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Little evidence for size-structured habitat use in a diverse *Anolis* community

Introduction

The partitioning of structural microhabitat among *Anolis* lizards is a well-studied phenomenon, with replicate patterns observable across independent island radiations (Losos 2011). Though a substantial body of literature describes the predictable nature of habitat partitioning *between* species, fewer studies have investigated how partitioning *within* species (and within sexes) may also be consistent among species.

One theory of intraspecific habitat partitioning is that patterns of habitat use may be driven by body size (Werner & Gilliam 1984), as optimal habitat may be preferentially used by larger individuals most capable of winning agonistic interactions. In anoles, complex behavioral intraspecific interactions are characterized by dewlap displays, lateral body presses (head bobs and push ups), which can escalate to aggressive physical confrontations, particularly among males (Johnson et al. 2010, Losos 2011). Body size correlates positively with success in agonistic interactions, in other words social dominance increases with body size (Tokarz 1985), which suggests that larger lizards should use perches which are most preferential. This is known as the size-structured habitat use (SSHU) hypothesis, and evidence for it has been found in some anole studies (Tokarz 1985, Jenssen et al. 1998, Kamath and Losos 2017). It is possible that intraspecific size-structured habitat use may be the underlying mechanism driving interspecific divergence in perch use, if intraspecific relationships exist to different perch optima. Therefore, testing the SSHU hypothesis may be incredibly important in identifying the mechanisms that underlie interspecific habitat partitioning and community structure.

In this study, we test the SSHU hypothesis in anoles by examining perch height and diameter use among four different species of the anole community of Fairchild Tropical Botanic Gardens, Miami FL USA. We tested two specific hypotheses; (i) anoles of different ecomorphs used different portions of the structural habitat, and (ii) that a relationship exists between perch use and body size in each species.

Methods

Fairchild Tropical Botanical Garden (FTBG) is located in Miami FL USA (25.403°N, 80.163°W, WGS 84; < 1 m elev.), and hosts a diverse, lizard assemblage, which includes 5 species of native and non-native anoles: *Anolis carolinensis* (native), *A. cristatellus* (Puerto Rico), *A. distichus* (Hispaniola), *A. equestris* (Cuba), and *A. sagrei* (Cuba and the Bahamas). We examined SSHU for all anole species present in the FTBG assemblage with the exception of *Anolis equestris* because of low efficacy in matching body size to perch use; *A. equestris* are large and highly arboreal, meaning that while perch use data may be empirically collected, it can be difficult to accurately estimate body size from a far distance. *Anolis carolinensis* are trunk-crown ecomorphs, primarily utilizing the upper portions of tree trunks and canopy branches. *Anolis cristatellus* and *A. sagrei* are both trunk-ground ecomorphs, primarily using the lower portions of tree trunks for perching and display, while actively foraging on the ground. *Anolis distichus* are trunk specialists, utilizing the full strata of broad perches – primarily trunks of palm trees (especially palm, such as *Roystonea* sp.).

Data collection was conducted opportunistically from 12/12/14 to 22/10/15, between 0800h – 1600h. Lizards were found by walking paths in FTBG while visually scanning all trees and vegetation from ground level to approximately 6 meters above the ground. On observation, lizards were quickly identified to species-level, and perch data were recorded empirically. Data were only collected for adult male lizards, and only on those individuals whereby perch use could be determined from distance, prior to any effect from the observer. Perch height was determined as the direct vertical distance from the mid-point of the perching lizard to the ground, while perch diameter was the width of the perching substrate. All perch use data were recorded empirically using a metric tape measure, although the diameter of perches of lizards observed at >2.5m in height were estimated.

