



Does ecological specialization transcend scale? Habitat partitioning among individuals and species of *Anolis* lizards

Ambika Kamath^{1,2} and Jonathan B. Losos¹

¹Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

²E-mail: ambikamath@gmail.com

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Ecological specialization is common across all levels of biological organization, raising the question of whether the evolution of specialization at one scale in a taxon is linked to specialization at other scales. *Anolis* lizards have diversified repeatedly along axes of habitat use, but it remains unknown if this diversification into habitat use specialists is underlain by individual specialization. From repeated observations of individuals in a population of *Anolis sagrei* in Florida, we show that the extent of habitat use specialization among individuals is comparable to the extent of specialization in the same traits among ten sympatric *Anolis* habitat specialist species in Cuba. However, the adaptive correlations between habitat use and morphology commonly seen across species of *Anolis* were not observed across individuals in the sampled population. Our results therefore suggest that while patterns of ecological specialization can transcend scale, these parallels are the consequence of distinct ecological processes acting at microevolutionary and macroevolutionary scales.

KEY WORDS: *Anolis*, *Anolis sagrei*, anole, habitat use, individual, perch height, perch diameter, partitioning, specialization.

Ecological specialization is common across a range of scales, from individual specialists to whole clades comprised of specialist species (MacArthur 1972; Cox and Ricklefs 1977; Futuyma and Moreno 1988; Losos and de Queiroz 1997; Johnson and Steiner 2000; Araújo et al. 2011; Siefert et al. 2015). Conceptual and mathematical models have long considered whether and how resource-use specialization at one scale can influence ecological interactions and evolutionary trajectories at other scales (Roughgarden 1972; Dieckmann and Doebeli 1999; Bolnick et al. 2003, 2011; Ravnigné et al. 2009; Pfennig and Pfennig 2012; Violle et al. 2012; Gilbert et al. 2015; Hart et al. 2016). Though the specifics of these models vary, together they raise the question of whether the extent of ecological specialization is linked across scale.

At one extreme, it is possible that populations made up of individual specialists diversify into clades of specialized species (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000; Ravnigné et al. 2009), suggesting that interspecific interactions and macroevolutionary patterns are simply intraspecific interac-

tions and microevolutionary patterns “writ large” (Mayr 1942; Eldredge 1985). At the other extreme, it is possible that the degree of specialization across species in a clade is not influenced by whether these species are made up of individuals that are specialists or generalists, thereby indicating that populations’ evolutionary trajectories over macroevolutionary timescales are relatively unaffected by individuals’ ecological interactions and the population’s microevolutionary dynamics (Gould 1981). Most clades likely lie between these two extremes, with specialization transcending scale to some extent (Brooks and McLennan 1999; Bolnick et al. 2003; Gilbert et al. 2015). However, relatively few taxa are well-suited for empirical examinations of ecological specialization across a range of scales, from clades to species to populations to individuals.

A group especially well-poised for such examinations is *Anolis* lizards. Anoles have undergone repeated evolutionary diversification in the Greater Antilles, wherein ancestral species on each island have diverged into a community of species, each of

which is morphologically specialized to use a different microhabitat (Williams 1972; Losos et al. 1998). Two key traits involved in anole specialization are toepad dimensions and limb length: more arboreal anoles tend to have better developed toepads for clinging to smooth surfaces high in trees, whereas variation in limb length reflects conflicting demands for rapid movement on broad surfaces and agility on narrow surfaces (reviewed in Losos 2009). These ecomorphological correlations are also seen at the scale of populations within the same species—populations of anoles in different localities that differ in perch height or diameter also differ predictably in toepad dimensions or limb length (Schoener 1975; Lister 1976; Janssen et al. 1984; Losos et al. 2006; Stuart et al. 2014).

