

Habitat selection by the Puerto Rican yellow-chinned anole, *Anolis gundlachi*

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Abstract: Habitat selection can directly affect the fitness of an individual and the evolutionary dynamics of the population to which that organism belongs. We studied habitat use of the Puerto Rican yellow-chinned anole (*Anolis gundlachi* Peters, 1876) to examine whether this arboreal lizard uses its environment in a nonrandom manner. Males and females preferred woody vegetation substrates over nonwoody plants and sierra palms (*Prestoea acuminata* var. *montana* (Graham) A. Henderson and G. Galeano) as perching sites, and they also selected wider vegetation than what was randomly available. Selection for minimizing conspicuousness to potential predators and for increased locomotion capacity may help explain the preference for woody substrates and broader surfaces, respectively. *Anolis gundlachi* relies almost exclusively on visual cues for foraging and social interactions, and using wider perches also increases an individual's ability to scan a larger proportion of its territory. Our findings thus indicate that the nonrandom habitat use of free-ranging *A. gundlachi* leads to the selection of perching substrates that may increase performance of ecologically relevant capabilities.

Résumé : La sélection de l'habitat peut affecter directement la fitness d'un individu ainsi que la dynamique évolutive de la population à laquelle il appartient. Nous avons étudié l'utilisation de l'habitat chez l'anolis de Gundlach (*Anolis gundlachi* Peters, 1876) de Porto Rico pour voir si ce lézard utilise son environnement de façon non aléatoire. Les mâles et les femelles préfèrent les substrats de végétation ligneuse aux perchoirs de végétation non ligneuse et de palmiers *Prestoea acuminata* var. *montana* (Graham) A. Henderson and G. Galeano; ils choisissent aussi des parcelles de végétation plus grandes que celles qui sont disponibles au hasard. La préférence pour les substrats ligneux et les grandes surfaces peut s'expliquer en partie respectivement pour minimiser la visibilité aux prédateurs potentiels et pour accroître la capacité de locomotion. *Anolis gundlachi* dépend presque exclusivement de signaux visuels pour la recherche de sa nourriture et ses interactions sociales; l'utilisation de perchoirs plus vastes permet aussi à l'individu de pouvoir surveiller une partie plus étendue de son territoire. Nos résultats indiquent donc que l'utilisation non aléatoire de l'habitat par les *A. gundlachi* libres en nature mène à la sélection de substrats pour se percher qui peuvent augmenter la performance de tâches d'importance écologique.

[Traduit par la Rédaction]

Introduction

Habitat selection is a central theme in studies of behavioral and evolutionary ecology because the habitat that an individual occupies can directly affect fitness and the evolutionary dynamics of the population to which that organism belongs (Morris 2003). For example, habitat choice can have important effects on foraging behavior and reproductive success (Steele 1993; Doligez et al. 2002), as well as have significant consequences for the organization of ecological communities (Forstmeier et al. 2001; Losos et al. 2003) and evolutionary diversification (Borowsky 1990; Leal and Fleishman 2004). Habitat selection can be more easily assessed at smaller spatial scales, such as an individual's choice of microhabitat conditions (e.g., temperature, humidity, light characteristics). Theoretical models predict that in-

dividuals should select those microhabitats that allow them to increase their fitness by maximizing their performance of ecologically relevant tasks such as growth, survival, and reproduction (Cody 1985; Orians and Wittenberger 1991).

The ecology of West Indian anole lizards has been intensively studied for the past four decades (reviewed in Schoener 1977; Williams 1983; Losos 1994; Roughgarden 1995). When comparing the anoles found on the Greater Antilles (Cuba, Jamaica, Hispaniola, Puerto Rico), the most striking observation is that the same set of habitat specialists — termed ecomorphs — evolved independently on each of these four islands (Losos et al. 1998). These ecological types are named for the microhabitat that they usually occupy: grass-bush, twig, trunk-ground, trunk, trunk-crown, and crown giant (Williams 1983). Among ecomorphs, differences in the structural niche have been clearly demonstrated at the interspecific

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level (e.g., twig anoles routinely use twigs as perching sites, whereas trunk anoles are typically found on tree trunks; Collete 1961; Schoener 1968; Schoener and Schoener 1971; Estrada and Silva-Rodríguez 1984).

