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# RESOURCE USE IN ARBOREAL HABITATS: STRUCTURE AFFECTS LOCOMOTION OF FOUR ECOMORPHS OF *ANOLIS* LIZARDS

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*Abstract.* Previous laboratory studies have frequently determined the maximal running speeds of lizards. However, neither the extent to which animals use maximal speeds in nature nor the effects of arboreal habitat structure on undisturbed speeds of locomotion have been well documented. Furthermore, quantitative data describing the physical structure of arboreal habitats are lacking. Thus, we quantified available habitat, perch use, and the undisturbed locomotor behavior of four syntopic ecomorphs of *Anolis* lizards (*A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps*) in the field. Fifty percent of the cumulative perch length available in the habitat had values of diameter, length, and incline <0.8 cm, 54 cm, and 67°, respectively, indicating that narrow, short, and steep perches dominated the study site. The selection of all perch attributes by *A. distichus* was biased, whereas each of the remaining species randomly used at least one of the three attributes describing perch structure. Narrow breadth of resource use most often reflected the narrow breadth of available resources rather than selective use of resources. Interestingly, the behavioral and morphological specializations of *A. angusticeps* facilitate the use of the most common type of perch (twig) rather than a rare resource. Based on median values, the undisturbed speeds and distances of locomotion of *A. sagrei* (8.9 cm/s and 5.3 cm), *A. distichus* (31.5 cm/s and 2.8 cm), *A. carolinensis* (1.6 cm/s and 5.0 cm), and *A. angusticeps* (2.7 cm/s and 3.9 cm) were exceedingly slow and short, suggesting that neither maximal sprinting speeds nor endurance capacities were used frequently by any species in the field. The effects of habitat structure on undisturbed locomotor speeds and movement distances were highly species specific.

*Key words:* Anolis; *arboreal habitat; Bahamas; ecomorphology; habitat use; intermittent locomotion; lizard; lizard locomotion; performance; physiological ecology; preferred speeds.*

## Introduction

The ability to move actively from one location to another is a fundamental feature of animal ecology and behavior. As animals move through their environment, some attributes of habitat structure may obstruct locomotion. However, for habitats that are accessible, some structural features may affect the speed or energetic cost of movement while other features may be of no consequence to locomotion. Thus, a combination of habitat structure and the physiological capacities of an animal may affect locomotion during a variety of ecologically important activities such as dispersal, resource use, escape from predators, and territorial defense (Turchin 1998).

Maximum physiological capacities are often determined with tests of whole-organism performance in the laboratory (Arnold 1983), and comparing performance among species often facilitates correlating variation in performance with variation in morphology. For example, lizards are a model group for testing locomotor performance (reviewed in Garland and Losos 1994), and the large radiation of arboreal species belonging to the genus *Anolis* has been studied extensively (Losos 1994). Many species of *Anolis* have evolved convergent morphologies and microhabitat preferences, and these species are often categorized as the same ecomorph (Rand and Williams 1969, Williams 1972, 1983). Ecomorphs of *Anolis* with relatively long limbs generally have greater sprinting speeds and jumping distances, and they are found on thicker branches than relatively short-limbed ecomorphs (Losos 1990, Losos and Irschick 1996, Irschick and Losos 1999). The maximum running speeds of all ecomorphs decline with decreased perch diameter, and this effect of diameter is most pronounced for the long-limbed ecomorphs (Losos and Sinervo 1989, Irschick and Losos 1999). Thus, some expected effects of habitat structure on locomotor performance depend on the ecomorph.

Different ecomorphs are usually found at different heights and on perches of different diameter (Schoener 1968, Moermond 1979*a*, Pounds 1988, Losos 1990, Irschick and Losos 1996). However, several additional attributes of arboreal habitat structure might affect locomotion. For example, steeper inclines often decrease maximal speeds, decrease acceleration, and increase energetic cost (Taylor et al. 1972, Huey and Hertz 1982, Farley and Emshwiller 1996, Irschick and Jayne 1998).

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To date, the only documented effects of incline on the locomotion of lizards in the field have involved terrestrial species (Jayne and Ellis 1998, Jayne and Irschick 2000). In laboratory trials, an increased angle between perches at a branching point decreases maximal running speeds and increases the amount of pausing of *Anolis* lizards (Higham et al. 2001). Thus, the unobstructed length of a perch between successive branching points (nodes) may also affect the speed and distance of continuous movement in the field. However, no previous study has quantified the lengths of perches used by *Anolis* lizards or the extent to which lizards pause between bouts of continuous movement.

In addition to several potential effects of habitat structure on maximal speed, sometimes animals simply may choose to move with submaximal speeds. An important but largely unresolved question for physiological ecology is how often animals in nature use maximal physiological capacity (Hertz et al. 1988). The only lizard species for which speeds have been quantified for total locomotor effort in the field is a terrestrial species, *Uma scoparia*. Only a small fraction of the locomotion of *U. scoparia* occurs near maximal locomotor speeds, and the speeds of undisturbed locomotion vary significantly with physical attributes of the habitat (Jayne and Irschick 2000). Unexpectedly, much of the escape locomotion of *U. scoparia* is also substantially below maximal speed (Jayne and Ellis 1998), and large fractions of both escape and undisturbed locomotion have similar speeds (Jayne and Irschick 2000).

To better understand the adaptive radiation of *Anolis* lizards, many previous studies have related perch use to both morphology and the effects of perch diameter on maximal performance (Schoener 1968, Moermond 1979*a*, Pounds 1988, Losos 1990, Irschick and Losos 1996, 1999). However, data are lacking regarding the availability of different types of perches within a habitat. Thus, if two species from different sites use different perch types, these differences in perch use could result from either random use of perches in two sites with different habitat structure or selective use of perches in different sites with identical habitat structure. Furthermore, if several species at a single site have different modal values of perch use, then one cannot determine which of these species is using a relatively rare or common resource without knowing the distributions of perch types in the habitat. Thus, quantifying the availability of different perch types is important for interpreting the diversity of perches occupied by different *Anolis* species both among different sites and within a single site.

For flightless animals in arboreal habitats, all of the propulsive forces necessary for locomotion are generated by interacting with the available perch surfaces (Cartmill 1985). Unlike aquatic and terrestrial environments, the discontinuities in the networks of perches in arboreal habitats severely constrain the pathways available for animal locomotion. Furthermore, the diameters, lengths, and inclines of the perches forming these distinct arboreal pathways can be quantified, and these perch attributes are likely to be relevant to locomotion.

To better understand the relationships between morphological diversity, habitat use, and the effects of habitat structure on function, we conducted a field study that quantified the undisturbed speeds of locomotion and the habitat use of four syntopic ecomorphs of *Anolis* with the following major goals. We tested whether the use of perch diameter, length, and incline was random with respect to the available habitat and whether perch use differed among ecomorphs. Based on previous studies of *Anolis* ecomorphs, we expected different ecomorphs to use habitat differently such that the diameter of perches used would decrease with decreased relative limb length. For the entire locomotor effort of these ecomorphs, we determined how commonly the undisturbed speeds of locomotion approached the maximal sprinting capacities and whether the undisturbed speeds differed among ecomorphs. Finally, we tested whether the structural attributes of an arboreal habitat significantly affected the speeds of undisturbed locomotion in a natural setting.

## METHODS

### *Study site and species*

We conducted all field work within a single 50 × 50 m plot of forest (25°42′7″ N, 79°18′5″ W) on South Bimini, Bahamas, between 1 July and 31 August 2001. The vegetation in the study site is a community of blackland forest (Howard 1950). The structure of the vegetation was relatively homogeneous, and the plot was within a larger area of forest such that none of the plot included forest edge. Although some large trees were in the study site (e.g., *Bursera simaruba* and *Ficus* spp.), many trees had a trunk diameter <20 cm and a height <10 m (Fig. 1).