Because these ecomorphological relationships at the species and population levels are adaptive, it is plausible that similar adaptive habitat specialization is also present across individuals within a population. Indeed, mechanisms of diversification that begin with individual specialization in habitat use have been proposed to explain the *Anolis* adaptive radiation (Doebeli and Dieckmann 2000; Shaw et al. 2000; Thomas et al. 2003). However, it remains unknown if individual anoles do actually specialize in habitat use and whether individuals' habitat use is correlated with their morphology, as it is at the among-population and among-species levels.

In this study, we quantify the extent of individual specialization in habitat use in a population of *Anolis sagrei*, from repeated observations of marked individuals over a six-week period. We compare the degree of specialization between individuals in this population to the degree of habitat use specialization among ten sympatric Greater Antillean *Anolis* species, to assess if ecological specialization is similar at different scales. We also examine if variation in habitat use across individuals in the sampled population of *A. sagrei* is a consequence of variation in habitat availability. Finally, we test if individual habitat use is associated with morphology. Specifically, we predict that correlations between habitat use and morphology across individuals within a population will be similar to the well-established adaptive ecomorphological correlations (between perch height and toepad dimensions and between perch diameter and limb length) seen across populations and species of anoles (Williams 1972; Schoener 1975; Lister 1976; Janssen et al. 1984; Losos et al. 1998, 2006; Stuart et al. 2014).

Methods

STUDY SPECIES

Anolis sagrei, the brown anole, is native to Cuba and the Bahamas, but has been established in Florida for over 70 years (Collette 1961; Kolbe et al. 2004) and has spread northward to South Carolina and has also dispersed to Louisiana and Texas

since its introduction. A member of the “trunk-ground” habitat specialist type or “ecomorph,” *A. sagrei* perches at low heights and on broad surfaces, and consequently has longer limbs and smaller toepads with fewer lamellae, compared to other habitat specialist types (reviewed in Losos 2009). Throughout most of its range in the United States, *A. sagrei* co-occurs with the native trunk-crown species *Anolis carolinensis*; this was true in our sampled population as well, though densities of *A. carolinensis* were low (pers. obs.).

FIELD DATA COLLECTION

Anolis sagrei lizards were observed in a forested area in Possum Creek Skate Park in Gainesville, FL (29.70209°N, 82.38125°W) from 12th June to 1st August, 2014. We surveyed an area of about 1300 m² between 0800 and 1700 hours almost daily, and recorded all locations at which lizards were observed. We also measured the height at which each lizard was observed, and the diameter of the perch on which it was seen. Lizards were caught at the first observation, at which time we measured their snout vent length (SVL) as an estimate of body size and tagged them with unique bead tags for individual identification (Fisher and Muth 1989). Lizards were released at their initial location within 24 hours of capture. A total of 31 males and 49 females were marked. In subsequent surveys, marked lizards were identified from a distance by their tags; their location, perch height, and perch diameter were recorded. Observations of the same individual were separated by at least 60 minutes.

At the end of the survey period, we recaptured 18 male and 20 female lizards to remeasure SVL as well as measure the total length of both forelimbs and hindlimbs, using calipers. All caliper measurements were made by one person (A.K.). We imaged the lizards' toepads on a flatbed digital scanner to measure toepad area and count the number of lamellae on the toepad of the longest toe on each foot using ImageJ (third toe of the forelimb, fourth toe of the hindlimb; Schneider et al. 2012). Toepad area and lamella number on both right and left hindlimbs were measured independently by two people (R.M. and C.P.) and the four values were averaged for analysis. Right and left measurements were averaged for limb length, toepad area, and lamella number on the forelimbs, as well as hindlimb length. We then took the mean of forelimb and hindlimb measurements, yielding one value per individual for limb length, toepad area, and lamella number (results were similar for forelimbs and hindlimbs considered separately, and are not shown here).

To assess the habitat available to individual lizards, we quantified perch diameters in the vicinity of 158 locations of the 38 recaptured lizards (6.1 ± 2.6 locations per lizard; multiple lizards were often seen at a single location). Specifically, we randomly picked three of the locations at which each recaptured lizard was seen during the survey period (except one individual that was seen

Table 1. Tests to compare the proportional similarity (PSi) of distributions of Perch Height (PH) and Perch Diameter (PD) in the sampled population of *A. sagrei*.