An underlying assumption of studies comparing habitat use among ecomorph types is that individuals do not perch randomly, but instead select the subset of available perches that best match their morphological adaptations. Surprisingly, few studies (e.g., Schoener 1975; Mattingly and Jayne 2004) have documented perch availability and perch use at a given locality to test whether this assumption is correct. Furthermore, because females are significantly smaller than males in most species of Caribbean anoles (Butler and Losos 2002), the sexes may differ in their patterns of habitat choice. If perch selection occurs, we expect individuals to use preferentially perches that allow them to maximize performance of ecological activities which are tightly coupled with morphology (e.g., locomotion, foraging behavior; Wainwright and Reilly 1994). To test this prediction, we characterized perch availability and documented habitat use in a natural population of *Anolis gundlachi* Peters, 1876, the Puerto Rican yellow-chinned anole.

Methods

Study species and field site

Anolis gundlachi is a medium-sized (males and females can reach 75 and 45 mm, respectively, in snout–vent length) montane lizard characterized by a rust–brown dorsal coloration with irregular patterns. This trunk–ground ecomorph (Rand 1964) is sexually dimorphic (females are smaller than males and typically have a conspicuous, light-colored, mid-dorsal line; Rivero 1998; Butler et al. 2000) and occurs exclusively in the interior wet forests of Puerto Rico (Rivero 1998), where it is common in several localities. Although individuals descend to the ground to feed and lay eggs, they predominantly use the lower portion of tree trunks as perching and foraging sites (Rand 1964; Irschick and Losos 1998; Rivero 1998).

We conducted this study near the El Verde Field Station (18°20'N, 65°49'W), in the Luquillo Experimental Forest in northeastern Puerto Rico. The general topography of the area is mountainous with deeply dissected drainages and steep northeast- and southwest-facing slopes. The site lies within Holdridge's Subtropical Wet Forest life zone and the tabonuco forest type (Ewel and Whitmore 1973). The forest is dominated by tabonuco (*Dacryodes excelsa* Vahl) and sierra palms (*Prestoea acuminata* var. *montana* (Graham) A. Henderson and G. Galeano), and has a closed canopy at 20–25 m, many understory trees and shrubs, and only sparse vegetation on the forest floor (Parrotta and Lodge 1991).

Experimental design and statistical analyses

Our design consisted of nine 20 m × 20 m plots, ranging in elevation from 360 to 490 m. Because the purpose of this study was to document patterns of habitat use by male and female *A. gundlachi*, vegetation surveys and assessments of lizard perch selection were conducted on different days to minimize the possibility that our vegetation surveys affected the behavior of the anoles. The vegetation was surveyed by establishing five 1.75 m wide × 20 m long linear transects

inside each plot, which allowed us to cover approximately 44% of the total area of the plot. Inside each transect we categorized each plant as woody, nonwoody (no bark), or sierra palm, and recorded its diameter at breast height (in centimetres). Selection of perching sites by anoles was assessed by conducting one census per plot. We censused three plots per day on three consecutive days, in the morning (0900–1100), midday (1130–1330), or afternoon (1400–1600). We randomly chose which plot to census on a given day and at what time. For each lizard observed during a census, we recorded sex (male, female, juvenile), tree type (woody, nonwoody, sierra palm), perch diameter (in centimetres), and perch height (in 0.5-m intervals) at the location where the anole was first seen. We spent approximately the same amount of time searching for anoles in each plot. To avoid pseudoreplication (i.e., repeated sampling of the same individual), we caught all lizards seen during a census, and released them inside the plot at the end of the survey. Because we only recorded nine juveniles from five of the nine plots, these individuals were excluded from the study.