Four syntopic species of *Anolis* lizards with similar body sizes occur within the blackland forest: *A. sagrei* (trunk–ground ecomorph), *A. distichus* (trunk ecomorph), *A. carolinensis* (trunk–crown ecomorph), and *A. angusticeps* (twig ecomorph) (Fig. 2). The rank order of species from the least to the greatest amount of time required for us to locate an individual was *A. sagrei*, *A. distichus*, *A. angusticeps*, and *A. carolinensis*. *Anolis sagrei* was extremely conspicuous and more abundant than the other three species, and we were often able to locate one adult male for every five minutes of searching. Within the study site, *A. carolinensis* was rare compared to the other three species, and sometimes we could locate only a few adult males in an entire day. Our impressions of the relative abundance of these *Anolis* species correspond well with those described previously for the blackland forest of South Bimini (Schoener 1968). We made focal observations of each

FIG. 1. Photograph of the study site in blackland forest on South Bimini, Bahamas. The diameter of the largest tree in the foreground is ~12 cm.

species at haphazardly chosen locations throughout the study site.

Ecomorphs of *Anolis* are defined primarily by the microhabitat preferences and morphology of adult males (Williams 1972), and the effects of perch structure on the maximum running speeds of *Anolis* species have only been studied for adult males (Losos and Sinervo 1989, Losos and Irschick 1996, Irschick and Losos 1999). We also did not want variation in size within a species to confound our attempt to relate locomotor speed to habitat structure. Thus, we only studied adult males. Immediately after conducting focal observations, we captured several individuals of *A. sagrei* (*n* = 17), *A. distichus* (*n* = 4), *A. carolinensis* (*n* = 12), and *A. angusticeps* (*n* = 11), for which the mean values (and range) of snout–vent length and mass were 5.5 cm (5.0–5.8 cm) and 7.6 g (5.8–9.0 g), 4.9 cm (4.7–5.1 cm) and 5.9 g (5.5–6.3 g), 5.3 cm (4.7–5.8 cm) and 5.6 g (4.8–6.5 g), and 4.6 cm (4.4–4.9 cm) and 4.6 g (4.3–5.0 g), respectively. The size of the observed individuals that eluded capture appeared to be within the size range of the captured individuals.

### *Quantification of available habitat*

We trisected the 50 × 50 m plot with two parallel transects and measured the diameter, length, and incline of every woody perch intersecting a 1-m wide plane at heights of 1 and 2 m along each 50-m transect. To quantify habitat structure, we chose heights of 1 and 2 m for several reasons. Two meters was the greatest height at which it was practical to make the large number of measurements required to characterize the habitat, and the 1-m height provided an intermediate value. All of our videotaped focal observations were for lizards <3 m above the ground, and for *A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps*, the percentages of observations at heights <2 m were 95%, 90%, 81%, and 62%, respectively. A previous study involving point sightings of adult males of *A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps* on South Bimini found that the frequencies of occurrence on perch heights <2.6 m were 98%, 93%, 91%, and 64%, respectively (Schoener 1968). Thus, all of our focal observations were within 1 m of a transect height, and the heights used to quantify habitat and observe lizards encompassed the vast majority of the heights of perches used by these *Anolis* species.

Where each perch intersected the 1- or 2-m high reference plane, we used calipers to measure the diameter (±1 mm) and a digital level (Smart Tool Builder's Angle finder, Macklanburg-Duncan, Oklahoma City, Oklahoma) to measure the angle of inclination (±1°). We calculated values of rise per meter as the sine of the angle of inclination. For example, a rise of 0.5 indicates a vertical gain of 0.5 m for 1 m of perch with a 30° incline. We measured perch length (±1 mm) as the straight-line distance between two successive branching points (i.e., the internode distance). We pooled all data from the two transects to determine the cumulative frequency distribution of each perch attribute in the habitat.

### *Focal observations of lizard locomotion*

We used a Sony TRV520 digital camcorder (Sony, Tokyo, Japan) to videotape the undisturbed locomotion of *Anolis* lizards within the study site. During each taping session, we remained ~5 m from the lizard. We observed several individuals feeding and some individuals mating, which suggests that our presence was

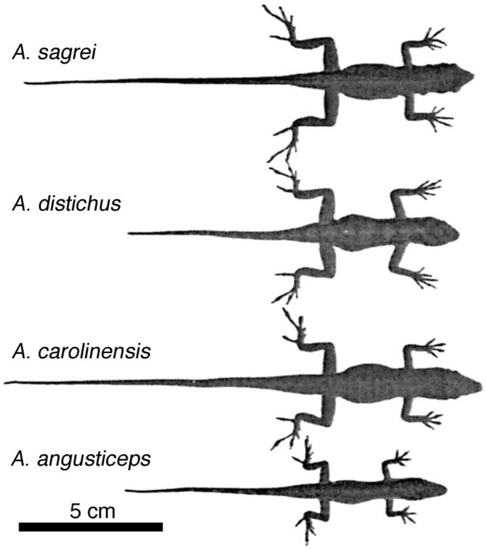

FIG. 2. Dorsal views of anesthetized specimens of each of the four *Anolis* species. Although the overall body size is similar in each species, the relative lengths of the limbs and tail differ.

not substantially affecting behavior. We recorded ~20 bouts of continuous movement per individual, where each bout was defined as all movement between a distinct start and a pause (>0.03 s) in locomotion. We defined striding locomotion as the alternate use of the hindlimbs, whereas jumping involved the simultaneous retraction and extension of both hindlimbs. Following each focal observation, we attempted to capture the lizard to measure its snout–vent length (±1 mm) and mass (±0.1 g).

We used the video playback feature of the camera to facilitate the reconstruction of locomotor paths. At the endpoint of each movement within a perch, we measured the perch diameter (±1 mm), angle of inclination (±1°), and height (±1 cm), and perch length was measured as the straight-line distance (±1 mm) between successive nodes. Unlike the angles of inclination describing available habitat, which were all positive values, the values for perches within locomotor paths were positive and negative for uphill and downhill locomotion, respectively. We also measured the elapsed time (±0.03 s) and straight-line distance (±1 mm) of continuous movement upon each perch. Thus, if a bout of continuous movement spanned three perches, we recorded three sets of values for elapsed time, movement distance, and each perch attribute, and the distance traveled on the second perch would equal the length of that perch. For continuous bouts of movement that crossed more than one perch, we also measured the three-dimensional interperch angle (±5°) between successive perches in the locomotor path from the perspective of the moving lizard. Thus, an interperch angle of 0° indicated that the two perches formed a straight path, and values between 90° and 180° indicated a partial reversal in the forward direction of travel of the lizard. We categorized each perch involved in a locomotor path as one of three substrate types: trunk base (the basal portion of a tree below the lowest node), trunk (the structure with the largest diameter at a given height above the lowest node), or branch (neither trunk base nor trunk).

For each bout of continuous movement by a lizard, we calculated the within-perch speed by dividing the distance of continuous movement along a single perch by the elapsed time of the movement. If a bout of continuous movement involved more than one perch, we also summed the distances traveled on each perch and divided by the respective sum of elapsed times to calculate the average speed per whole movement. For each focal observation, we also determined pause durations (±0.03 s) between continuous bouts of movement.

We observed a total of 30 individuals each of *A. sagrei*, *A. distichus*, and *A. angusticeps*, and 27 individuals of *A. carolinensis*. We observed the following total numbers of within-perch movements and whole-movement bouts for *A. sagrei* (456 and 350), *A. distichus* (579 and 563), *A. carolinensis* (536 and 355), and *A. angusticeps* (635 and 487). Because of the similar number of individuals observed for each species and the similar number of movement bouts observed per individual, no one individual had an undue influence on the values characterizing a species.