Test	Distribution A	Distribution B	PSi (mean \pm SD)
I	Individual used PH	All used PH	0.62 \pm 0.17
II	Individual used PD	All used PD	0.61 \pm 0.16
III	Species used PH	All species used PH	0.69 \pm 0.21
IV	Species used PD	All species used PD	0.72 \pm 0.14
V	Habitat specialist type used PH	All habitat specialists used PH	0.62 \pm 0.22
VI	Habitat specialist type used PD	All habitat specialists used PD	0.68 \pm 0.14
VII	Individual available PD	All available PD	0.94 \pm 0.04
VIII	Individual used PD	Individual available PD	0.25 \pm 0.11

Values of PSi closer to 1 indicate higher similarity between the distributions being compared. *P*-values, which indicate if the similarity between Distributions A and B is significantly different than the similarity of Distribution B to random samples drawn from Distribution B, were all < 0.001.

only at two locations). We then counted the perches within a 50 cm radius of the flagged location at three heights: 25, 100, and 125 cm. Perches were categorized into the following five classes based on their diameters: 0–1 cm, 1–5 cm, 5–10 cm, 10–20 cm, > 20 cm. Perches included all stems, branches, and trunks. We limited our counts at a single location and height to a maximum of 30 perches per diameter class; this limit was reached in only 2% of the 2370 location \times height \times diameter classes in which perches were counted. Additionally, we incorporated the ground as one available perch in the >20 cm category for each location. For each individual, we calculated a distribution of perch diameters available to that lizard by summing the number of perches in each diameter category across heights and locations. Availability of perch heights was not quantified as we thought it unlikely to vary across individuals, and thus unlikely to influence individual specialization in habitat use; most trees in the sampled site were much taller than 5 m, whereas the maximum observed perch height in the population was 4.55 m.

STATISTICAL ANALYSES: INDIVIDUAL AND SPECIES SPECIALIZATION

All statistical analyses were performed in R v. 3.2.2 (R Core Team 2015). First, we examined if individuals specialize in perching at particular heights. Specifically, we calculated the mean proportional similarity (mean PSi, also referred to as IS, an index of individual specialization) between individual and population distributions, to ask if distributions of perch heights used by each individual are similar to the distribution of perch heights used by all individuals (Test I in Table 1; Bolnick et al. 2002). We used the *PSi* function in the *RInSp* package (Zaccarelli et al. 2013), which also calculates a *P*-value by randomly sampling individual distributions from the population distribution. Values of PSi closer to 1 indicate high overlap between the two distributions being considered and, in this case, demonstrate low individual specialization. In contrast, lower values of PSi indicate lower overlap

Table 2. Species sampled by Rodríguez-Schettino et al. (2010), with their habitat specialist type categorizations, used here to calculate the degree of specialization in habitat use among sympatric *Anolis*.

Species	Habitat specialist type
<i>Anolis allogus</i>	Trunk ground
<i>Anolis alutaceus</i>	Grass bush
<i>Anolis angusticeps</i>	Twig
<i>Anolis homolechis</i>	Trunk ground
<i>Anolis loysianus</i>	Trunk
<i>Anolis luteogularis</i>	Crown giant
<i>Anolis mestrei</i>	Trunk ground
<i>Anolis porcatus</i>	Trunk crown
<i>Anolis sagrei</i>	Trunk ground
<i>Anolis vermiculatus</i>	Aquatic

between distributions and, in this case, demonstrate higher individual specialization. To calculate distributions, we classified observations of perch height into five classes (0–50 cm, 50–100 cm, 100–150 cm, 150–200 cm, >200 cm). We similarly calculated individual specialization in perch diameter (Test II in Table 1), with observations classified into diameter categories as above.