We used the χ^2 goodness-of-fit test to determine whether male and female *A. gundlachi* used tree types nonrandomly, and the nonparametric Mann–Whitney *U* test to investigate whether significant differences existed between available perch diameters and those used by anoles in each plot. We used Fisher's test for combining probabilities to create an overall test of significance from the combined probability values of the independent significance tests calculated for each plot (Sokal and Rohlf 1995). Statistical tests were performed with StatView® version 4.51 (Abacus Concepts, Inc. 1996). Values reported are means ± SD and all *P* values are two-tailed.

Results

Male and female *A. gundlachi* preferentially selected woody vegetation substrates over nonwoody plants and sierra palms as perching sites (Fig. 1). Both sexes also selected vegetation with larger diameter at breast heights than what was randomly available (Fig. 2). Because tree types may differ in diameter, we compared perch diameter versus perch availability within woody plants in each plot to determine whether anoles used broader trees than what was randomly available. Even within woody plants, both sexes selected perches with the largest diameters (combined probability for significance tests of selection of perching diameters: $\chi^2_{\text{male}} = 51.46$, *df* = 18, *P* < 0.0001; $\chi^2_{\text{female}} = 31.52$, *df* = 18, *P* = 0.025). The sexes also selected woody, nonwoody, and sierra palms as perching substrates with similar frequency (106:8:12 woody : nonwoody : sierra palms (males) and 132:16:18 woody : nonwoody : sierra palms (females); $\chi^2 = 1.25$, *df* = 2, *P* = 0.54), but males occupied slightly wider perches than females (males: 10.6 ± 10.3 cm, range = 0.4–50.0 cm, *n* = 126; females: 8.7 ± 9.5 cm, range = 0.6–50.0 cm, *n* = 166; combined probability for significance tests of intersexual differences in perch diameter, $\chi^2 = 28.69$, *df* = 18, *P* = 0.052), even when the comparison was restricted to woody plants (males: 11.9 ± 10.6 cm, *n* = 106; females: 10.2 ± 10.0 cm, *n* = 132; $\chi^2 = 27.54$, *df* = 16, *P* = 0.036). There were no significant differences between male and female *A. gundlachi* on perch height (males: 1.62 ±

0.91 m, range = 0.5–4.5 m, $n = 126$; females: 1.49 ± 0.79 m, range = 0.5–4.0 m, $n = 165$; Mann–Whitney U test, $z = -1.03$, $P = 0.30$).

Discussion

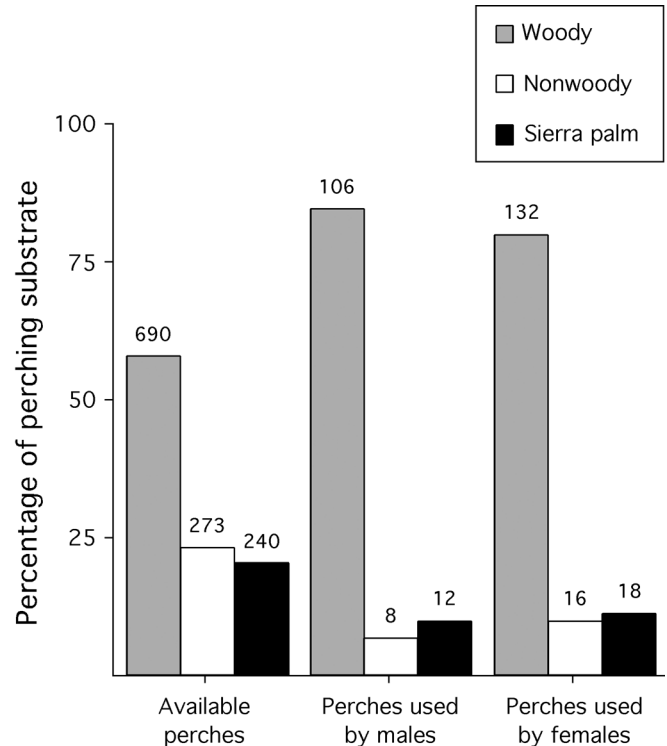
Although interspecific studies on *Anolis* lizards suggest that perch use is not random (Williams 1983; Losos 1994), this proposition has rarely been tested. We have demonstrated here that *A. gundlachi* does, indeed, use its habitat non-randomly; individuals preferentially used woody plants over nonwoody vegetation and sierra palms, and also selected vegetation with wider diameters as perching sites.

