

# Do Lizards Avoid Habitats in Which Performance Is Submaximal? The Relationship between Sprinting Capabilities and Structural Habitat Use in Caribbean Anoles

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**ABSTRACT:** Recent years have seen an increased emphasis on measuring ecologically relevant performance capabilities to understand associations between morphology and habitat use. Such studies presume that performance is invariant, but in eight Caribbean *Anolis* lizard species, we found that maximal sprinting ability depends on surface diameter. Moreover, these species differ in the degree to which sprint speed declines with decreasing surface diameter, defined as "sprint sensitivity" (high sprint sensitivity = substantial declines in speed between broad and narrow dowels). The habitat constraint hypothesis postulates that *Anolis* lizards will avoid structural habitats in which their maximal sprinting capabilities are impaired. The habitat breadth hypothesis postulates that species whose performance is less affected by substrate will use a greater variety of habitats than species whose performance varies to a greater extent on surfaces of different diameters. Field observations quantified the proportion of time that lizards spent on different perch diameters. Both hypotheses were confirmed: species with high values of sprint sensitivity avoided using perches on which their maximal sprinting abilities are impaired, whereas species with low sprint sensitivity used such "submaximal" surfaces more frequently. Species with low sprint sensitivity used a broader range of structural habitats than species with high sprint sensitivity.

**Keywords:** phylogeny, sprinting, habitat use, comparative, performance.

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Only by investigating the functional capabilities conferred by a trait can one understand whether it is favored by

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natural selection in a particular environmental situation and, if so, why (Arnold 1983; Lauder 1990; Wainwright 1994). Arnold (1983) codified this approach by breaking the study of aptation (sensu Gould and Vrba 1982) into two components: laboratory studies to investigate whether variation in a trait leads to differences in functional capabilities and field studies to determine whether variation in functional capabilities is related to differences in fitness. Although this approach is explicitly intrapopulational (see Emerson and Arnold 1989), analogous approaches have been taken to study whether trait variation among species represents aptation (and potentially adaptation) to different parts of the environment (Wainwright 1988; Losos 1990b; Arnold 1994; McPeck 1995).

This morphology → performance → fitness approach makes the assumption that the relationship between morphology and performance is invariant. However, for many organisms and many tasks, performance ability depends on the environmental context. For example, lizards with toe fringes can run substantially faster than fringeless lizards on sandy surfaces but not on solid surfaces (Carothers 1986). Hence, fringes are aptations providing increased performance in some habitats but not others.

This context dependence of performance has important consequences for the study of aptation: laboratory comparisons of the functional capabilities of individuals or species are only meaningful to the extent that comparable environments are used in the field, and, conversely, the ability of organisms or species to use their maximal capabilities may be a function of the parts of the environment they choose to utilize. In other words, habitat selection behavior is an important filter in the morphology → performance → fitness paradigm (Garland and Losos 1994).

Nonetheless, few studies have evaluated the extent to which organisms use habitats in which they are constrained to perform submaximally. One exception concerns the relationship between temperature and performance. In ectotherms, performance ability for many

activities (e.g., digestion, hearing) is temperature dependent, yet under some circumstances, the costs associated with attaining the optimal temperature outweigh the benefits, leading these organisms to use habitats in which they maintain body temperatures that result in suboptimal performance (Huey 1982).

Another environmental variable that has a strong effect on performance is the structural habitat (i.e., the matrix of surfaces that organisms live in and move upon; Moermond 1979; Pounds 1988). For many small organisms, especially arboreal species, the structural environment poses substantial challenges for many important activities (Moermond 1979; Pounds 1988). Moreover, locomotor capabilities of many vertebrates are strongly affected by structural habitat (rodents: Thompson 1990; marsupials: Pridmore 1992; lizards: Losos and Irschick 1996). Although these studies have demonstrated that locomotor capabilities are affected by structural habitat, no previous study has investigated the extent to which species use structural habitats in which their maximal sprinting abilities are substantially impaired.

Studying the effects of structural habitat use on sprinting ability in lizards is especially appropriate because previous studies have shown that maximal sprinting ability in reptiles is heritable (van Berkum and Tsuji 1987; Garland et al. 1990; Garland 1994), repeatable (Huey and Dunham 1987), and, in a few cases, important to fitness (Bennett and Huey 1990; Jayne and Bennett 1990). Here, we investigate whether lizards avoid structural habitats in which their maximal sprinting capabilities are impaired, which we term the habitat constraint hypothesis. We also examined whether species whose performance varies little among different structural habitats use a broader range of habitats than species whose performance is maximal over only a limited set of habitats (the habitat breadth hypothesis). To test these hypotheses, we examine both maximal sprinting ability and the breadth of structural habitat use in eight species of Caribbean *Anolis* lizards.

### Background on Caribbean *Anolis* Lizards

Caribbean *Anolis* lizards provide an excellent opportunity for examining how maximal sprinting ability affects structural habitat use. *Anolis* lizards have diversified tremendously, producing nearly 150 species in the Caribbean, including extensive radiations on each of the Greater Antillean islands of Cuba, Hispaniola, Jamaica, and Puerto Rico (Williams 1983; Jackman et al. 1999). In many ways, Caribbean *Anolis* lizards have been a model system for studying how species adapt morphologically and behaviorally to different habitats. Numerous studies on Caribbean *Anolis* lizards over the past 30 yr have shown that *Anolis* species on each Greater Antillean island have in-

dependently evolved into a series of ecologically and morphologically distinct habitat specialists (Rand and Williams 1969; Williams 1983; Losos et al. 1998) that partition the environment by perch height and diameter (Schoener 1968; Rand and Williams 1969; Schoener and Schoener 1971a, 1971b; Moermond 1979; Williams 1983; Losos 1990b; Irschick et al. 1997).