### *Data analysis*

To quantify the availability and use of habitat, we determined the frequency distributions of perch attributes based on the percentage of the total pathway distance rather than using frequencies based simply on a percentage of a total number of occurrences. We primarily used this method for the following reasons. First, we were interested in locomotion, and distance is one of the most useful currencies for describing locomotor effort of animals since it is directly proportional to the energetic cost of movement on a terrestrial surface (Bennett 1985). Second, for our particular system, the vast majority of perches were very narrow and effectively all of the lizard locomotion occurred along the length of perches rather than around their circumference. Third, we wanted frequency distributions describing habitat that best reflected the probability that a lizard moving randomly would be on a perch with a particular attribute. Therefore, the percentage of the total distance traveled by an animal best indicates the relevance to the animal, and the same units (percentage total distance) must be used to permit direct comparisons of cumulative frequency distributions describing the availability and use of habitat.

We compared pairs of cumulative frequency distributions for a given variable using Microsoft Excel 2000 (Redmond, Washington) to calculate the value of $D$ for a two-sample Kolmogorov-Smirnov (K-S) test based on the equations in Kim and Jennrich (1970). To facilitate the spreadsheet calculations of the cumulative frequencies for perch diameter, perch length, perch rise, movement distance, and average speed per movement, we used bin widths of 1 mm, 1 cm, 0.01, 1 cm, and 1 cm/s, respectively, to compute a bin-wise sum of the relevant distance. Each bin sum was divided by the total distance and converted to a cumulative frequency (frequency of last bin = 1). We then subtracted the cumulative frequencies of homologous bins of one distribution (with $m$ cumulative frequencies) from those of the other distribution (with $n$ cumulative frequencies), and $D$ was the largest value of these pairwise subtractions. We used $m$ and $n$ as the sample sizes to determine the critical values of $D$ for these K-S tests. Rather than indicating the total numbers of original observations, the sum of $m$ and $n$ indicated the upper limit on the number of pairwise subtractions performed between the cumulative frequencies. For each perch attribute, we examined 10 pairwise comparisons among species and between each species and the habitat. Thus, to correct for multiple comparisons, we emphasized results for which the $P$ value of an individual test was $<0.005$. To facilitate evaluating the effects of multiple comparisons, we provide the relevant exact (uncorrected) $P$ values for individual comparisons.

To further clarify the patterns of habitat use by each *Anolis* species, we calculated values of niche breadth ($B$) using the index provided by Levins (1968): $B = (\Sigma p_i^2)^{-1}$ where $p_i$ represents the frequency of use of perch type $i$. To determine the values of $p_i$ for each species, we used the frequency distributions of perch diameter, length, and rise to calculate the frequency of use of perch types with the same bin widths as for the K-S analyses.

Because we quantified the available habitat structure of the study site, we were able to determine the preference of each species for particular perch types using the resource selectivity index provided by Schoener (1974): $B_s = (\Sigma(d_k/f_k)^2)^{-1}$ where $d_k$ represents the frequency of use of perch type $k$ by a species, and $f_k$ represents the relative availability of perch type $k$ within the habitat. Thus, this index of resource selectivity provides a measure of niche breadth weighted by the relative availability of resources. To determine values of $f_k$ and $d_k$ for each species, we used the frequency distributions of perch diameter, length, and rise with bin widths of 5 mm, 5 cm, and 0.05, respectively. The bin widths for the calculations of $B$ and $B_s$ differ because we pooled several bins when calculating values of $B_s$ to avoid having values of $f_k = 0$. Thus, for perch diameters $>10$ cm and perch lengths $>130$ cm, we used bin widths of 24 and 25 cm, respectively, to calculate values of $B_s$ for each species.

We used SYSTAT version 5.0 (Wilkinson 1992) to perform forced-fit multiple regressions that related the effects of habitat structure to both the within-perch movement distances and speeds of each species. We examined all combinations of the independent variables, which included perch diameter, length, rise (both linear and quadratic terms), and within-perch movement distance (used only for the regressions predicting speed). For the average speed per movement for each species, we also performed forced-fit multiple regressions to assess the effects of total movement distance and the number of nodes crossed per bout. For all multiple regression analyses, our final choice of a model was the analysis with the greatest value of $R^2$ and for which each partial regression coefficient was significant ($P < 0.05$).

## RESULTS

### *Available habitat*

The cumulative frequency distributions of each perch attribute describing habitat structure did not differ significantly between 1- and 2-m heights within each transect or between the two transects (K-S tests, all $P$ values $> 0.05$). Thus, we pooled all habitat data for each perch attribute before making comparisons with the habitat used by each species of *Anolis*.

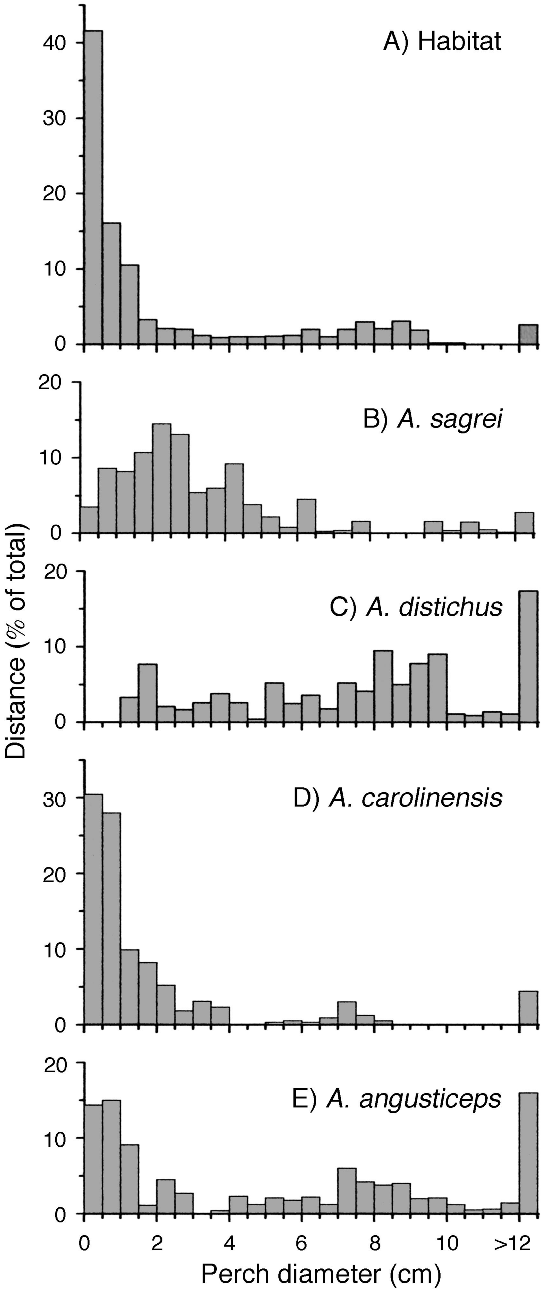

FIG. 3. (A) Frequency distribution of the percentage total distance of available perch diameters in the habitat and (B–E) frequency distributions of the percentage cumulative distance traveled on perch diameters by each species. For (B) *A. sagrei*, (C) *A. distichus*, (D) *A. carolinensis*, and (E) *A. angusticeps*, 50% and 90% of the cumulative distance occurred on perches with diameters <2.8, 8.2, 0.8, and 4.7 cm; and 6.3, 15.4, 6.5, and 13.2 cm, respectively.