We propose three nonexclusive hypotheses to account for the observed pattern of habitat selection in *A. gundlachi*. First, perch choice in this species may reflect selection for minimizing conspicuousness to potential predators. Second, perch selection may indicate selection for maximizing locomotor capabilities. Third, perch use may reflect selection for efficiency of visual tasks such as foraging, predator detection, and social communication.

Male and female *A. gundlachi* preferred woody vegetation substrates over nonwoody plants and sierra palms as perching sites. Mechanisms that reduce predation pressure may be responsible for this pattern of habitat use. An animal's color pattern is cryptic if it resembles a random sample of the visual background the individual is most likely to be found in (Endler 1978). At our field site, woody substrates were usually darker than other perch types. Because of the irregular, rust–brown dorsal coloration of male and female *A. gundlachi*, woody perches may provide a chromatic background against which individuals are harder to detect by a visually oriented predator (such as the Puerto Rican lizard-cuckoo, *Saurothera vieilloti* Bonaparte, 1850; cf. Fernández-Juricic et al. 2004). Furthermore, the main antipredator response displayed by *A. gundlachi* during staged predatory encounters in the wild is immobility (J.A. Rodríguez-Robles, personal observation), which enhances crypsis.

Male and female *A. gundlachi* selected larger vegetation than what was randomly available. The likely reason for this preference for wider substrates is that those perches may allow individual anoles to move more effectively. In the wild, *A. gundlachi* and many other anole species frequently rely on sprinting ability to escape from predators and to catch prey (Leal and Rodríguez-Robles 1997a, 1997b; Irschick and Losos 1998). Relatively longer limbed lizards such as *A. gundlachi* have correspondingly greater strides and hence run more rapidly, which likely allow them to capture faster moving prey and escape predators sooner. Because sprint speed and balance for long-legged taxa increase significantly with increasing surface diameter (Losos and Sinervo 1989; Losos and Irschick 1996; Irschick and Losos 1999), using wider perches would improve locomotor efficiency in *A. gundlachi*. (However, the relationship between sprint speed and surface diameter must eventually reach an asymptote, because as a tree gets wider, it will become functionally equivalent to a flat surface (Spezzano and Jayne 2004).) Many of the lizards (38% of males, 50% of females) that we observed were on tree trunks whose diameters were in the range where a relationship has been documented between perch diameter and speed in for this species. Our findings