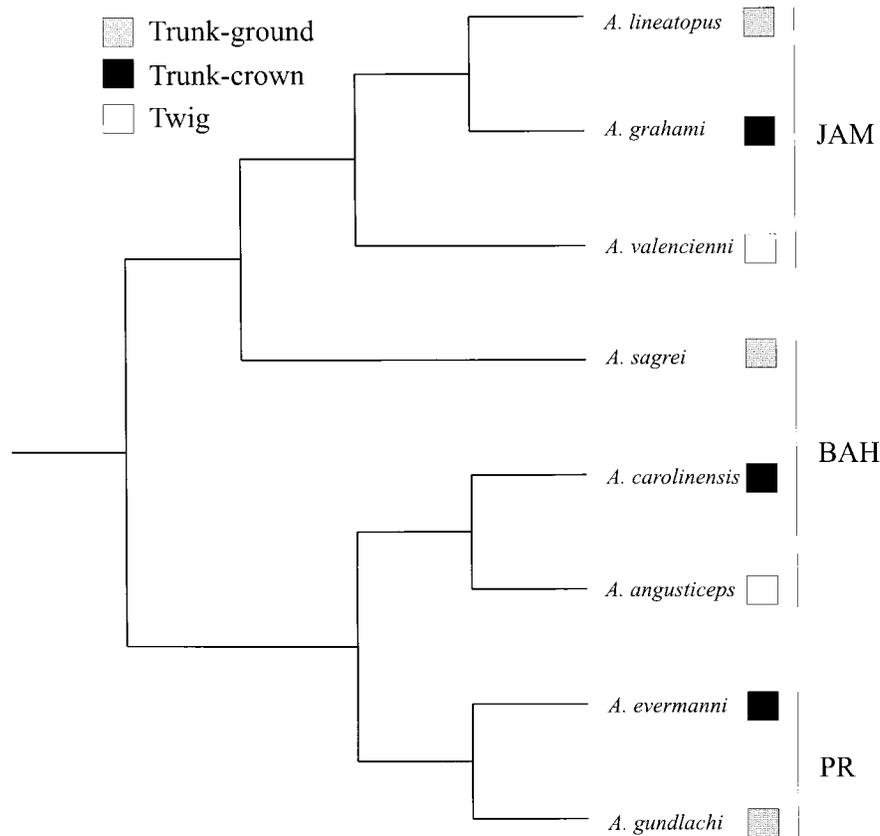
Although the habitat use of these species has been extensively investigated, previous studies have focused on the mean ecological characteristics of species when they are initially spotted (but see Pounds 1988 for work on Central American anoles). No attempt has been made to systematically quantify the range of perch heights and perch diameters that Caribbean anoles use as they move throughout their habitats. Consequently, previous studies may provide a biased view of anole habitat use if perch locations are not a random sample of the substrates used during locomotion (Pounds 1988).

Anoles use their maximal sprinting capabilities to escape predators and, to a lesser extent, to capture prey (Irschick and Losos 1998). However, in some anole species, maximum sprinting performance is markedly affected by substrate diameter (Losos and Sinervo 1989; Losos and Irschick 1996). We predict that such species should limit their activities to those surfaces on which they sprint well (i.e., close to their physiological maximum). By contrast, species whose sprint speed is less affected by surface diameter should both spend a greater percentage of their time on "submaximal" surfaces and use a greater variety of surfaces in nature (i.e., have greater habitat breadth).

To examine whether habitat effects on performance are relevant to habitat use, we examined the sprinting capabilities of eight *Anolis* species on a range of substrate diameters under controlled laboratory conditions to establish the degree to which maximal sprinting performance declines on surfaces of different diameters (sprint sensitivity). We then conducted focal animal samples in the field for all species to determine the breadth of habitat use for each species and the extent to which these species vary in the use of surfaces on which sprint performance is impaired.

### Methods

We chose eight species to examine performance capabilities and habitat use (fig. 1). The species chosen vary substantially in both morphology (from the short-legged and slender *Anolis valencienni* and *A. angusticeps* to the long-legged and stocky *A. gundlachi*, *A. lineatopus*, and *A. sagrei*) and habitat use (twig dwellers to species that use broad tree trunks; for discussion of anole ecomorphology, see Williams 1983; Losos 1990b; references therein). In addition, we chose study sites at which ecologically and morpho-



**Figure 1:** Phylogenetic tree for eight *Anolis* lizard species (see the text for details). Locality headings next to species names represent the Caribbean islands on which these species occur, although *Anolis carolinensis* was studied in Louisiana. JAM = Jamaica, BAH = Bahamas, and PR = Puerto Rico.

logically different species co-occur so that differences in habitat availability would not confound our analyses.

#### Laboratory Performance Trials

Sprinting data for six of the eight anole species (*A. carolinensis*, *A. sagrei*, *A. gundlachi*, *A. lineatopus*, *A. valencienni*, and *A. grahami*) were taken from prior studies (Losos and Sinervo 1989; Losos and Irschick 1996). The sprinting data for *A. evermanni* and *A. angusticeps* were collected using similar protocols. Lizards were collected by hand or by a slip noose attached to a fishing pole a day before performance trials. Only healthy adult male lizards (e.g., none with shrunken tail bases) were used in performance trials. Lizards were later released at the original site of capture. Maximal sprinting ability was measured on dowels of four different diameters—0.7, 1.6, 2.5, and 5.1 cm—corresponding to those used in studies of *A. carolinensis* and *A. sagrei* (Losos and Irschick 1996). The sprinting capabilities of the other four species were mea-

sured on five slightly different dowel sizes: 1.2, 2.1, 2.6, 3.3, and 4.6 cm (Losos and Sinervo 1989). Each dowel was covered with fiberglass window screening (1.6-mm mesh) to provide good traction. We used a portable microcomputer-operated racetrack to measure sprinting ability. Plexiglas boards were positioned on both sides of the track to prevent lizards from jumping off the track platform. Infrared emitters and receptors positioned every 25 cm along a 1.5-m track were triggered by lizards sprinting along the dowel. These sensors were connected to a laptop computer that calculated speed over each interval. A cloth was draped over the end of the racetrack to provide a refuge toward which lizards ran.