The mean and median values ($n = 2819$ perches) of perch diameter (0.74 and 0.30 cm), length (27.3 and 13.7 cm), and rise (0.75 and 0.83) indicate that most perches were narrow (Fig. 3A), short (Fig. 4A), and steep (Fig. 5A). The cumulative perch length of the

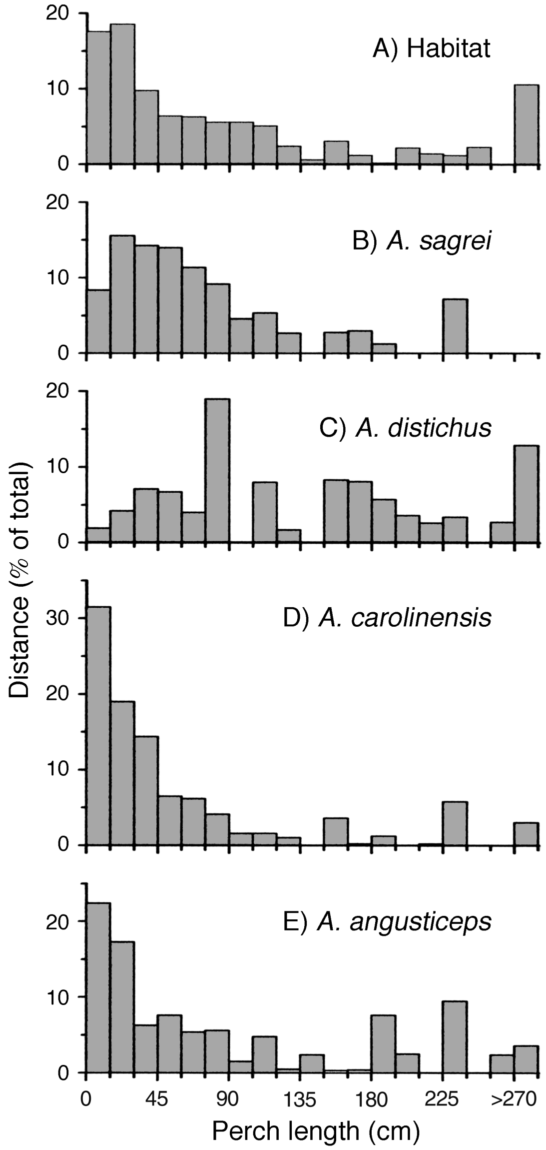

FIG. 4. (A) Frequency distribution of the percentage total distance of available perch lengths in the habitat, and (B–E) the percentage cumulative distance traveled on perch lengths by each species. For (B) *A. sagrei*, (C) *A. distichus*, (D) *A. carolinensis*, and (E) *A. angusticeps*, 50% and 90% of the cumulative distance occurred on perches with lengths <60, 120, 29, and 56 cm; and 180, 289, 190, and 229 cm, respectively.

sampled habitat was 769 m. Based on the number of perches measured, 50% and 90% had diameters <0.4 and 1.4 cm, lengths <13.8 and 61.0 cm, and values of rise <0.828 and 0.996, respectively. Based on the cumulative lengths of available perches, 50% and 90% had diameters <0.8 and 8.2 cm (Fig. 3A), lengths <54 and 280 cm (Fig. 4A), and values of rise <0.921 and 0.996 (Fig. 5A), respectively.

### *Habitat use*

Most of the distance traveled by *A. sagrei*, *A. carolinensis*, and *A. angusticeps* occurred on branches,

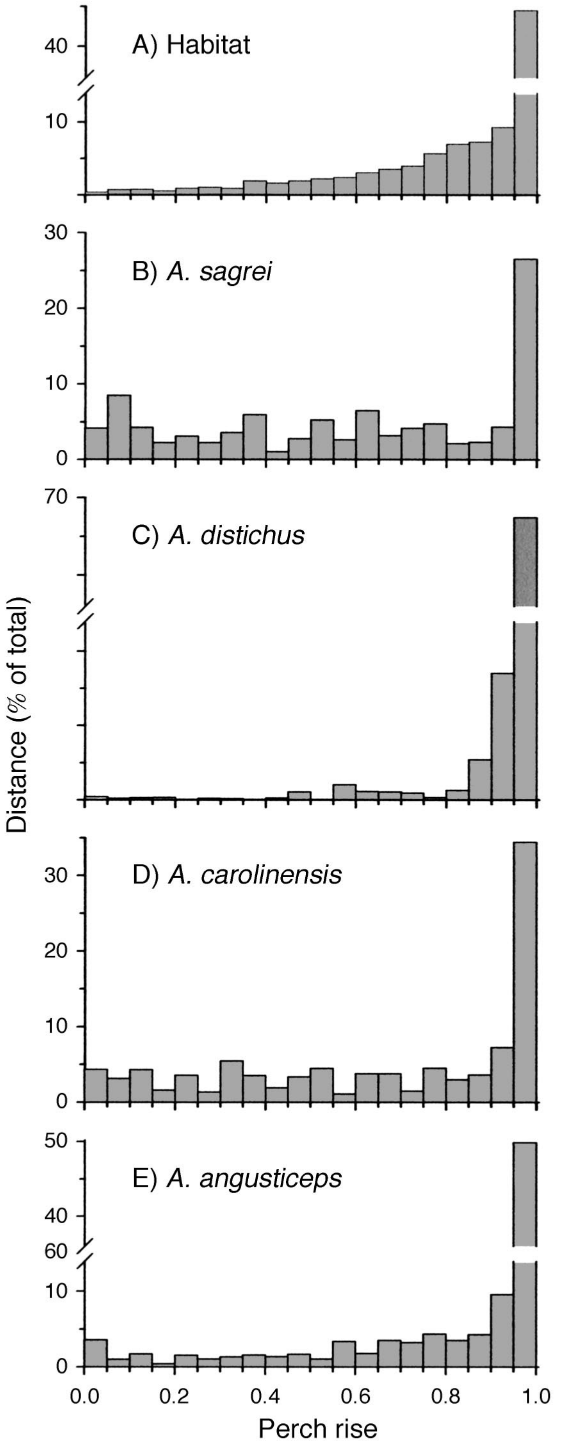

FIG. 5. (A) Frequency distribution of the percentage total distance of available perch inclines in the habitat, and (B–E) the percentage cumulative distance traveled on perch inclines by each species. For (B) *A. sagrei*, (C) *A. distichus*, (D) *A. carolinensis*, and (E) *A. angusticeps*, 50% and 90% of the cumulative distance occurred on perches with values of rise <0.639, 0.978, 0.782, and 0.950; and 0.992, 0.997, 0.995, and 0.995, respectively.

TABLE 1. Summary of the use of particular perch types and the turning and jumping frequencies of each *Anolis* species.

| Species | Distance traveled on perch type (%) | | | Mean nodes crossed/bout | Bouts with node crossed (%) | Nodes crossed with turn >5° (%) | Bouts with jump (%) |
|---|---|---|---|---|---|---|---|
| | Trunk base | Trunk | Branch | | | | |
| *A. sagrei* | 6.6 | 22.6 | 70.8 | 0.30 | 18.6 | 21.7 | 14.9 |
| *A. distichus* | 33.5 | 31.6 | 34.9 | 0.03 | 2.8 | 4.8 | 78.7 |
| *A. carolinensis* | 8.1 | 13.2 | 78.7 | 0.51 | 31.5 | 29.0 | 11.0 |
| *A. angusticeps* | 11.4 | 16.0 | 72.6 | 0.30 | 21.1 | 24.4 | 8.8 |

whereas *A. distichus* traveled nearly equal distances on each of the three types of perches (Table 1). Although *A. sagrei* is categorized as a trunk–ground ecomorph, this species had the smallest percentage of total distance traveled on trunk bases (i.e., <30%). Nearly two-thirds of the distance traveled by *A. distichus* occurred on either trunk bases or trunks. *Anolis carolinensis* and *A. angusticeps* used trunks and branches in similar proportion (Table 1). Based on the endpoint of each within-perch movement, the rank order of species based on increasing median values of perch height was *A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps* (Table 2), and the values for the ranges in perch height were 4–272, 4–284, 1–300, and 1–300 cm, respectively.