After recording perch height and width, lizards were captured using a 10ft Cabela's telescopic fishing pole with a dental floss noose at the end. Snout vent length was measured for each individual using 15cm digital calipers accurate to 0.01 mm (Neiko 01407A) by measuring from the anterior tip of the snout to the cloaca. Data were log transformed. Single factor analysis of variance (ANOVA) was used to assess differences in body size (SVL) among the different anole species, and differences in perch use (both perch height and perch diameter). We tested for differences in perch height and perch width independently, significant ANOVAs being followed by Student's t-tests. We performed linear regressions, with perch height and perch diameter being the response variable against snout-vent length to investigate SSHU relationships.

Results

We recorded perch use data of 330 lizards during the course of our sampling. In general, structural habitat use was consistent among species as expected under the ecomorph hypothesis, such that Trunk-Ground species (*A. sagrei* and *A. cristatellus*) perched lowest, Trunk species (*A. distichus*) perched at an intermediate height on very broad perches (e.g. tree trunks), and Trunk-Crown species (*A. carolinensis*) most frequently used high, thin perches (Table 1).

We found significant difference in body size among the four anoles assessed in this community (ANOVA, $p < 0.0001$); *A. cristatellus* were generally the largest followed by *A. carolinensis*, *A. sagrei*, and *A. distichus* (Table 1). We also found significant differences in both perch height (ANOVA, $p < 0.0001$), and perch diameter (ANOVA, $p < 0.0001$) among species. *Anolis cristatellus* and *A. sagrei* did not differ significantly in perch height ($p = 0.341$), nor did *A. carolinensis* and *A. distichus* ($p = 0.729$). *Anolis cristatellus* and *A. sagrei* perched significantly lower than *A. carolinensis* and *A. distichus* ($p < 0.0001$ for all comparisons) (Table 1). Only *A. distichus* differed significantly in perch diameter ($p < 0.0001$ for all comparisons), occupying significantly wider perches than the other three species (Table 1); removal of *A. distichus* showed no significant difference in perch diameter among the three remaining anoles (ANOVA, $p = 0.366$) (Table 1).

Table 1. Size-structured habitat use (SSHU) for four species of anole coexisting in the same community at Fairchild Tropical Botanic Gardens in Miami FL. All quantative data are means ± 1 S.E. Ecomorph categories follow each species name in parentheses as follows: TG, "*trunk-ground*", T, "*trunk*", TC, "*trunk-crown*". Significant relationships at α = 0.05 are presented in bold and at α = 0.1 in italic.

Species	***N***	**SVL (mm)**	**Perch height (cm)**	**R^2**	***P* value**	**Perch diameter (cm)**	**R^2**	***P* value**
A. sagrei (TG)	72	58.4 ± 0.30	107.8 ± 8.30	0.001	0.742	14.4 ± 1.52	0.001	0.850
A. cristatellus (TG)	81	66.7 ± 0.36	110.5 ± 5.26	*0.036*	*0.091*	16.8 ± 1.86	0.004	0.568
A. distichus (T)	89	49.1 ± 0.38	193.0 ± 11.14	0.022	0.183	33.9 ± 3.12	0.001	0.819
A. carolinensis (TC)	88	62.5 ± 0.52	194.1 ± 9.52	0.000	0.885	15.3 ± 2.51	**0.069**	**0.015**

We found no evidence in support of SSHU in any of the species examined in this study in either perch height (Fig. 1) or perch diameter (Fig. 2), with all R^2 values explaining less than 5% of variation (Table 1), with the exception of a significant positive SSHU relationship in *A. carolinensis* for perch diameter ($p = 0.015$). Incidentally, there is also a negative SSHU relationship of *A. cristatellus* in perch height ($p = 0.091$).