Using data from Rodríguez-Schettino et al. (2010), we calculated the mean PSi for 10 sympatric *Anolis* species from Soroa, Cuba, to ask if distributions of perch heights used by each species are similar to the distribution of perch heights used by the whole community of species (Test III in Table 1). Because four of the 10 species belonged to the trunk-ground habitat specialist type (Table 2) and are expected to show similar habitat use, we repeated the mean PSi calculations after grouping perch height distributions by habitat specialist type instead of species (Test V in Table 1). Specialization in perch diameter was calculated similarly for species and for habitat specialist type (Tests IV and VI in Table 1).

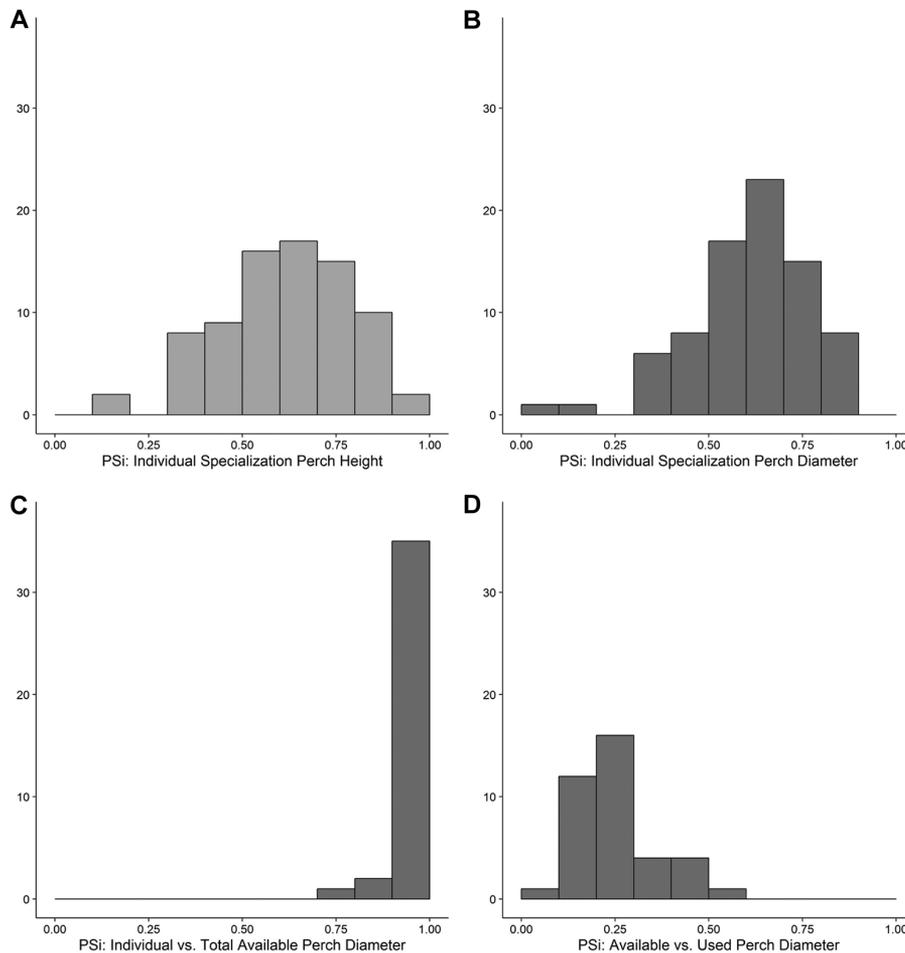


Figure 1. Distributions of proportional similarity (PSi) indicating (A) individual specialization in perch height and (B) perch diameter; (C) high similarity between the distributions of perch diameters available to each individual and the total distribution of available perch diameters; and (D) low similarity between perch diameters available to and the perch diameters used by each individual.