*Anolis carolinensis* used perch diameters randomly with respect to the available habitat, whereas the remaining *Anolis* species used significantly greater diameters than expected (Fig. 3, Table 3). The cumulative frequency distributions of distance traveled on particular perch diameters had highly significant differences for all pairwise comparisons among species (K-S tests, all $P$ values $< 0.0001$; Fig. 3). Based on median values of the total distance traveled on perch diameters, the rank order of species from the smallest to largest value was *A. carolinensis*, *A. sagrei*, *A. angusticeps*, and *A. distichus*.

After correcting for multiple comparisons, the lengths of perches used by *A. sagrei*, *A. carolinensis*, and *A. angusticeps* conformed to a random sample of the habitat, whereas *A. distichus* used significantly longer perches than expected (Fig. 4, Table 3). The cumulative frequency distributions of distance traveled on perches of a particular length by *A. sagrei* and *A. angusticeps* were the most similar, and the use of perch length did not differ significantly between *A. carolinensis* and *A. angusticeps*. However, the cumulative frequency distributions of the use of perch length differed significantly for all remaining pairwise species comparisons after the Bonferroni correction (Fig. 4, Table 4).

After correcting for multiple comparisons, both *A. carolinensis* and *A. angusticeps* used perch inclines randomly with respect to the available habitat. *Anolis sagrei* used fewer steep perches than expected for this habitat, whereas *A. distichus* used more steep perches (Fig. 5, Table 3). The use of perch incline did not differ between *A. sagrei* and *A. carolinensis*, *A. carolinensis* and *A. angusticeps*, or *A. angusticeps* and *A. distichus*. However, the cumulative frequency distributions of distance traveled on given perch inclines differed significantly for all remaining pairwise species comparisons after the Bonferroni correction (Fig. 5, Table 4).

The rank order of species based on increasing mean values of interperch angles traversed was *A. distichus*, *A. sagrei*, *A. angusticeps*, and *A. carolinensis* (Table 2). The paths taken by *A. distichus* when crossing nodes rarely involved turns >5°, whereas the turning frequencies of the remaining species were greater and had similar values (Table 1). For all pairwise comparisons among species, the frequency distributions of the interperch angles taken did not differ significantly (K-S tests, all $P$ values $> 0.17$).

The rank order of species differed among the three measures of breadth for the use of perch diameter, length, and incline. For the use of perch diameter and length, *A. carolinensis* had the narrowest breadths, whereas *A. distichus* had the greatest breadths. For use of perch incline, *A. sagrei* and *A. distichus* had the greatest and narrowest breadths, respectively (Table 5). The rank order of species also differed among the three measures of resource selectivity. Furthermore, rank orders of species for a particular perch attribute were not consistent between the measures of $B$ and $B_s$ (Table 5).

### *Lizard locomotion*

The rank order of species based on increasing median values of the distance traveled per movement bout was

TABLE 2. Summary of mean and median values of used perch attributes and the locomotor behavior of each *Anolis* species.

| Variable | *A. sagrei* | *A. distichus* | *A. carolinensis* | *A. angusticeps* |
|---|---|---|---|---|
| Perch height (cm) | 118, 113 (456) | 113, 118 (579) | 146, 138 (536) | 183, 181 (635) |
| Interperch angle (°) | 7.6, 0 (106) | 1.7, 0 (21) | 15.0, 0 (186) | 12.2, 0 (156) |
| Movement distance (cm) | 11.5, 5.3 (350) | 4.4, 2.8 (563) | 9.7, 5.0 (355) | 7.3, 3.9 (487) |
| Movement speed (cm/s) | 13.4, 8.9 (350) | 32.8, 31.5 (563) | 2.6, 1.6 (355) | 4.9, 2.7 (487) |
| Pause duration (s) | 67.3, 12.8 (320) | 18.0, 2.5 (533) | 30.3, 4.2 (328) | 32.8, 10.3 (457) |

*Note:* Values are mean, median ($n$).

TABLE 3. $P$ values from two-sample Kolmogorov-Smirnov tests comparing the cumulative frequency distributions of available habitat structure with perch use by each *Anolis* species.

| Perch attribute | *A. sagrei* | *A. distichus* | *A. carolinensis* | *A. angusticeps* |
|---|---|---|---|---|
| Diameter | <0.0001 (95, 95) | <0.0001 (95, 118) | 0.2458 (95, 56) | <0.0001 (95, 120) |
| Length | 0.2168 (162, 90) | 0.0001 (162, 54) | 0.0160 (162, 68) | 0.8542 (162, 78) |
| Incline | <0.0001 (101, 95) | 0.0034 (101, 53) | 0.0065 (101, 100) | 0.9627 (101, 97) |

*Note:* Sample sizes are indicated parenthetically after each $P$ value.

*A. distichus*, *A. angusticeps*, *A. carolinensis*, and *A. sagrei*, and most of the movement distances were short and often less than the snout–vent length of the lizard (Table 2). Although *A. sagrei* and *A. distichus* were the least similar in the distances traveled per movement bout (K-S test, $P = 0.04$), none of the pairwise species comparisons of the cumulative frequency distributions of distance traveled per movement differed significantly after correcting for multiple comparisons (K-S tests, all remaining $P$ values $> 0.25$; Fig. 6).

The rank order of species based on increasing median values for the average speeds per whole movement was *A. carolinensis*, *A. angusticeps*, *A. sagrei*, and *A. distichus*, and the vast majority of undisturbed speeds of locomotion were very slow (Table 2). The fastest 10% of the total distance traveled by *A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps* occurred with speeds >37.3, 57.0, 8.3, and 19.1 cm/s, respectively. The cumulative frequency distributions of average speed per movement of *A. carolinensis* and *A. angusticeps* did not differ significantly (K-S test, $P = 0.08$; Fig. 7C, D), whereas all remaining pairwise species comparisons had highly significant differences (K-S tests, all remaining $P$ values $< 0.0001$; Fig. 7).

The rank order of species based on increasing median values of pause durations between continuous bouts of movement was *A. distichus*, *A. carolinensis*, *A. angusticeps*, and *A. sagrei* (Table 2). The cumulative frequency distributions of pause durations differed significantly for all pairwise comparisons between species (K-S tests, all $P$ values $< 0.005$).

From the highest to the lowest mean value of nodes crossed per movement bout, the rank order of species was *A. carolinensis*, *A. angusticeps*, *A. sagrei*, and *A. distichus* (Table 1). On average, *A. carolinensis* crossed a node during one out of every two bouts, which was more often than the twig ecomorph, *A. angusticeps*.

Most of the movement bouts of *A. distichus* included a jump (Table 1). However, fewer than 15% of the bouts of the remaining three species involved jumps. Nearly 97% of the jumps by *A. distichus* occurred within a perch, whereas fewer than 5% of jumps were within a single perch for each of the remaining species. Thus, with the exception of *A. distichus*, all species usually jumped between different perches.

### *Effects of habitat on locomotion*

Multiple regressions of within-perch movement distances revealed that the effects of habitat structure were species dependent both in the number of significant variables and in the sign of the coefficients (Table 6). For example, the within-perch movement distances of *A. carolinensis* increased significantly with decreased perch diameter, the distances traveled by *A. distichus* increased with greater diameters, and the movement distances of the remaining two species were not significantly affected by perch diameter. Within-perch movement distances increased significantly with perch length for all species except *A. distichus*. The within-perch movement distances of both *A. distichus* and *A. angusticeps* increased significantly with a positive quadratic polynomial of perch rise, whereas the distances traveled by the other two species were unaffected by perch rise. These regression models accounted for up to 21% of the observed variance in within-perch movement distances (Table 6).