Because *Anolis* lizards tend to hop on horizontal surfaces, the racetrack was angled upward at 37° to match earlier experimental conditions (Losos and Irschick 1996) (lizards in Losos and Sinervo 1989 were sprinted at a 45° angle). Comparison of speeds of one species (*A. lineatopus*) on the broadest dowels at 37° (Macrini and Irschick 1998) and 45° (Losos and Sinervo 1989) shows great similarity

( $\bar{X}_{37^\circ} = 1.70$  m/s,  $\bar{X}_{45^\circ} = 1.71$  m/s). Furthermore, previous studies have shown that slope does not greatly affect maximal sprinting ability in small lizards (Huey and Hertz 1982, 1984a). For each trial, lizards were positioned at the beginning of the dowel and induced to run by repeated taps to the tail.

Lizards that cycled limbs rapidly and exerted significant effort were given a "good" rating, whereas lizards that moved their limbs only partially and exerted suboptimal effort were given a "poor" rating. Only speeds from good runs were used in subsequent analyses. The greatest speed over a 25-cm interval was considered the estimate of maximal sprinting ability for each lizard. Four trials per dowel were carried out for each lizard (16 trials total for each lizard). All performance trials took place between 28° and 30°C, temperatures that are close to preferred temperatures of most of the anoles used in this study (Huey and Webster 1976; Hertz 1981, 1992). Previous studies have demonstrated that anole species typically perform optimally (i.e., within 95% of maximum) at temperatures close to their preferred temperatures (Huey 1983; van Berkum 1986). For each of the species, trials were completed over a 2-d period (eight trials per day). The lizards were run twice on each dowel each day, with the order of dowels randomized.

#### Habitat Data

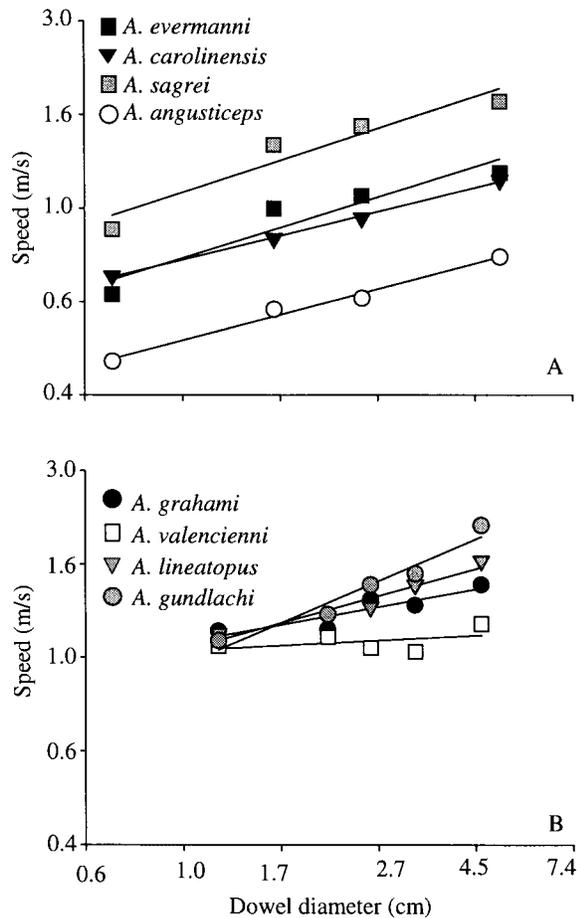
Field data were collected in habitat surrounding Discovery Bay marine laboratory (Jamaica; *A. grahami*, *A. lineatopus*, *A. valencienni*), Luquillo National Forest (Puerto Rico; *A. gundlachi*, *A. evermanni*), South Bimini Island (Bahamas; *A. angusticeps*, *A. sagrei*), and Jean Lafitte State Park (Louisiana; *A. carolinensis*). Field data were gathered from the same localities from which specimens used in maximal performance trials were collected. Field data were collected in Puerto Rico from the beginning of May until mid-June 1995; in Jamaica from May to mid-June 1996; in the Bahamas from July 8 to July 28, 1996; and in Louisiana from September 8 to September 15, 1996.

Lizards were quietly videotaped for periods ranging from 5 to 40 min with a Hi8 video camera from a distance (2–7 m). After each trial, videotapes were reviewed in the field to determine the perch diameters of all substrates used during the observation period. In this way, we are able to establish a distribution of all perch diameters used by a lizard during an observation period. We also measured the distance from a lizard's initial location to the nearest perch <1.5 cm in diameter to provide an estimate of the availability of narrow perches for different species.

#### Statistical Analyses

All statistical analyses were carried out in SYSTAT 5.03 (Wilkinson 1990). The species we examined in this study are similar in body length, with the exception that *A. angusticeps* is slightly smaller than the other seven species. However, we found no significant relationship among species between body mass and sprint sensitivity (defined below; Pearson  $r$  among independent contrasts = 0.41, 6 df,  $P > .25$ ). Thus, we did not remove the effects of body size from any performance or habitat use measure. For each species, we define sprint sensitivity as the slope of the line for the regression (linear least squares) of sprint speed (dependent variable) on dowel diameter (independent variable), which shows the degree to which sprint speed varied as a function of diameter. High values of sprint sensitivity indicate a substantial decline in sprinting performance from broad to narrow dowels. For each species, mean values of all individuals were calculated for sprint speed on each dowel size. Natural log transformation of both speed and dowel diameter produced generally linear fits for each species (fig. 2). We tested for differences in slopes among species using ANCOVA. To identify which species were responsible for the significant differences identified in the overall analysis, we then conducted ANCOVAs between all pairs of species. This approach entails 28 pairwise comparisons; we therefore provide estimates of  $P$  values to allow readers to judge for themselves the biological significance of the differences (note that one would expect 1.4 significant differences at the  $P = .05$  level by chance with 28 comparisons, but we report nine such differences).