STATISTICAL ANALYSES: HABITAT AVAILABILITY

We divided our investigation of whether individual variation in perch diameter was a consequence of habitat availability into three parts. First, we assessed the proportional similarity between the distributions of perch diameters available in the vicinity of each individual's locations and the common distribution of available perch diameters across all individuals (Test VII in Table 1). Here, a mean PSi value closer to 1 would indicate that similar distributions of perch diameters are available to all individuals. Next, we calculated the proportional similarity between the distribution of perches available to an individual and the distribution of perch diameters used by that individual (Test VIII in Table 1). Here, a mean PSi value close to 1 would indicate that individuals tend to use perches of certain diameters in proportion to their availability. For the latter comparison, we simulated a distribution of mean PSi values under the criterion that individuals sampled from their available perches at random, to calculate a *P*-value for the comparison. Third, we used a chi-square test to compare the proportion

of perches in each diameter category between all available and all used perches.

STATISTICAL ANALYSES: ECOMORPHOLOGICAL CORRELATIONS

To account for variation in habitat use with body size (Schoener 1968; Jenssen et al. 1998), we first assessed the relationship between mean perch height and SVL, and mean perch diameter and SVL using linear models, weighted by the number of observations for each individual. Because female anoles both perch lower than males and are smaller than males (Schoener 1968; Perry 1996), we also split the dataset by sex and examined the correlation for males and females separately. Regressions of habitat variables against SVL were conducted for all sampled individuals, as we measured SVL when they were first captured.

We then used linear models to assess if individual morphology was related to individual habitat use. In particular, we examined if mean perch height was positively correlated with toepad

area or lamella number, and if mean perch diameter was positively correlated with limb length, in concordance with the patterns of ecomorphological variation seen across species and populations of anoles (reviewed in Losos 2009). Each linear model included SVL as a covariate to account for variation in body size, and was weighted by the number of observations for each individual. All morphological variables were log transformed.

Results

INDIVIDUAL SPECIALIZATION

Lizards were observed between one and 46 times (mean \pm SD: 12.6 ± 11.2 observations). Individuals in this population were specialized in both perch height and diameter, as indicated by the indices of specialization for both perch height (Fig. 1A; Test I in Table 1) and perch diameter (Fig. 1B; Test II in Table 1). This specialization implies that different individuals used perches of particular heights and diameters in different proportions. The degree of specialization in habitat use between 10 species (Tests III and IV in Table 1) and seven types of habitat specialists (Tests V and VI in Table 1) of sympatric anoles from Soroa, Cuba, was comparable to the degree of specialization between individuals in the sampled population (Fig. 2).

HABITAT AVAILABILITY

Individual specialization in perch diameter was not determined by available habitat, as the distributions of perch diameters available to each individual were very similar to the distribution of perch diameters available across all individuals in this population (though not identical; Fig. 1C; Test VII in Table 1). Moreover, the distributions of perch diameters used by individuals was different than the distribution of perch diameters available to that individual, suggesting that, with respect to diameter, individuals do not use perches in proportion to their availability (Fig. 1D; Test VIII in Table 1). The distributions of diameters of all available and all used perches were different from one another ($\chi^2_4 = 2667$, $P < 0.001$), with lizards primarily avoiding the narrowest perches (Fig. 3; results [not shown] were similar when excluding the narrowest perch diameter category).

ECOMORPHOLOGICAL CORRELATIONS

Variation in habitat use across individuals was partly related to body size: mean perch height, but not mean perch diameter, was positively correlated with SVL (perch height: $\beta \pm$ SE = 201 ± 31 , $t_{78} = 6.6$, $P < 0.001$; perch diameter: $\beta \pm$ SE = 4 ± 4 , $t_{73} = 1.06$, $P = 0.29$). Splitting the dataset by sex, we found that mean perch height and SVL were positively correlated for males ($\beta \pm$ SE = 484 ± 117 , $t_{29} = 4.1$, $P < 0.001$), but not for females ($\beta \pm$ SE = 147 ± 121 , $t_{47} = 1.2$, $P = 0.23$).