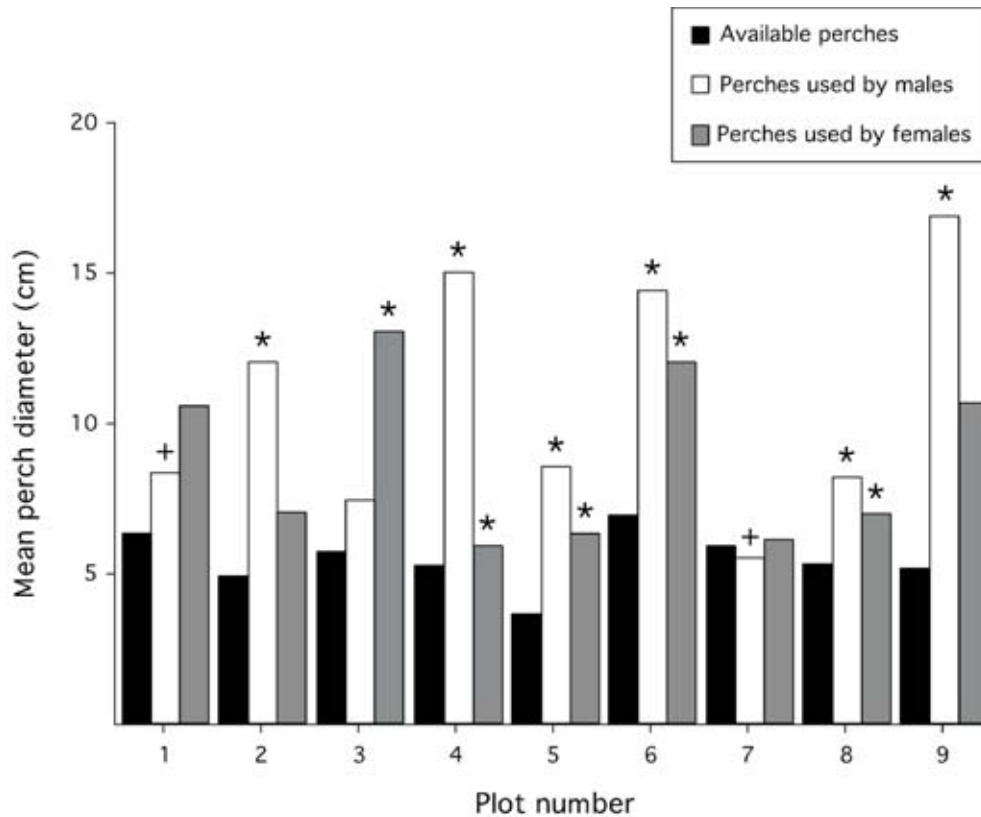
Fig. 1. Percentage of woody, nonwoody, and sierra palm substrates available to and used by male and female *Anolis gundlachi*. Numbers above bars are sample sizes. Combined probabilities for significance tests of selection of perching substrates by males and females: $\chi^2_{\text{male}} = 57.14$, $df = 18$, $P < 0.0001$; $\chi^2_{\text{female}} = 44.07$, $df = 18$, $P = 0.0006$.



thus suggest that the pattern of habitat selection by individual *A. gundlachi* leads them to use environments in which their locomotor ability is greater than it would be if they used the habitat randomly (see also Irschick and Losos 1999).

Increased efficiency of visual tasks may also play a significant role in habitat selection by *A. gundlachi*. For visually oriented, arboreal lizards such as *A. gundlachi* (Fleishman et al. 1993), habitat complexity is a critical factor that may hinder the efficiency of tasks such as prey and predator detection and social interactions. Perching sites are often visually cluttered owing to stems, branches, and leaves emanating from a particular perch and nearby vegetation. In tropical forests, tree distribution tends to correlate with the age of the tree, with older trees usually found isolated with regard to distance to the nearest tree and younger trees or stems more frequently occurring in clumps (Janzen 1970; Clark and Clark 1984; Okuda et al. 1997); a pattern that suggests that mature trees may constitute a less visually cluttered perch for visually oriented animals. At our study site, perch heights of approximately 1.5 m on mature trees are usually clear of branches (J.A. Rodríguez-Robles, personal observation), which coincides well with the mean perch height of male (1.62 m) and female (1.49 m) *A. gundlachi* recorded during this study (see Results). Furthermore, wider substrates may provide more secure perching sites against visually oriented predators by increasing the probability of detecting the approach of such animals (Scott et al. 1976). Accordingly, the pattern of habitat selection of *A. gundlachi*, particularly its

Fig. 2. Mean perch diameters available to and used by male and female *A. gundlachi*. Asterisks indicate significant differences ($P < 0.05$) between available and selected perches in separate comparisons for males and females, whereas pluses indicate comparisons for which probability levels were $0.05 < P < 0.08$. Combined probability for significance tests of selection of perching diameters by *A. gundlachi*: $\chi^2_{\text{male}} = 77.37$, $df = 18$, $P < 0.0001$; $\chi^2_{\text{female}} = 56.62$, $df = 18$, $P < 0.0001$.



preference for wider perches, may reflect selection for efficiency of visual tasks.