Maximal sprinting ability decreases in anoles owing to decreased support diameter and smooth surface texture (Losos and Sinervo 1989; Losos and Irschick 1996; D. J. Irschick, unpublished data) and is independent of slope in small lizards (Huey and Hertz 1982), with the exception of some bipedal specialists (Irschick and Jayne 1998). Hence, broad surfaces with rough texture should promote maximal sprinting performance. Consequently, we consider sprinting performance on the broadest dowels in this study to approximate the maximal speeds of which *Anolis* lizards are capable. By contrast, narrower surfaces should result in submaximal sprinting, at least for some anole species. Based on regression equations between speed and dowel diameter for the eight species in this study (table 1), anoles can attain, on average, only 85% of their maximal speed on dowels of 3 cm (range among species = 76%–92%) and 75% of their maximal speed on dowels of 2 cm (range = 63%–89%). Thus, there is substantial variation among species in the predicted percentages of maximum speed that can be attained on 2- and 3-cm diameter surfaces. We thus tested the predictions of the habitat con-



**Figure 2:** Log-log plots of mean values of speed (*Y*-axis) versus dowel diameter (*X*-axis) for eight *Anolis* lizard species. Plot A is for species that were examined on dowels ranging from 0.7 to 5.1 cm in diameter, whereas plot B is for species that were examined on dowels ranging from 1.2 to 4.6 cm in diameter. The regression lines are linear least squares.

straint hypothesis: that a negative relationship should exist between sprint sensitivity and the percentage of time that lizards spend using narrow perches, which we defined as supports  $\leq 3$  cm in diameter (a second analysis lowered the cutoff to 2 cm). We used the following procedure to determine the extent to which lizards utilized different perch diameters. For each individual lizard, we categorized the percentage of time (in seconds) that it spent on perch diameters in 17 categories (range = 0–8 cm, bin widths = 0.5 cm). All perch diameters  $>8$  cm were lumped into the final bin (rationale explained later). We averaged these percentages among individuals for each species, and mean values of percentage of time spent on particular perch diameters were used in comparative analyses. For clarity, we only present the mean percentages of time that each species spent in the following perch diameter cate-

gories, all in centimeters (0–2, 2.1–4, 4.1–6, 6.1–8, and  $>8$ ), but we tested for statistical differences among species using all 17 categories. To test whether the eight species differed in their habitat use, we carried out two-sample Kolmogorov-Smirnov tests between each pair of species comparing the percentage of time species spent on different perch diameters (as earlier, the number of significant results far exceeds that expected by chance).

We also calculated the coefficient of variation of all substrate diameters used by each species (termed “habitat breadth”). To calculate habitat breadth, we pooled data from individuals within each species to create a single distribution of substrate diameters (because most individuals used relatively few different supports over the course of an observation period, individual measurements of habitat breadth use were not meaningful). The coefficient of variation of this pooled distribution (expressed as a percentage of the mean) was our estimate of habitat breadth. Because substrate diameters above a particular size tend to be functionally equivalent (i.e., approximate a flat surface) to a small lizard (Cartmill 1985), we examined habitat breadth only over perch diameters from 0 to 8 cm. All perch diameters  $>8$  cm were given a value of 8.

Because we had an a priori expectation that anole species with high sprint sensitivity should avoid using submaximal habitats and should utilize a narrow range of habitats, we used one-tailed *P* values for correlations between sprinting performance and habitat use.

#### Phylogenetic Analyses

Because species are related to one another in a hierarchical fashion, species means cannot be considered statistically independent (e.g., Felsenstein 1985; Martins and Garland 1991; Garland et al. 1992). The independent contrasts method (Felsenstein 1985) has been demonstrated to be successful for analyzing quantitative data within a phylogenetic context (Martins and Garland 1991). This

**Table 1:** Least squares regression statistics describing the relationship between dowel diameter (cm) and sprinting performance (m/s) within each of eight anole species

| Species                | Slope       | <i>Y</i> -intercept | <i>r</i> <sup>2</sup> |
|------------------------|-------------|---------------------|-----------------------|
| <i>Anolis sagrei</i>   | .316 ± .054 | .111 ± .054         | .95                   |
| <i>A. lineatopus</i>   | .291 ± .046 | .039 ± .047         | .93                   |
| <i>A. gundlachi</i>    | .445 ± .066 | -.036 ± .068        | .94                   |
| <i>A. carolinensis</i> | .235 ± .016 | -.252 ± .016        | .99                   |
| <i>A. evermanni</i>    | .306 ± .063 | -.242 ± .062        | .92                   |
| <i>A. grahamsi</i>     | .190 ± .052 | .080 ± .053         | .82                   |
| <i>A. angusticeps</i>  | .257 ± .016 | -.687 ± .016        | .99                   |
| <i>A. valencienni</i>  | .056 ± .063 | .035 ± .065         | .21                   |

Note: Values are ± 1 SE.

**Table 2:** Results from ANCOVA comparing slopes among species for regressions of speed (dependent variable) versus dowel diameter (independent variable)

| Genus and species | AS   | AL   | AGu    | AC    | AE   | AGr | AA    | AV  |
|-------------------|------|------|--------|-------|------|-----|-------|-----|
| AS                | ...  |      |        |       |      |     |       |     |
| AL                | .3   | ...  |        |       |      |     |       |     |
| AGu               | 1.0  | 3.6  | ...    |       |      |     |       |     |
| AC                | 1.4  | .7   | 9.2*   | ...   |      |     |       |     |
| AE                | .1   | .1   | 1.3    | .8    | ...  |     |       |     |
| AGr               | 2.6  | 2.1  | 9.3*   | 1.6   | 1.8  | ... |       |     |
| AA                | .7   | .1   | 6.4*   | 1.0   | .4   | 2.5 | ...   |     |
| AV                | 8.3* | 9.1* | 18.1** | 10.7* | 6.5* | 2.7 | 11.8* | ... |

Note: AS = *Anolis sagrei*, AL = *A. lineatopus*, AGu = *A. gundlachi*, AC = *A. carolinensis*, AE = *A. evermanni*, AGr = *A. grahami*, AA = *A. angusticeps*, and AV = *A. valencienni*. Numbers in each cell are *F* values. Comparisons between species that ran on dowel sizes from 0.7 to 5.1 cm had *df* = 1, 4. Comparisons between species that ran on dowel sizes from 1.2 to 4.6 cm had *df* = 1, 6. Comparisons between species that ran on dowel sizes from 0.7 to 5.1 cm and on dowel sizes from 1.2 to 4.6 cm had *df* = 1, 5.

\*  $P < .05$ .