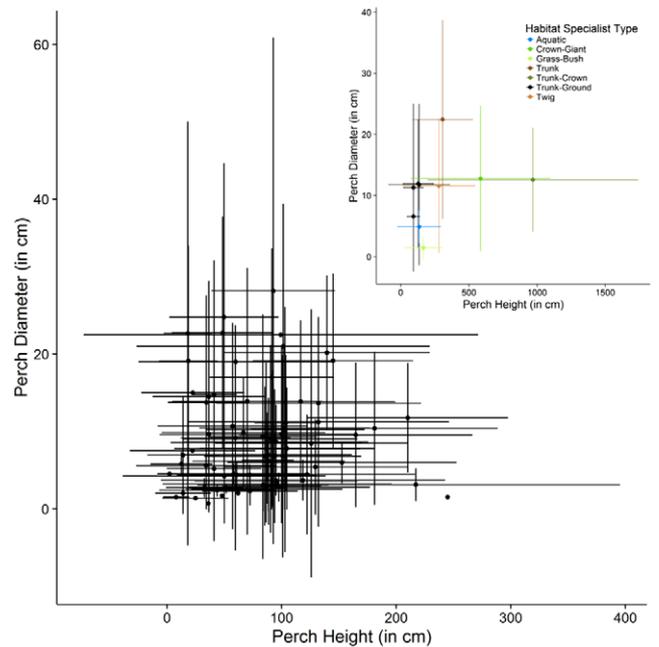


Figure 2. Mean \pm SD of perch height and diameter for individuals of *A. sagrei* from a population in Gainesville FL, and (inset) sympatric species of Greater Antillean anoles (data from Rodríguez-Schettino et al. (2010)). Note that the scales of the two graphs are different, indicating differences in the total breadth of habitat used in the two contexts. Mean Ψ_i (\pm SD) for perch height and perch diameter respectively were 0.62 ± 0.17 and 0.61 ± 0.16 for individuals, and 0.69 ± 0.21 and 0.72 ± 0.14 for species (see text, Table 1 for details). [Color figure can be viewed at wileyonlinelibrary.com]

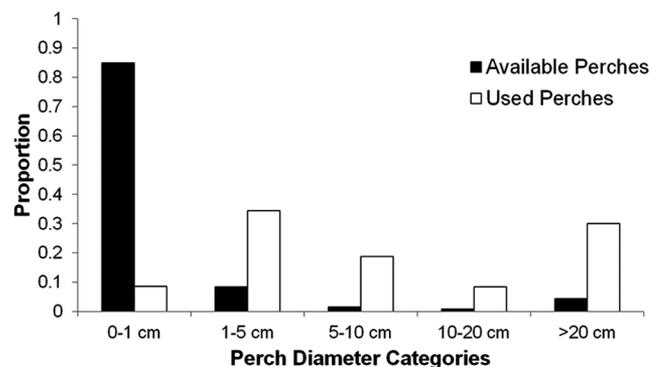


Figure 3. Comparison of the diameters of available and used perches in the sampled population of *A. sagrei*.

However, after accounting for body size, none of our predictions for relationships between habitat variables and morphological variables were met. Mean perch height was not positively correlated with toepad area ($\beta \pm$ SE = -91 ± 48 , $t_{35} = -1.9$, $P_{\text{one-tailed}} = 0.97$) or lamella number ($\beta \pm$ SE = -48 ± 109 , $t_{35} = -0.4$, $P_{\text{one-tailed}} = 0.67$), and mean perch diameter was not positively correlated with limb length ($\beta \pm$ SE = -13 ± 23 ,

$t_{35} = -0.6$, $P_{\text{one-tailed}} = 0.72$). Relationships were similar (results not shown) between the residuals from a regression of habitat variables against SVL and the residuals from a regression of morphological variables against SVL.

Discussion

Ecological specialization is widespread across taxonomic scales, from clades of specialist species to specialized individuals within populations. Parallels in ecological specialization across scales can suggest whether microevolutionary forces determine macroevolutionary patterns (Dieckmann and Doebeli 1999; Doebeli and Dieckman 2000; Ravigné et al. 2009; Bolnick et al. 2003, Gilbert et al. 2015). With their well-documented specialization in habitat use across species and populations, *Anolis* lizards are well-suited to test if macroevolutionary patterns of ecological specialization are paralleled at the microevolutionary scale of individuals within a population.