Anolis lizards also rely almost exclusively on visual cues for social communication (Jenssen 1977; Fleishman 1992). Territorial males frequently signal spontaneously throughout their ranges using visual displays consisting of motion patterns of the head and body and of a colorful throat fan (i.e., the dewlap) to advertise their position, repel other males, and attract potential mates (Jenssen 1977; Stamps 1977; Fleishman 1992). Strong selection may act on male anoles, including *A. gundlachi*, favoring individuals that choose perches which maximize the probability of advertising their presence to conspecifics and of detecting an intruder male (Stamps 1977; Fleishman 2000), suggesting that selection for social interactions in *A. gundlachi* may account in part for its pattern of habitat use.

Both sexes of *A. gundlachi* occupied larger perches, but males used wider substrates than females. A possible explanation for this finding is that males need to use broader surfaces because they are larger. In other words, females can probably use narrower surfaces than males without impairing locomotion abilities. Alternatively, the observed pattern may be caused by intraspecific agonistic interactions. Competitive interference between the sexes could lead to habitat partitioning. Larger lizards (i.e., males) may aggressively exclude females from preferred arboreal perches, leaving them to occupy less contested sites (Jenssen et al. 1998). Although this may explain the observed differences in habitat

use in *A. gundlachi*, it is not clear which limiting factor may cause agonistic interactions between the sexes.

Differences in the width of perches occupied by male and female *A. gundlachi* may have consequences for the escape behavior of the sexes. As previously indicated, *A. gundlachi* and other anoles run faster on wider perches (Losos and Irschick 1996; Irschick and Losos 1999). At the same time, the frequency of attempting to escape a potential predator by jumping increases on narrower substrates. Jumping is a relatively infrequent (ca. 15% of the time) means of escape from perches greater than 5 cm in diameter, but increases in frequency (to ca. 50%) on narrower perches. Because of the wider perches occupied by male *A. gundlachi* in nature, we expect males to try to escape a potential predator by running more frequently, and females to resort to jumping more often.

The distribution of perch diameters used by *A. gundlachi* in this study differed from previous reports for the species. In one instance, individuals used smaller perches more frequently (Rand 1964), whereas in another they used wider perches than documented herewithin (Reagan 1992). Additionally, perch diameters used by male *A. gundlachi* in our survey (10.6 ± 10.3 cm, range = 0.4–50.0 cm, $n = 126$) were narrower than reported elsewhere (33.5 ± 5.36 cm, $n > 20$ (Losos and Sinervo 1989); 14.9 ± 15.8 cm, $n = 88$ (Butler and Losos 2002)). These discrepancies are most readily explainable by a combination of two factors: the distribution of available perches and the presence or absence of syntopic

anole species at a given site. Clearly, local habitat structure will determine which perches are selected (Mattingly and Jayne 2004), and a large body of evidence documents shifts in habitat use in anoles as a function of sympatry with other species (cf. Schoener 1975; Pacala and Roughgarden 1985; Leal et al. 1998; for reviews see Losos 1994 and Roughgarden 1995).

One other factor that could affect perch choice, particularly in ectothermic animals, is ambient temperature. However, the extent of variation in ambient temperature in habitats occupied by *A. gundlachi* is small (Rogowitz 1996). More importantly, the species is a passive thermoconformer that does not use behavioral thermoregulation (e.g., basking in sunlight) to adjust to changes in environmental conditions with altitude (Huey and Webster 1976; Hertz 1992), an observation that suggests that temperature is not a critical factor affecting habitat selection in *A. gundlachi*.