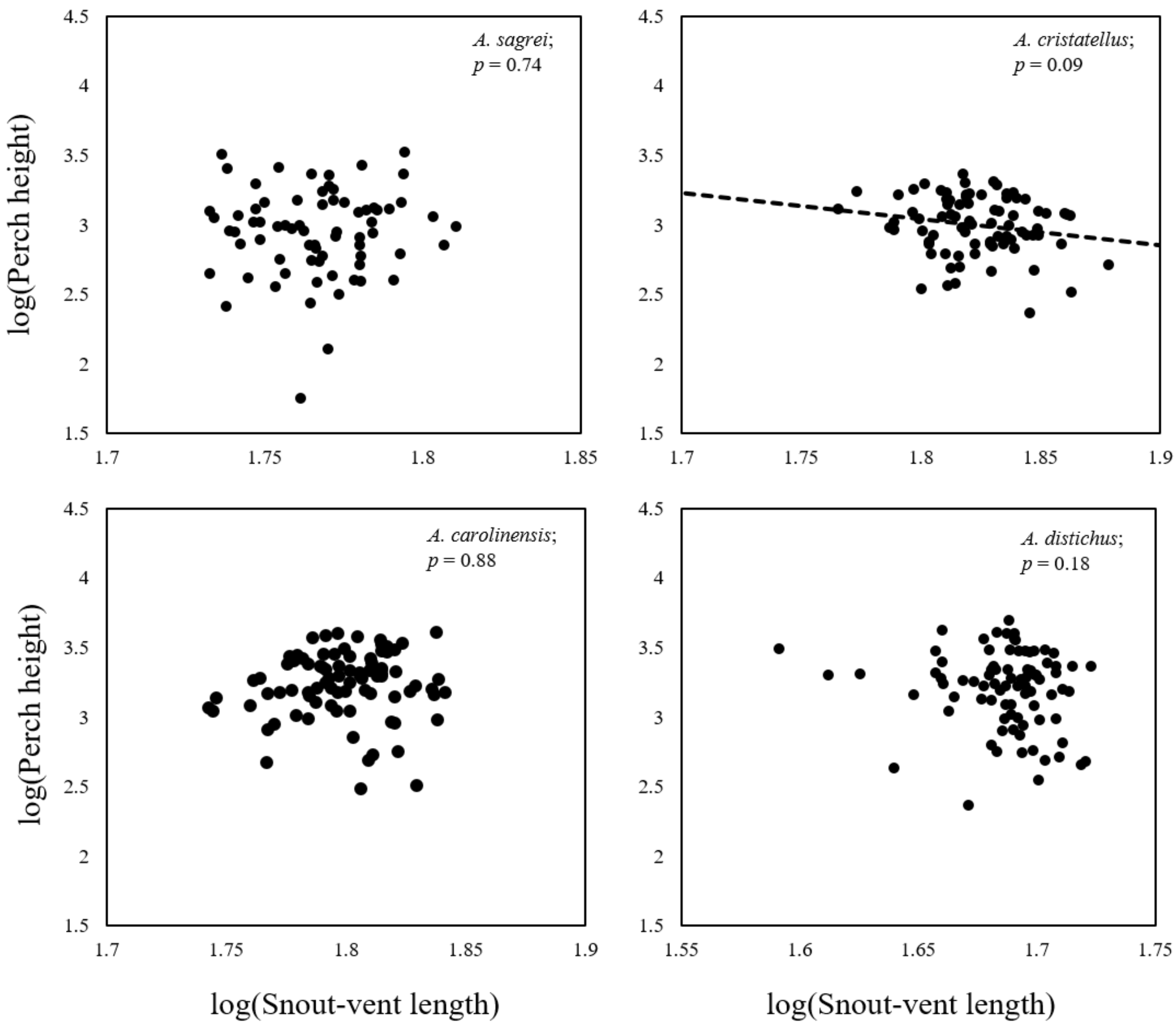

Figure 1. The Size Structured Habitat Use (SSHU) relationship between body size (snout-vent length) and perch height for four species of *Anolis* lizard in Fairchild Tropical Botanic Gardens, Miami FL. Solid lines represents significance at $\alpha = 0.05$, while dashed lines at $\alpha = 0.1$. Note that the x-axis scale of *A. distichus* is not the same as the other species due to a relatively smaller body size.

