using lizards from natural habitats with distinct perch types, and detailed biomechanical analyses of locomotion on different perch types, will further test the plasticity hypotheses against other evolutionary alternatives.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Comparisons of limb morphologies and SVL in adult male, adult female, and juvenile green anoles. Significant interactions between sex/age class and SVL indicate allometry across these groups in hindlimb length (a) and length of the fourth toe (b).