In conclusion, our study indicated that male and female *A. gundlachi* chose a subset of the available vegetation as perching sites. This nonrandom pattern suggests that individuals perform ecologically relevant activities such as foraging and predator detection more efficiently in certain habitats. Obviously, the outcome of these tasks is critical for individual survival and reproduction. Furthermore, through its influence on habitat choice, the interplay between an animal's behavior and ecology also plays an important role in the structuring of ecological communities.

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References

- Abacus Concepts, Inc. 1996. StatView®. Version 4.51 [computer program]. Abacus Concepts, Inc., Berkeley, Calif.
- Borowsky, R. 1990. Habitat choice by allelic variants in *Xiphophorus variatus* (Pisces; Poeciliidae) and implications for maintenance of genetic polymorphism. *Evolution*, **44**: 1338–1345.
- Butler, M.A., and Losos, J.B. 2002. Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecol. Monogr.* **72**: 541–559.
- Butler, M.A., Schoener, T.W., and Losos, J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, **54**: 259–272.
- Clark, D.A., and Clark, D.B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen–Connell model. *Am. Nat.* **124**: 769–788.
- Cody, M.L. (Editor). 1985. *Habitat selection in birds*. Academic Press, Orlando, Fla.
- Collete, B.B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bull. Mus. Comp. Zool.* **125**: 137–162.
- Doligez, B., Danchin, E., and Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science* (Wash., D.C.), **297**: 1168–1170.
- Endler, J.A. 1978. A predator's view of animal color patterns. *Evol. Biol.* **11**: 319–364.
- Estrada, A.R., and Silva-Rodríguez, A. 1984. Análisis de la eco-morfología de 23 especies de lagartos cubanos del género *Anolis*. *Cienc. Biol.* **12**: 91–104.
- Ewel, J.J., and Whitmore, J.L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. U.S. For. Serv. Res. Pap. ITF-18.
- Fernández-Juricic, E., Erichsen, J.T., and Kacelnik, A. 2004. Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**: 25–31.
- Fleishman, L.J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* **139**: S36–S61.
- Fleishman, L.J. 2000. Signal function, signal efficiency and the evolution of anoline lizard dewlap color. In *Animal signals: signalling and signal design in animal communication*. Edited by Y. Espmark, T. Amundsen, and G. Rosenqvist. Tapir Academic Press, Trondheim, Norway. pp. 209–236.
- Fleishman, L.J., Loew, E.R., and Leal, M. 1993. Ultraviolet vision in lizards. *Nature* (Lond.), **365**: 397.
- Forstmeier, W., Bourski, O.V., and Leisler, B. 2001. Habitat choice in *Phylloscopus* warblers: the role of morphology, phylogeny and competition. *Oecologia* (Berl.), **128**: 566–576.
- Hertz, P.E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology*, **73**: 1405–1417.
- Huey, R.B., and Webster, T.P. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *crisatellus* group on Puerto Rico. *Ecology*, **57**: 985–994.
- Irschick, D.J., and Losos, J.B. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, **52**: 219–226.
- Irschick, D.J., and Losos, J.B. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between spring capabilities and structural habitat in Caribbean anoles. *Am. Nat.* **154**: 293–305.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**: 501–528.
- Jenssen, T.A. 1977. Evolution of anoline lizard display behavior. *Am. Zool.* **17**: 203–215.
- Jenssen, T.A., Hovde, K.A., and Taney, K.G. 1998. Size-related habitat use by nonbreeding *Anolis carolinensis* lizards. *Copeia*, 1998: 774–779.
- Leal, M., and Fleishman, L.J. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *Am. Nat.* **163**: 26–39.
- Leal, M., and Rodríguez-Robles, J.A. 1997a. Signalling displays during predator–prey interactions in a Puerto Rican anole, *Anolis crisatellus*. *Anim. Behav.* **54**: 1147–1154.
- Leal, M., and Rodríguez-Robles, J.A. 1997b. Antipredator responses of the Puerto Rican giant anole, *Anolis cuvieri*. *Biotropica*, **29**: 372–375.
- Leal, M., Rodríguez-Robles, J.A., and Losos, J.B. 1998. An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. *Oecologia* (Berl.), **117**: 273–278.
- Losos, J.B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annu. Rev. Ecol. Syst.* **25**: 467–493.
- Losos, J.B., and Irschick, D.J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.* **51**: 593–602.
- Losos, J.B., and Sinervo, B. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* **145**: 23–30.