Multiple regressions of within-perch speeds revealed that the combined effects of habitat structure and within-perch movement distances were also species dependent (Table 7). For example, perch diameter and length only affected the within-perch speeds of *A. angusticeps*. The speeds of *A. sagrei* increased with a linear term of perch rise. The speeds of *A. distichus* changed significantly with a negative linear and a positive quadratic term of rise such that the slowest predicted speed was for a shallow uphill incline, and the fastest predicted speed was for running down the steepest (vertical) surface (rise $= -1$). The within-perch speeds of

TABLE 4. $P$ values from two-sample Kolmogorov-Smirnov tests comparing the cumulative frequency distributions for use of perch length (upper right) and perch incline (lower left) for all pairwise species combinations.

| Species | *A. sagrei* | *A. distichus* | *A. carolinensis* | *A. angusticeps* |
|---|---|---|---|---|
| *A. sagrei* | | <0.0001 (54, 90) | 0.0020 (68, 90) | 0.0651 (78, 90) |
| *A. distichus* | <0.0001 (95, 53) | | <0.0001 (54, 68) | 0.0005 (54, 78) |
| *A. carolinensis* | 0.3903 (95, 100) | <0.0001 (100, 53) | | 0.0467 (78, 68) |
| *A. angusticeps* | <0.0001 (95, 97) | 0.0185 (97, 53) | 0.0281 (100, 97) | |

*Note:* Sample sizes are indicated parenthetically after each $P$ value.

TABLE 5. Measures of niche breadth ($B$) and resource selectivity ($B_s$) for the use of perch diameter, length, and incline by each *Anolis* species.

| Measure | Perch diameter | Perch length | Perch incline |
|---|---|---|---|
| Niche breadth ($B$) | | | |
| *A. sagrei* | 11.8 | 22.4 | 9.6 |
| *A. distichus* | 18.8 | 22.5 | 2.0 |
| *A. carolinensis* | 5.2 | 13.5 | 6.9 |
| *A. angusticeps* | 14.6 | 18.1 | 3.7 |
| Resource selectivity ($B_s$) | | | |
| *A. sagrei* | 0.0034 | 0.0070 | 0.0027 |
| *A. distichus* | 0.0032 | 0.0030 | 0.1013 |
| *A. carolinensis* | 0.0211 | 0.0224 | 0.0037 |
| *A. angusticeps* | 0.0062 | 0.0253 | 0.0081 |

*Notes:* For each species, we used 47, 50, and 20 bins to calculate values of $B$ for perch diameter, length, and incline, respectively. We calculated values of $B_s$ for perch diameter, length, and incline using 21, 35, and 20 bins, respectively.

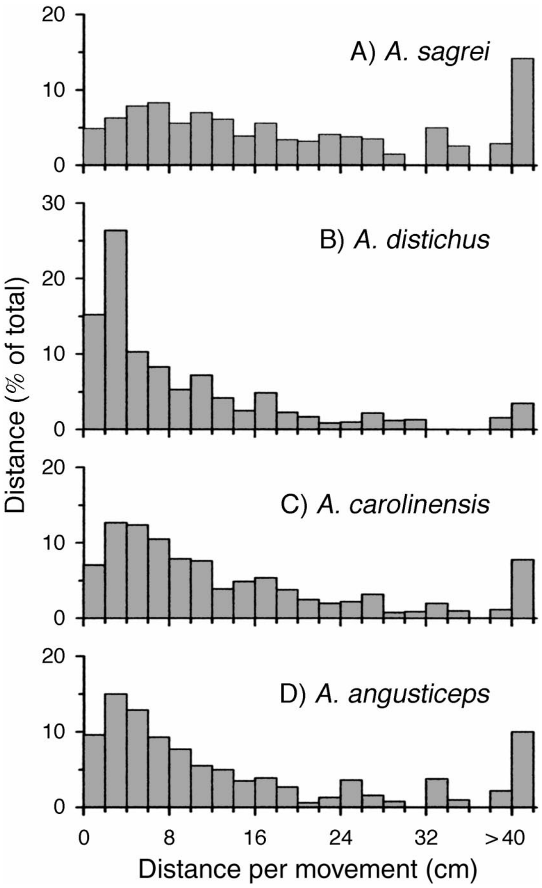

FIG. 6. Frequency distributions of the percentage cumulative distances traveled using particular movement distances by each species. For (A) *A. sagrei*, (B) *A. distichus*, (C) *A. carolinensis*, and (D) *A. angusticeps*, 50% and 90% of the cumulative distance occurred with movement distances $<$16, 6, 10, and 9 cm; and 46, 25, 34, and 40 cm, respectively.

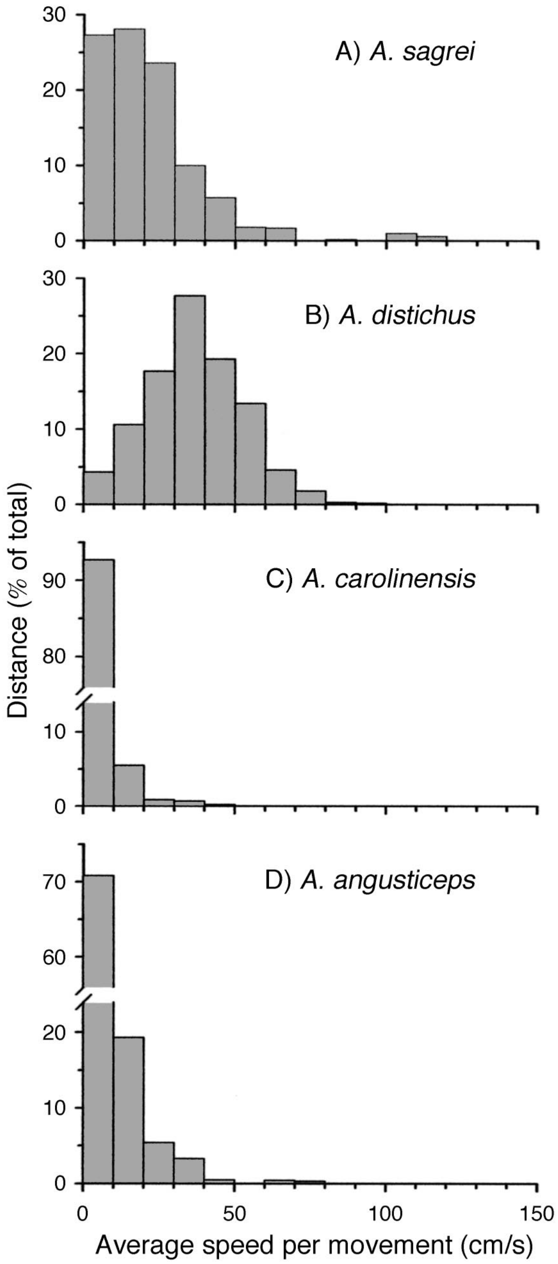

FIG. 7. Frequency distributions of the percentage cumulative distance traveled at average speeds per movement for each species. For (A) *A. sagrei*, (B) *A. distichus*, (C) *A. carolinensis*, and (D) *A. angusticeps*, 50% and 90% of the cumulative distance occurred with average speeds $<$18, 37, 2, and 6 cm/s; and 37, 57, 8, and 19 cm/s, respectively.

all four species increased significantly with within-perch movement distance. These regression models accounted for up to 16% of the observed variance in within-perch speeds (Table 7).

Multiple regressions of whole-movement speeds revealed that the average speed per bout increased significantly with whole-movement distance for all species. However, the number of nodes crossed per bout

TABLE 6. Standardized partial regression coefficients from separate multiple regression analyses testing the effects of each perch attribute on the within-perch movement distance of each *Anolis* species.

| Species | *n*† | $R^2$ | Overall *P* value | Independent variables | | | |
|---|---|---|---|---|---|---|---|
| | | | | Diameter | Length | Rise | $\text{Rise}^2$ |
| *A. sagrei* | 456 | 0.009 | 0.038 | | 0.097* | | |
| *A. distichus* | 579 | 0.058 | <0.001 | 0.133*** | | 0.129** | 0.162*** |
| *A. carolinensis* | 536 | 0.208 | <0.001 | −0.251*** | 0.545*** | | |
| *A. angusticeps* | 635 | 0.087 | <0.001 | | 0.204*** | | 0.161*** |

*Notes:* Empty cells indicate nonsignificant results.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† The number of within-perch movements.

only affected the whole-movement speeds of *A. sagrei* ($R^2 = 0.14$, $\beta = -0.366$, $P < 0.0001$). These regression models accounted for up to 17% of the observed variance in whole-movement speeds.