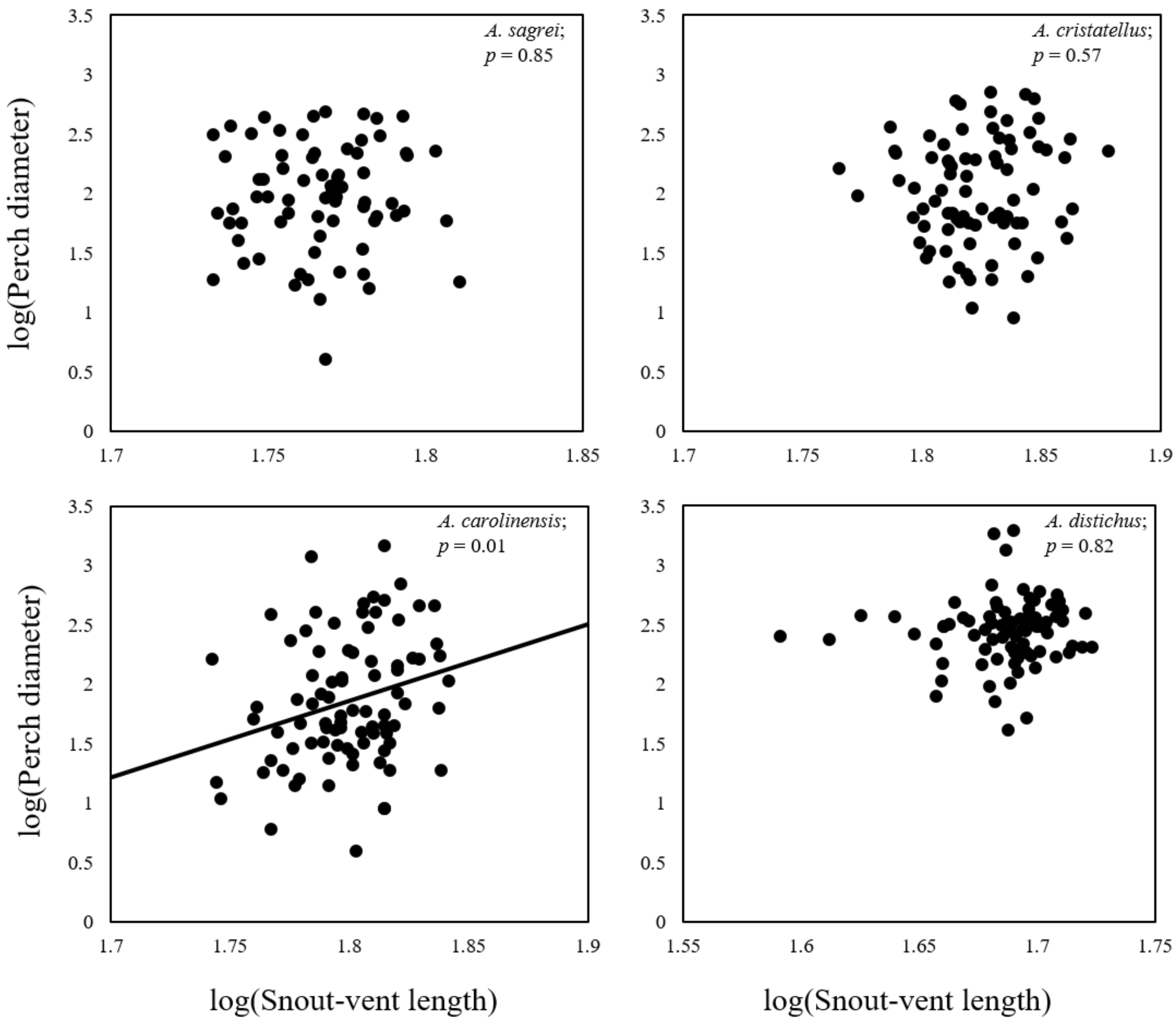

Figure 2. The SSHU relationship between body size (snout-vent length) and perch diameter for four species of *Anolis* lizard in Fairchild Tropical Botanic Gardens, Miami FL. Solid lines represents significance at α = 0.05, while dashed lines at α = 0.1. Note that the x-axis scale of *A. distichus* is not the same as the other species due to a relatively smaller body size.