- Losos, J.B., Jackman, T.D., Larson, A., de Queiroz, K., and Rodríguez-Schettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* (Wash., D.C.), **279**: 2115–2118.
- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodríguez-Schettino, L., Chamizo L., A., Jackman, T.R., and Larson, A. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* (Lond.), **424**: 542–545.
- Mattingly, W.B., and Jayne, B.C. 2004. Resource use in arboreal habitats: structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, **85**: 1111–1124.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* (Berl.), **136**: 1–13.
- Okuda, T., Kachi, N., Yap, S.Y., and Manokaran, N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rain forest — implications for regeneration and maintenance of species diversity. *Plant Ecol.* **131**: 155–171.
- Orians, G.H., and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* **137**(Suppl.): S29–S49.
- Pacala, S.W., and Roughgarden, J. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology*, **66**: 129–141.
- Parrotta, J.A., and Lodge, D.J. 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. *Biotropica*, **23**: 343–347.
- Rand, A.S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology*, **45**: 745–752.
- Reagan, D.P. 1992. Congeneric species distribution and abundance in a three-dimensional habitat: the rain forest anoles of Puerto Rico. *Copeia*, 1992: 392–403.
- Rivero, J.A. 1998. Los anfibios y reptiles de Puerto Rico. 2nd ed. Editorial de la Universidad de Puerto Rico, San Juan.
- Rogowitz, G.L. 1996. Evaluation of thermal acclimation and altitudinal variation of metabolism in a Neotropical lizard, *Anolis gundlachi*. *Copeia*, 1996: 535–542.
- Roughgarden, J. 1995. *Anolis* lizards of the eastern Caribbean: ecology, evolution, and plate tectonics. Oxford University Press, New York.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, **49**: 704–726.
- Schoener, T.W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecol. Monogr.* **45**: 233–258.
- Schoener, T.W. 1977. Competition and the niche. *In* *Biology of the Reptilia*. Vol. 7. Ecology and behaviour A. Edited by C. Gans and D.W. Tinkle. Academic Press, London. pp. 35–136.
- Schoener, T.W., and Schoener, A. 1971. Structural habitats of West Indian *Anolis* lizards. I. Lowland Jamaica. *Breviora*, **368**: 1–53.
- Scott, N.J., Jr., Wilson, D.E., Jones, C., and Andrews, R.M. 1976. The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **10**: 75–84.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W.H. Freeman and Company, New York.
- Spezzano, L.C., Jr., and Jayne, B.C. 2004. The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). *J. Exp. Biol.* **207**: 2115–2131.
- Stamps, J.A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. *Ecology*, **58**: 349–358.
- Steele, B.B. 1993. Selection of foraging and nesting sites by black-throated blue warblers: their relative influence on habitat choice. *Condor*, **95**: 568–579.
- Wainwright, P.C., and Reilly, S.M. (Editors). 1994. *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago.
- Williams, E.E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. *In* *Lizard ecology: studies of a model organism*. Edited by R.B. Huey, E.R. Pianka, and T.W. Schoener. Harvard University Press, Cambridge, Mass. pp. 326–370.