## DISCUSSION

### *Arboreal habitats*

The complex, three-dimensional structure of arboreal habitats poses a challenge to quantitative sampling methods. Consequently, few studies have thoroughly quantified the types of perches available within arboreal communities. Previous methods for studying perch use by *Anolis* lizards have measured the nearest distance between a focal perch and each perch type within a series of five or fewer diameter categories (Pounds 1988, Losos 1990, Losos and Irschick 1996, Irschick and Losos 1998). Some studies of arboreal primate locomotion have grouped perch types within a series of six or fewer diameter and incline categories (Morbeck 1977, Garber 1991, McGraw 1998). On a larger scale, vertical profiles of arboreal habitats have quantified the dimensions of individual tree crowns (Terborgh and Petren 1991, Cannon and Leighton 1994, Garber and Pruetz 1995) as well as the abundance of perch types within each diameter and incline category at particular height intervals (McGraw 1998). In the present study, we quantified perch diameter, length, and incline as continuous variables to obtain a finer scale understanding of available habitat.

Moffett (2001) emphasized that the ecological processes of arboreal communities should be viewed in light of the three-dimensional structure of arboreal habitats. The three-dimensional complexity of arboreal habitats arises in part from variation in surface inclines. For example, the steepest 10% of available perches in our study site had inclines >85°, and the maximum perch incline in this arboreal habitat was 90°. In contrast, for 1-m intervals of a terrestrial dune system with a maximum substrate incline of 32°, the steepest 10% of surfaces had inclines >20° (Jayne and Irschick 2000). Whether a particular habitat is perceived as three-dimensional depends on the scale of an organism relative to its immediate substrate. For example, a rock protruding 20 cm out of the ground could momentarily force a small terrestrial lizard to move on a nearly vertical surface, whereas a large animal such as a human could readily step over such a rock.

Arboreal habitats are further distinguished by the discontinuity of available surfaces (Moermond 1986), and the discontinuities of arboreal surfaces pose many functional challenges unlike those of most terrestrial environments. In our study, most of the locomotion of lizards paralleled the long axis of the perch. Consequently, the networks of perches involved in locomotor paths often forced anoles to turn or to secure footholds on an array of perch diameters and inclines. Arboreal lizards must also bridge gaps between discontinuous perches through reaching and jumping. Alternatively, a more circuitous path must be traveled when discontinuous perches cannot be spanned successfully.

Arboreal habitats are often cluttered with obstructions that may arise from either branches emanating from a particular perch or branches and leaves not directly connected to the perch upon which locomotion

TABLE 7. Standardized partial regression coefficients from separate multiple regression analyses testing the effects of each perch attribute and within-perch movement distance on the within-perch speed of each *Anolis* species.

| Species | *n*† | $R^2$ | Overall *P* value | Independent variables | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Diameter | Length | Rise | $\text{Rise}^2$ | Distance |
| *A. sagrei* | 456 | 0.136 | <0.001 | | | 0.088* | | 0.354*** |
| *A. distichus* | 579 | 0.160 | <0.001 | | | −0.131*** | 0.253*** | 0.261*** |
| *A. carolinensis* | 536 | 0.048 | <0.001 | | | | | 0.219*** |
| *A. angusticeps* | 635 | 0.141 | <0.001 | 0.205*** | −0.134* | | | 0.332*** |

*Notes:* Empty cells indicate nonsignificant results.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† The number of within-perch movements.

occurs. In this study, the mean total hindlimb spans (distance between the toetips of outstretched limbs) for *A. sagrei* and *A. angusticeps* were 9.2 and 5.2 cm, respectively. For perches giving rise to two branches on opposite sides, perch diameters of 5.9 and 3.3 cm would be required to provide an unobstructed 180° arc equal to the hindlimb spans of *A. sagrei* and *A. angusticeps*, respectively. Thus, when perch diameters exceed ~6 cm, the probability of side branches interfering with the limbs is greatly reduced for all species. In contrast, side branches on perches with diameters <3 cm are likely to impede limb movements of all species when crossing a node.

### *Use of habitat by* Anolis

Comparative studies of resource use often provide insight into the mechanisms by which communities of syntopic species partition available resources. If the breadths of resource use are broad or narrow, then species are often recognized as either generalists or specialists, respectively (Brown 1984). In our study, none of the *Anolis* species consistently had all of the greatest or smallest values of breadth for the perch attributes, and thus no single species was uniformly the most generalized or specialized. However, based on the breadth of resource use for both perch diameter and perch length, *A. carolinensis* and *A. distichus* were the most specialized and generalized, respectively.

The tendency to distinguish generalists and specialists based solely on the breadth of resource use is in part due to the practical difficulties of determining the availability of resources. However, accounting for the availability of resources permits a more comprehensive evaluation of both habitat use and the extent to which *Anolis* species are specialized. In addition to a broad breadth of resource use, generalists are further characterized by the nonselective (random) use of resources. Despite the narrow breadth of perch diameter use, K-S tests revealed that *A. carolinensis* used diameter randomly. In our study site, narrow perches were simply the most abundant perch type. *Anolis carolinensis* also had the highest value of $B_s$ for the use of perch diameter, indicating that it was the least selective of the four species. In contrast to *A. carolinensis*, *A. distichus* selectively used rare (large) perch diameters. For many other perch attributes and species, both the K-S tests and $B_s$ indices supported overall similar conclusions regarding specialization, but both of these methods yielded very different conclusions from those based solely on habitat breadth.

We found the K-S tests particularly convenient for quantifying the extent to which habitat use was random because it avoided two of the drawbacks of using the $B_s$ index. First, the choice of bin widths substantially affects the values of $B_s$ (Pianka 1986). For example, the rank order of species based on $B_s$ changed substantially when we doubled the width of bins. Second, if any of the frequencies of resource availability in the habitat ($f_k$) equal zero, then $B_s$ cannot be calculated. In our study site, large trees were rare. Thus, when we used bins of equal width, several bins for perch diameter lacked observations. Consequently, for the rare resource types, we had to use larger bin widths than those used for the more common resources.

Among anoline lizards, twig ecomorphs are often considered specialists (Hicks and Trivers 1983, Irschick and Losos 1996). Twig ecomorphs have convergently evolved several derived morphological and behavioral traits including relatively short limbs, an elongated body, a prehensile tail, and reliance on crypsis rather than speed for avoiding predators (Hicks and Trivers 1983, Irschick and Losos 1996). These derived traits of twig ecomorphs make them well suited for living on short, narrow perches where attaining high speeds is difficult for all species of anoles (Williams 1983, Losos 1990). Interestingly, the evolutionary specializations in the morphology and behavior of *A. angusticeps* facilitate the use of the most common type of perch (twig) rather than a rare resource. Thus, morphological specialization in these *Anolis* lizards does not correspond to ecological specialization.

One of the clearest expectations for habitat use by *Anolis* based on morphology is that species with the greatest relative limb length use perches with the greatest diameter (Losos 1990). Based on increasing values of relative limb length for adult males, the rank order of species was *A. angusticeps*, *A. carolinensis*, *A. distichus*, and *A. sagrei*. In contrast, the rank order of species based on increasing median values of perch diameter use was *A. carolinensis*, *A. sagrei*, *A. angusticeps*, and *A. distichus*. Although *A. carolinensis* is designated as a trunk–crown ecomorph and does not have the shortest limbs, this species had both the lowest median value of perch diameter use as well as the narrowest breadth of perch diameter use.