\*\*  $P < .01$ .

method requires a fully resolved phylogeny as well as branch lengths in units of expected variance in phenotypic differentiation. A phylogenetic study of *Anolis* relationships based on mitochondrial DNA sequences (Jackman et al. 1999) included six of the eight species in this study. Although *A. evermanni* and *A. gundlachi* were not sequenced, two closely related species, *A. cristatellus* and *A. stratulus*, were included in those studies. Previous studies based on allozymic and karyotypic data have shown that *A. evermanni* and *A. stratulus* are sister taxa and that *A. cristatellus* and *A. gundlachi* are very closely related (Gorman et al. 1983). Figure 1 presents the phylogeny used in this study.

Branch lengths, assuming a molecular clock, were taken from Jackman et al. (1999). Using these branch lengths assumes that the amount of change on a branch should be proportional to the length, in time, of that branch. We investigated whether contrasts were appropriately standardized by examining the correlation between the standard deviations of branch lengths and the absolute values of independent contrasts (following Garland et al. 1992) and found that all contrasts were appropriately standardized (all Pearson correlation values  $< 0.50$ ,  $P$  values  $> .10$ ).

## Results

### Laboratory Data

In all species, perch diameter was significantly positively correlated with maximal speed (all  $P$  values  $< .05$ ; table 1; fig. 2), with the exception of *Anolis valencienni* ( $P > .25$ ), although this species did run slightly faster (12% faster) on the broadest dowel than on the narrowest dowel. Re-

gression slopes ranged from 0.056 (*A. valencienni*) to 0.445 (*A. gundlachi*). An overall ANCOVA revealed significant differences among slopes of the eight species ( $F = 3.2$ ,  $df = 7, 20$ ,  $P < .025$ ). Of the 28 comparisons of slopes between species, one was significant at  $P < .01$ , and eight were different at  $P < .05$  (table 2). Two species (*A. gundlachi* and *A. valencienni*) accounted for all of these significant differences, whereas the remaining six species did not differ significantly in sprint sensitivity (table 2). Thus, the eight slopes among the species can be divided into three categories: low (*A. valencienni*), medium (*A. grahami*, *A. lineatopus*, *A. sagrei*, *A. carolinensis*, *A. evermanni*, and *A. angusticeps*), and high (*A. gundlachi*).

### Habitat Data

We observed 123 lizards for a total of 33.3 h (average viewing time per lizard = 16.2 min). Initial perch diameters were generally similar to perch diameters for the entire movement bouts, with some exceptions. Most notably, initial perch diameters tended to underestimate the amount of time that two species (*A. valencienni* and *A. angusticeps*) used narrow (0- to 2-cm diameter) perches. For example, only 44% of the individual *A. valencienni* were initially sighted on perches between 0 and 2 cm, but this species spent 71% of its time on perches of this size class (fig. 3). This discrepancy occurred because *A. valencienni* would frequently be initially sighted on broad perches (e.g., trees) but subsequently would move onto narrow branches where they are less easily detected.

The mean distances ( $\pm 1$  SD) to the nearest perch  $< 1.5$  cm in diameter for each species were as follows: *A. sagrei* ( $10.5 \pm 6.6$  cm), *A. angusticeps* ( $13.0 \pm 7.9$ ), *A. grahami* ( $20.8 \pm 22.8$ ), *A. valencienni* ( $21.1 \pm 33.5$ ), *A. lineatopus*