We found that individuals in a population of *A. sagrei* were specialized in their habitat use, specifically in both the height and the diameter of the surfaces on which they perched. The degree of specialization of individuals in this population was comparable to the degree of specialization of ten sympatric species of *Anolis*, along the same axes of habitat use. In other words, habitat use was partitioned to a similar extent by individuals in a population of *A. sagrei* as by sympatric species of *Anolis*. Thus, anoles can be equally specialized whether considering individuals within a population or species within a community—ecological specialization in *Anolis* can transcend scale.

Habitat specialist species in the *Anolis* adaptive radiation also differ consistently in morphology, presumably as a result of adaptation to using different parts of the environment (reviewed in Losos 2009). If both within- and between-species specialization in habitat use that we observed are driven by the same adaptive processes, then we would expect the morphological relationships to also be parallel across scales. Theoretical work suggests a reason to expect such a parallel. Mechanisms of ecologically mediated sympatric speciation suggest that interspecific adaptive divergence arises out of within-population processes that drive an initially homogeneous population to diverge in situ as a result of disruptive selection, eventually becoming distinct species (Dieckmann and Doebeli 1999; Ravigné et al. 2009; reviewed in Via 2001). Critically, these theories posit the development of an intrapopulation link between individual habitat choice and phenotype as an important stage in this process (Via 2001; Bolnick et al. 2003). Repeated cycles of this process of disruptive selection on habitat use followed by speciation have been proposed to explain the *Anolis* adaptive radiation (Doebeli and Dieckmann 2000; Shaw et al. 2000; Thomas et al. 2003).

However, the adaptive correlations between habitat use and morphology that are common across populations and species of *Anolis* lizards were not observed across individuals within the sampled population of *A. sagrei*. Our results therefore do not support the model of disruptive selection leading to sympatric speciation as a path to adaptive diversification in *Anolis*. This conclusion is in accord with biogeographical evidence that suggests that sympatric speciation is not common in anoles (Losos 2009).

If the correlations among *Anolis* species between habitat and morphology are adaptive, why do we not see similar correlations, albeit at a reduced scale, among individuals within a single population? One possibility is that the variation in morphology across individuals in the sampled population was too low to result in differences in performance that are visible to selection. However, the variation we observed was comparable to that seen in studies documenting correlated shifts in habitat and morphology between populations of anoles (e.g., coefficient of variation for lamellae number in this study vs Stuart et al. [2014]: 0.099 vs 0.050). A second possibility is that our study was underpowered. However, our sampling appears sufficient to detect correlations comparable to those seen between habitat and morphology across populations (e.g., power analyses showed that we could detect correlations as low as $r^2 = 0.29$ with 95% power; in comparison, the correlation between mean lamellae number and perch height across populations in Stuart et al. [2014] had $r^2 = 0.37$). A third possibility is that differences among individuals in habitat use are entirely a consequence of variation in the habitat available to each individual, with little opportunity for individuals to choose preferred perches. However, we found that the distributions of available perch diameters were similar across locations inhabited by different individuals in the sampled *A. sagrei* population. Moreover, individuals did not use perches of different diameters in the proportion that they were available (see Rodriguez-Robles et al. 2005 for similar results across individuals in *Anolis gundlachi*). These results indicate that substantial interindividual variation exists in both morphology and habitat use, but this variation is not linked: individuals do not choose to use the habitats to which they are presumably best adapted according to morphology. In contrast, at the interspecific level, habitat choice is evident among sympatric species, with different species using habitat appropriate for their morphology (Irschick and Losos 1999; Johnson et al. 2006; these studies also reveal substantial intraspecific variation in habitat use, in agreement with our study).