Discussion

This study provides little support for the hypothesis of size-structure habitat use (SSHU) in an assemblage of anoles in Miami FL. *Anolis carolinensis* was the only species that demonstrated any significant SSHU relationship; a positive correlation between body size and perch diameter. However, the percent of variation explained by this relationship is extremely low (R^2 = 0.069; Table 1), and so, despite being statistically significant, may have little bearing in describing any ecologically relevant patterns. Similarly, a negative relationship between perch height and body size exists for *A. cristatellus,* although this also explained a low proportion of the variation (R^2 = 0.036; Table 1). These results suggest that either habitat use is not partitioned within species by the size of individuals in this community, or that perhaps perches are so abundant that intraspecific interactions for perches are not strong enough to drive a pattern of usage. In other words, perches are not so limiting that interactions have driven a size-structured pattern of usage. Alternatively, perch preference may instead be highly idiosyncratic to individuals and not a conserved behavior throughout the population. In this way, a preferential perch for one large lizard may not have the same characteristics as a preferred perch of another. This inter-individual variation, sometimes called individual specialization, has received relatively little attention so far in the anole literature (but see Kamath & Losos 2017). Further studies would benefit from exploring variation in perch use of focal individuals to tease apart this alternative hypothesis.

It is also possible that, in this anole community, perch height and diameter may not be the ecological axes which best reflect the perceived habitat quality which an individual is inhabiting. For example, future studies would benefit from examining whether a relationship exists with body size and other environmental qualities of microhabitats, such as thermal microsite characteristics or prey abundance and diversity. This may be especially important for *A. cristatellus* which generally occupy shaded microhabitats in Miami FL, such that it can be accurately used to predict the species distribution at the landscape scale (Kolbe et al. 2016). In this situation it is possible that more dominant (i.e. larger) males may drive smaller males to occupy habitats with less desirable thermal profiles, providing an alternative axis for which SSHU to operate. Similarly, for trunk-crown species such as *A. carolinensis*, variation in crown structure between different tree species may be a more important predictor of habitat quality than perch height or diameter. Variations in tree canopies may be especially pronounced in botanical gardens, such as in Fairchild Gardens (which has approx. 2,400 species), given the artificially high ecological and taxonomic diversity of tree species in the collection.

Future studies of SSHU may also benefit from examining natural anole assemblages, as it is possible the dynamics involved in this novel assemblage of primarily introduced non-native species may not be reflective of patterns occurring in the natural range of these species. It would also be beneficial to consider the SSHU hypothesis in other non-natural settings. For example, many anoles in urban environments utilize artificial perches (e.g. Kolbe et al. 2016, Winchell et al. 2016 2018, , Battles et al. 2018), which are generally less structurally complex than natural environments.

It is worth noting that these results contradict those of previous studies finding significant relationships between body size and perch height for *A. carolinensis* and *A. sagrei* (e.g. see Tokarz 1985, Jenssen et al. 1998, Kamath and Losos 2017). This may be attributable to the relatively narrow range in body size of individuals utilized in this study. These data were collected only from fairly large adult male lizards as they are easy to identify from afar; in many species, smaller males can look incredibly similar to mature females and so were excluded.

Examining individuals across a wider body size range may demonstrate varying patterns of habitat use in relation to body size more clearly as smaller males may be displaced by larger males (Jenssen et al. 1998, and Tokarz 1985). Similarly, further studies would also benefit from exploring this hypothesis in females, as well as across the entire body size range of all individuals (i.e. including juveniles).

Acknowledgements

We thank Carl Lewis and the Fairchild Tropical Botanic Gardens for permission to do this study.

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