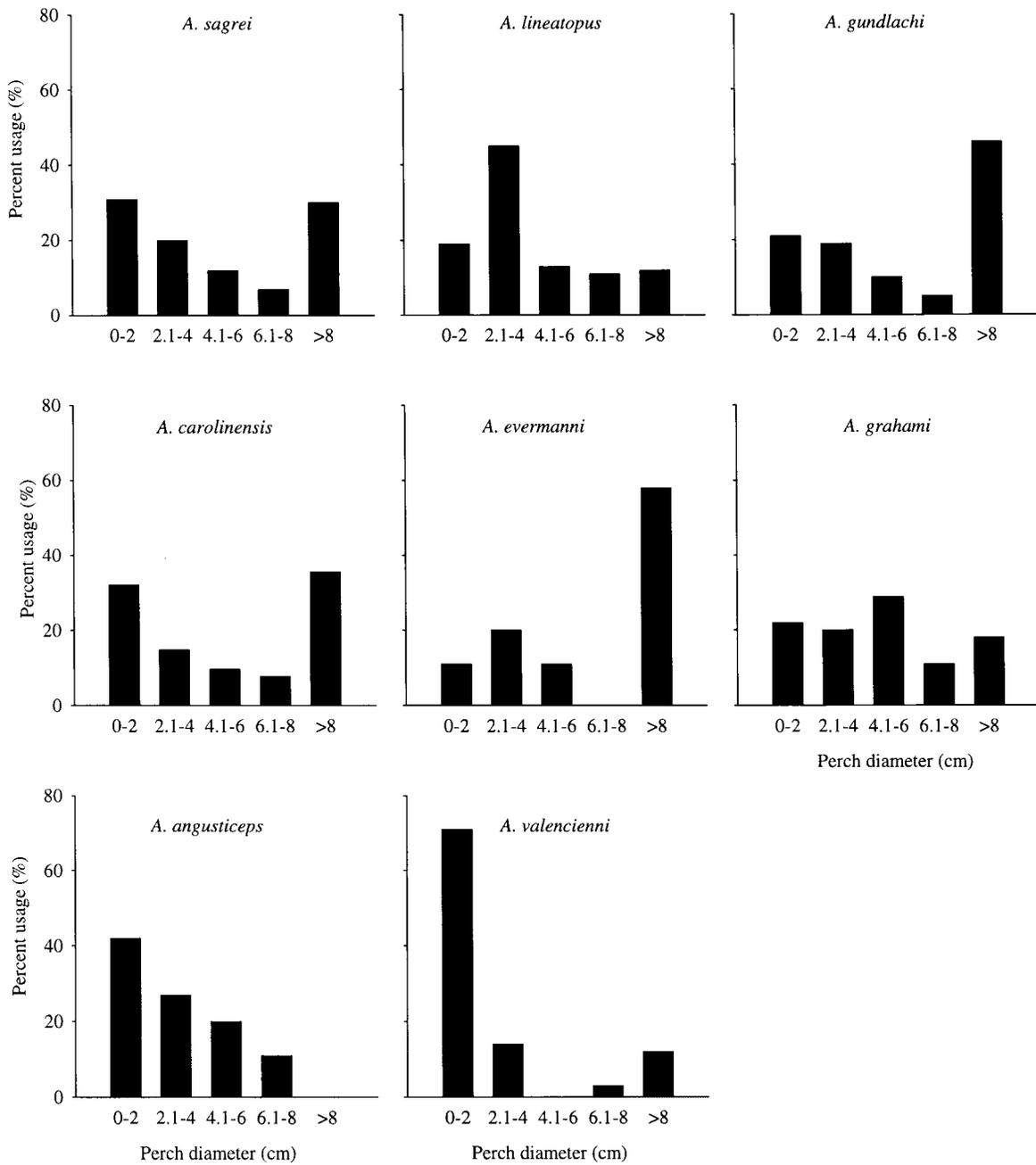


Figure 3: Histograms of habitat use for each of eight *Anolis* lizard species; each bar is a mean value for individuals within each species

(21.5 ± 19.2), *A. evermanni* (23.8 ± 13.3), *A. carolinensis* (25.0 ± 33.5), and *A. gundlachi* (37.8 ± 34.9). Two points are noteworthy here. First, all of the mean distances are <40 cm, which is well within the maximal jumping range of most *Anolis* species (including the seven species included in this study for which jumping performance data are available; Losos 1990c), which indicates that narrow

perches are easily available to all these species. Second, no correspondence exists among species between the average distance to perches <1.5 cm in diameter and how much time is spent on perches <1.5 cm ( $r^2 = 0.02$ , 6 df,  $P > .50$ ).

Figure 3 provides data on the percentage of time that each species spends on perches of different diameters. The

two short-legged species, *A. valencienni* and *A. angusticeps*, spent most of their time (71% and 42%, respectively) on perches  $\leq 2$  cm in diameter (fig. 3). By contrast, the long-legged species spent only 19% (*A. lineatopus*), 21% (*A. gundlachi*), and 31% (*A. sagrei*) of their time on perches  $\leq 2$  cm in diameter (fig. 3). Thirteen of the 28 pairwise comparisons of perch diameter distributions were statistically different at  $P < .001$ , two were significantly different at  $P < .01$ , and four were significantly different at  $P < .05$  (table 3), which indicates substantial differences in habitat utilization among the eight species (all comparisons employing two-sample K-S tests).

*Relationships between Habitat Use and Performance*

Values of habitat breadth for the eight species were as follows: *A. gundlachi*, 45.2; *A. evermanni*, 60.3; *A. sagrei*, 61.1; *A. lineatopus*, 64.8; *A. grahami*, 66.1; *A. carolinensis*, 75.1; *A. angusticeps*, 91.7; and *A. valencienni*, 102.4. Thus, the short-legged, twig-dwelling species tended to have the greatest habitat breadths, whereas the long-legged, trunk-ground anole *A. gundlachi* had the lowest value. Habitat breadth (fig. 4c) and the percentages of time each species spent on perches  $\leq 2$  (fig. 4a) or  $\leq 3$  cm (fig. 4b) in diameter were significantly and negatively correlated with sprint sensitivity (2 cm:  $r^2 = 0.75$ ,  $P < .01$ ; 3 cm:  $r^2 = 0.54$ ,  $P < .05$ ; habitat breadth:  $r^2 = 0.74$ ,  $P < .01$ , all tests have 6 df). Thus, both of our hypotheses are confirmed: species that sprint relatively poorly on narrow dowels (high values of sprint sensitivity) spend little time on narrow perches. Furthermore, species whose sprint capabilities are not strongly affected by dowel diameter tend to utilize a broader range of perch diameters in nature than species that do not sprint well on dowels of different diameters.

**Discussion**

The fundamental niche of a species is defined as the set of environmental conditions in which a population could persist indefinitely in the absence of competing, predatory, and parasitic species, whereas the realized niche is that subset of the fundamental niche that a population actually uses (Hutchinson 1957). Understanding the processes responsible for delimiting the realized niche, such as interspecific competition, has long been a central goal in ecology (Schoener 1974, 1986), but the mechanistic basis underlying these processes is less frequently examined. Why, for example, might predation be severe enough to prevent a population from occupying some habitats, but not others (e.g., Sih et al. 1985)? Extrinsic variation among habitats is one possibility, as the suite of predators, competitors, and parasites is likely to differ from one habitat to the next. In addition, intrinsic variation in a species' ability to perform in different habitats may prevent a species from using all portions of its fundamental niche.