Why such habitat selection behavior has not evolved at the individual level is an unanswered question. It is possible that the admixed genetic background of populations in the invasive range of *A. sagrei* (Kolbe et al. 2004, 2008) may have broken up adaptive genetic correlations between habitat use behavior and morphology, and that sufficient time has not passed since the invasion of

A. sagrei into Florida for these correlations to reform; similar studies in other populations of *A. sagrei* as well as other anole species could examine this possibility. In the absence of adaptive habitat use behavior, however, coupled disruptive selection cannot act on habitat use and morphology within populations, and thus cannot lead to sympatric speciation and adaptive radiation.

One potential mechanism that could partially explain the observed individual specialization in habitat use is suggested by the relationship we observed between perch height and body size in male, but not female, *A. sagrei*. This result suggests that intraspecific social interactions, specifically social conflict between males, may shape daily perch use choices. Perching higher than one's competitors is known to be important to male anoles in several social contexts—male anoles display from higher perches compared to their average perch use (Andrews 1971; Kamath et al. 2013), and the male that perches relatively higher than its rival during an agonistic encounter is more likely to win that encounter (Tokarz 1985). Body size is also known to influence the outcome of male–male agonistic interactions—large males win fights against small males (e.g., Tokarz 1985; Jenssen et al. 2005). Thus, the increase in perch height with body size in male *A. sagrei* may derive from larger males winning agonistic encounters and obtaining access to higher perches from which to display, in turn preventing smaller, competitively inferior, males from occupying high perches. But smaller individuals could gain access to higher perches as they grow older and larger, thereby becoming more likely to win agonistic interactions.

Though the relationship between male body size and perch height does not necessarily preclude the existence of other adaptive ecomorphological relationships, it may be that an individual's fitness via reproductive success depends more on the former than its fitness via survival depends on the latter. Thus, adaptive social behavior may act to impede the evolution of adaptive ecomorphological relationships within populations (Huey et al. 2003). Moreover, if the association between body size and perch height in male *A. sagrei* is largely due to ontogenetic change, it will have few direct consequences for the evolution of habitat use specialization at higher taxonomic levels (Lister 1976). Of course life-history traits with a genetic basis, such as those that influence growth rates, may consequently be subject to selection.

While the degree of specialization we observed was similar between individuals and species, the total extent of habitat used is different between the population of *A. sagrei* and the community of *Anolis*. In particular, a broader range of perch heights were used by ten species (and seven habitat specialist types) of anoles than by individuals in the sampled population of *A. sagrei* (Fig. 2). On one hand, this consideration points to the utility of metrics of specialization for facilitating comparisons across different ecological situations, including different taxa and resources (Bolnick et al. 2002, 2003; Araújo et al. 2011; Dall et al. 2012).

On the other hand, we run the risk of losing sight of the ecological relevance of such disparate comparisons. In particular, our results do not mean that an individual in a population of *A. sagrei*, a trunk-ground anole, is likely to have similar perch use to an individual belonging to a trunk-crown species, for example. Rather, they imply that individuals in a population of *A. sagrei* can be as nonoverlapping in their habitat use as sympatric *Anolis* species, even those belonging to different habitat specialist types. Similar studies conducted on multiple populations and in different species, especially across varying competition and predation regimes, will reveal the extent to which the degree of ecological specialization transcends both scale and ecological conditions. Such studies will shed light on how microevolutionary processes drive macroevolutionary patterns of diversification via ecological interactions.

In sum, our results suggest that while ecological specialization itself can be similar across scales in *Anolis* lizards, the morphological correlates, and thus the underlying causes, of this specialization, may differ between the within-population scale and the between-species scales. The transitions between microevolutionary processes and macroevolutionary patterns in *Anolis* therefore may not be seamless; understanding these transitions will require integrating an understanding of both ecological and social selective pressures on individuals within populations and forecasting the consequences of these pressures for population and species evolution.

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A.K. and J.B.L. designed the study, A.K. collected data and performed analyses, J.B.L. provided access to previously published data, A.K. and J.B.L. wrote the manuscript.

DATA ARCHIVING

Data are archived at 10.5061/dryad.9vk07.

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