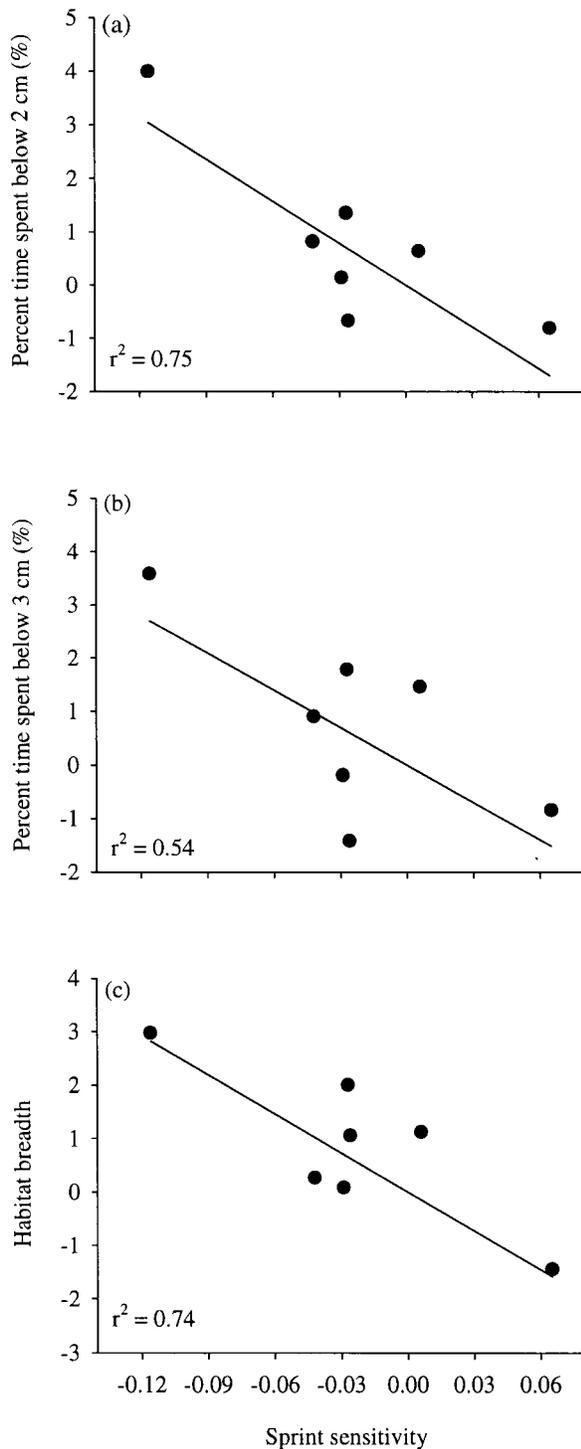
Testing this hypothesis requires information not only on how performance capabilities vary across an environmental gradient, but also the extent to which organisms actually use those parts of the environment in which their capabilities are maximal. Our studies with *Anolis* lizards illustrate how these two types of information can be integrated. All anole species decline in maximum sprinting performance as surface diameter decreases, but the extent to which speed declines varies among species. Moreover, species also differ in the degree to which they use habitats in which their sprinting abilities are impaired, and this variation is related to the sensitivity of sprint performance to surface diameter. As predicted by the habitat constraint hypothesis, species whose sprinting performance declines markedly with decreasing surface diameter tend not to use surface diameters that impair maximal performance, whereas species whose sprinting performance declines to

**Table 3:** Pairwise matrix of results from Kolmogorov-Smirnov tests comparing use of different perch diameter categories

| Genus and species | AS                 | AL                 | AGu                | AC                 | AE                 | AGr                | AA               | AV  |
|-------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|------------------|-----|
| AS                | ...                |                    |                    |                    |                    |                    |                  |     |
| AL                | .30                | ...                |                    |                    |                    |                    |                  |     |
| AGu               | .30                | .26                | ...                |                    |                    |                    |                  |     |
| AC                | .30                | .26                | .46 <sup>***</sup> | ...                |                    |                    |                  |     |
| AE                | .31                | .41 <sup>**</sup>  | .46 <sup>***</sup> | .36 <sup>*</sup>   | ...                |                    |                  |     |
| AGr               | .30                | .27                | .46 <sup>***</sup> | .36 <sup>*</sup>   | .58 <sup>***</sup> | ...                |                  |     |
| AA                | .35                | .37 <sup>*</sup>   | .47 <sup>***</sup> | .43 <sup>**</sup>  | .58 <sup>***</sup> | .46 <sup>***</sup> | ...              |     |
| AV                | .49 <sup>***</sup> | .61 <sup>***</sup> | .61 <sup>***</sup> | .47 <sup>***</sup> | .72 <sup>***</sup> | .62 <sup>***</sup> | .34 <sup>*</sup> | ... |

Note: Species abbreviations are the same as in table 2. Numbers in cells are  $D_{max}$  values. Each test has 17 df.

\*  $P < .05$ .  
 \*\*  $P < .01$ .  
 \*\*\*  $P < .001$ .



**Figure 4:** Sprint sensitivity versus (a) the percentage of time each anole species spends on supports  $\leq 2$  cm in diameter, (b) the percentage of time each anole species spends on supports  $\leq 3$  cm in diameter, and (c) habitat breadth. Values are independent contrasts.

a lesser extent are less restricted in their habitat selection. This is true even though the former species have greater absolute sprint speed on narrow-diameter surfaces than the latter species (fig. 2). Understanding why this should be so requires discussion of not only variation in performance abilities across environmental gradients but also how this variation relates to behavior and habitat use.

Previous studies (Losos and Sinervo 1989; Losos and Irschick 1996; Macrini and Irschick 1998) have shown that the relationship of sprint speed to surface diameter in anoles is a function of hind limb length. On broad surfaces, maximum sprint speed correlates with hind limb length such that, for example, the long-limbed *A. gundlachi* can run nearly twice as fast as short-limbed *A. valencienni* even though the two species are similar in body size (Losos and Sinervo 1989). By contrast, on narrow surfaces, differences in sprint speed between anole species are much less marked (fig. 2). The biomechanical basis for this trade-off is not well understood, but it may relate to the ability of lizards to effectively grip and maintain their center of balance on narrow branches (Cartmill 1985; Pounds 1988). Indeed, lizards that specialize on narrow branches appear to move their limbs in a vertical plane below their body, whereas more terrestrial lizards usually employ a more sprawling limb posture which may not be effective on narrow surfaces (D. J. Irschick, personal observation).

Nonetheless, the absolute speed of longer-limbed anole species on narrow surfaces is comparable to or greater than that of shorter-limbed species. For example, on a 1.2-cm dowel, *A. gundlachi* achieved a mean speed of 1.10 m/s, whereas on the same dowel size, *A. valencienni* achieved a very similar mean speed of 1.06 m/s. Why, then, do shorter-limbed species use narrower surfaces much more frequently than longer-limbed species? The answer appears to partially lie in interspecific differences in the behavioral ecology of anole species that affect the importance of sprint performance to individuals' fitness.

Many behavioral and physiological factors affect habitat use in *Anolis* lizards, such as foraging mode, territoriality, and complex fluctuations in food supply and population size. Therefore, establishing direct cause-effect relationships between performance capabilities and habitat use is difficult, but we can articulate some of the possible constraints on habitat use. Long-limbed species, such as *A. gundlachi*, *A. lineatopus*, and *A. sagrei*, are highly territorial species (Irschick and Losos 1996). Males of these species spend most of their time surveying their territory for conspecifics and food from a tree trunk or other prominent structures within a meter of the ground. Prey are attacked by rapid movements (running or jumping). Although this surveying behavior allows males to detect intruders, food, or potential mates quickly, it also makes them highly conspicuous to predators, which is exacerbated by their fre-

quent use of conspicuous display behaviors (e.g., dewlapping, head bobbing). As a result, these species rely greatly on maximal speed to escape predators (Irschick and Losos 1998). Thus, the ability to run quickly is an important facet of many aspects of their natural history.

By contrast, short-limbed, twig-dwelling species, such as *A. valencienni* and *A. angusticeps*, lead a very different lifestyle. Rather than being sit-and-wait predators, these species typically move slowly through the environment as they forage for slow and cryptic invertebrates (Hicks and Trivers 1983; Losos 1990a; Irschick and Losos 1996; see also Moermond 1981). The slow movements of twig anoles during feeding are not solely a result of the narrow perch diameters they are using. For instance, in the laboratory, *A. angusticeps* is capable of running up to 0.60 m/s on a 1.6-cm diameter perch, which is typically the perch diameter that they use in nature. However, their sprinting performance during feeding in nature averages only 0.39 m/s, which is only 65% of their maximal capabilities (Irschick and Losos 1998). Thus, stealth, not speed, may be more important for twig anoles when capturing prey. Furthermore, twig species tend to be cryptically colored, display infrequently, and rely on stealthy escape as their primary means of avoiding predators, although they will use rapid locomotion as a last resort (Irschick and Losos 1996). Rapid locomotion thus is of much less importance to short-limbed anole species. The other species included in this study are intermediate in the aforementioned morphological and behavioral characteristics.

Comparative studies support these generalizations by indicating that the degree to which species run quickly in nature is positively correlated with hind limb length (Losos 1990a). Thus, species that rely on rapid locomotion appear to be constrained to use habitats in which they can achieve maximal performance, whereas species for which rapid locomotion is less important are less constrained in their choice of habitat.

Although variation in the breadth of habitat use seems explicable by sprint capabilities, as predicted by the habitat breadth hypothesis, an alternative possibility is that species with greater habitat breadth have a greater variety of perch diameters from which to choose. The ideal means of testing this hypothesis would be to gather detailed data on habitat availability for each species, but such data are unavailable. Nonetheless, we find this explanation unlikely to explain the observed patterns for three reasons.

First, differences in the use of narrow perches constitute one of the primary differences in habitat use between the species (fig. 3), but all eight species use habitats in which individuals occur in close proximity to narrow-diameter surfaces (see "Results"). Second, detailed behavioral data for two relatively short-legged species (*A. valencienni* and *A. carolinensis*) indicate that they have relatively large

home ranges, move frequently, and encounter a wide variety of different perches (Hicks and Trivers 1983; Janssen et al. 1995). These data are noteworthy because these two species use broad surfaces relatively infrequently, yet their movement patterns clearly indicate that they must encounter such surfaces regularly. These two lines of evidence indicate that the failure of long-legged species to use narrow surfaces and the failure of shorter-legged species to use broad perches does not result because these species do not encounter such surfaces.

This conclusion is emphasized by our third line of argument. In three of our study sites (Jamaica, Puerto Rico, and the Bahamas), we collected data on two or three sympatric species simultaneously. Although these sympatric species differs in their average habitat use, the range of habitats used by these species overlaps substantially (e.g., Schoener 1968; Schoener and Schoener 1971a, 1971b). Hence, comparison of sympatric species sidesteps the issue of habitat availability because the habitat at any locality can be used by any anole of any coexisting species. Nonetheless, of all comparisons of sympatric species, only one (between *A. grahamsi* and *A. lineatopus* in Jamaica) fails to demonstrate a significant difference in habitat use (table 3).

Of course, factors other than sprinting ability may affect habitat use in anoles. For example, for territorial species, broad surfaces, such as tree trunks, provide excellent vantage points to display and look for prey, which suggests that habitat specialization may be partially driven by such factors. Nonetheless, our data strongly implicate sprinting performance as a primary determinant of habitat use in anoles. One means of testing this idea is to examine hypotheses that stem from it. If habitat specialization in *Anolis* lizards is driven by the relationship between sprinting ability and habitat use, then two predictions should be upheld. First, natural selection should favor maximum sprinting ability in long-limbed species but not, or to a much lesser extent, in short-limbed species. Second, if species were somehow constrained to use perches on which they perform submaximally, perhaps in laboratory trials, long-limbed species should be more greatly affected than short-limbed species.

#### *General Implications*

A trade-off exists among anole species between specialization for maximal speed, and thus having a narrow performance breadth, versus maintaining similar levels of speed across different structural habitats (see Bauwens et al. 1995 for a recent example relating thermal breadth to sprinting ability in lizards). Our results indicate that this performance trade-off has far-reaching ecological implications. Specialization for maximal sprinting performance

results in a behavioral ecology that limits which structural habitats can be occupied, whereas other species can use a broader range of habitats. Nonetheless, this situation is not an example of the “jack of all trades master of none” hypothesis (Huey and Hertz 1984b). In that scenario, specialists trade off poor performance in most contexts for exemplary performance in one context. By contrast, sprint performance specialists always perform better on surfaces of all diameters than anole species that exhibit similar speeds on different surfaces.

Consequently, if maximal speed translated directly into ecological success, then the sprint specialists would be competitively superior in all habitats. In fact, this is not the case because the importance of sprint speed varies among the anole species examined here. Thus, despite their superior sprinting speed on virtually all surfaces, long-limbed anole species are restricted to using surfaces on which they can achieve high speeds. Hence, the performance trade-off does translate into an ecological trade-off—relative sprint capabilities on different surfaces are more relevant to ecology than absolute capabilities. More generally, this study illustrates that measuring performance is only one component of studying the functional significance of a trait. Studies of adaptation must include both measures of the extent to which performance capabilities vary across environments and information on whether the performance ability is ecologically relevant to the organism (Hertz et al. 1988; Pough 1989; Irschick and Losos 1998).

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