### *Lizard locomotion*

A central issue in physiological ecology concerns how often organisms use their maximal physiological capacities in the field (Hertz et al. 1988). Maximal locomotor speeds of lizards have been determined frequently in the laboratory (reviewed in Garland and Losos 1994). However, complementary data for both undisturbed (Jayne and Irschick 2000) and maximal locomotor speeds (Jayne and Ellis 1998) are only available for a single species of lizard, *Uma scoparia*, which lives on the surface of sand dunes. *Uma scoparia* has a high degree of overlap between the distributions of undisturbed and escape speeds of locomotion. The undisturbed locomotor speeds of *U. scoparia* are distinctly bimodal, and ~11% of the total distance traveled is within the low speed mode (<0.7 m/s). The values of the faster mode of undisturbed locomotion (mean = 2.00 m/s) are very similar to those of the unimodal distribution of escape speeds (mean = 2.65 m/s). However, only a small fraction (11%) of escape locomotion is within 90% of the maximal speeds of this species. Additional field studies of voluntary locomotion have documented bimodal frequency distributions of undisturbed speed for mammals (Pennycuick 1975, Kenagy and Hoyt 1989). In contrast, the frequency distributions of undisturbed speed for all Bahamian *Anolis* species were clearly unimodal and very slow.

From slowest to fastest based on laboratory tests of maximal locomotor speeds, the rank order of species is *A. angusticeps* (0.8 m/s), *A. carolinensis* (1.2 m/s), *A. distichus* (1.6 m/s), and *A. sagrei* (1.8 m/s) (Losos and Irschick 1996, Irschick and Losos 1998; W. B. Mattingly and B. C. Jayne, *unpublished data*). In the present field study, the rank order of species based on the average speed of undisturbed locomotion was *A. carolinensis* (0.03 m/s), *A. angusticeps* (0.05 m/s), *A. sagrei* (0.13 m/s), and *A. distichus* (0.33 m/s). Thus, the rank order of species differed between laboratory escape and average undisturbed speeds in the field.

The observed locomotor effort of each *Anolis* species in the field was an extremely small fraction of the respective maximal speeds. For example, the 50th and 90th percentiles for undisturbed speeds of *A. sagrei*, *A. distichus*, *A. carolinensis*, and *A. angusticeps* represent only 4.9% and 22.8%, 19.7% and 35.9%, 1.3% and 6.7%, and 3.4% and 25.0% of their maximal locomotor speeds, respectively. The behavioral motivations for voluntary locomotion may contribute to the considerable difference between maximal and undisturbed speeds. For example, twig ecomorphs rely on cryptic behavior and actively forage by moving slowly through twig microhabitats (Hicks and Trivers 1983, Irschick and Losos 1996). Although we observed relatively slow speeds of undisturbed locomotion for all ecomorphs, anoles may use a greater percentage of their maximal capacities in nature during certain locomotor behaviors, such as escaping from predators (Irschick and Losos 1998). However, this faster behavior appears to be a very small fraction of the total locomotor effort that we observed for the Bahamian anoles.

The cluttered arboreal habitats commonly used by *Anolis* species may provide cover from visually oriented predators, which could reduce the need for rapid bouts of locomotion between distant points of refuge. Similarly, in a terrestrial dune system, the slower undisturbed speeds of *U. scoparia* were commonly associated with vegetative cover, whereas high speeds were often used to traverse open areas (Jayne and Irschick 2000).

Speeds that can be maintained for several minutes are usually aerobically sustainable (John-Alder et al. 1983), and the low speed mode of the undisturbed locomotion of *U. scoparia* is probably aerobically sustainable (Jayne and Irschick 2000). The mean endurance capacity of *A. carolinensis* while moving at 0.28 m/s is 95 s (Garland 1999). After aerobically sustainable speeds are exceeded, endurance times decline very rapidly, and thus speeds of *A. carolinensis* below 0.2 m/s are likely to be aerobically sustainable. If the endurance of *A. carolinensis* is similar to the other *Anolis* ecomorphs we studied, then most of the movement bouts we observed were aerobically sustainable. However, more than half of the locomotor bouts of *A. distichus* may be supported primarily by anaerobic metabolism. Thus, in contrast to the undisturbed locomotion of *U. scoparia*, a large fraction of the locomotion of anoles in nature is aerobically sustainable. The median values for the durations of undisturbed movement of *A. sagrei* (0.7 s), *A. distichus* (0.1 s), *A. carolinensis* (3.5 s), and *A. angusticeps* (1.4 s) were also exceedingly brief and punctuated by relatively long pauses (median values of 12.8, 2.5, 4.2, and 10.3 s, respectively). Thus, neither the maximal speeds nor the endurance capacities of any *Anolis* species we studied were frequently taxed in nature.

Intermittent locomotion can increase the ability of an animal to move a greater distance per unit time than steady speed locomotion (Weinstein 2001), but the detailed effects of pausing depend on both the speed and duration of movement as well as the duration of pausing (Gleeson and Hancock 2001). Few field studies have quantified the extent to which arboreal animals move intermittently or considered the significance of intermittent movement during undisturbed locomotion in nature (Kramer and McLaughlin 2001). If the frequent pauses we observed for *Anolis* have primarily a physiological function of promoting recovery from exertion, then we would expect the speed or distance of movement immediately before or after a pause to increase significantly with pause duration. However, the only positive correlation was for *A. angusticeps*, for which the pause duration increased with the speed before pausing ($r = 0.10$, $n = 457$, $P = 0.039$). For *A. carolinensis*, pause durations were not significantly correlated with either the movement distance or speed immediately preceding or following the pause, and some negative correlations occurred between speeds and pause durations of *A. sagrei* and *A. distichus*. Consequently, our field observations do not suggest that the intermittent locomotion of anoles primarily serves a physiological function. However, the intermittent locomotion of *Anolis* species may facilitate scanning for prey (Moermond 1979*b*), predators, intruders, or mates.

### *Effects of habitat structure on* Anolis *locomotion*

In our study, the effects of habitat structure on locomotion were remarkably species specific (Tables 6 and 7). Not only did different perch attributes affect the locomotion of different species, the directionality of the effects of some perch attributes also differed among species. Consequently, the mechanical effects of perch attributes are unlikely to provide a sufficient explanation of the observed variation in locomotion.

Species-specific effects occur for laboratory trials, in which decreased perch diameter (from 5.1 to 0.6 cm) causes the greatest decrease in the sprinting speeds of

*Anolis* ecomorphs with the longest limbs (Losos and Sinervo 1989, Losos and Irschick 1996, Irschick and Losos 1999). Although the mechanism for this decrease in performance is not fully understood, short-limbed ecomorphs may have less difficulty than long-limbed species in maintaining a generalized sprawling stance and securing footholds on relatively narrow perches. However, in the laboratory, the sprinting speeds of all ecomorphs do decrease with decreased perch diameter. Thus, the magnitude but not the directionality of this diameter effect is species specific.

Unexpectedly, diameter did not affect the undisturbed speeds of three of the *Anolis* species in our study. In contrast to laboratory trials of sprinting speeds, most undisturbed speeds in the field may simply be so slow that perch diameter is of little consequence. The only species for which we did observe a significant positive effect of perch diameter on undisturbed speed was the one with the shortest limbs, *A. angusticeps*. Perhaps this effect of diameter reflects that *A. angusticeps* has a greater reliance on cryptic behavior on narrow perches in cluttered areas.

No previous laboratory or field study has assessed the effects of perch length on the arboreal locomotor behavior of anoles. We expected within-perch movement distances to increase significantly with perch length, and this was observed for all species except *A. distichus*. Most of the locomotion of *A. distichus* consisted of single short ($<$6 cm) jumps followed by a pause. High-speed videos of other species of *Anolis* in the laboratory have previously revealed that lizards commonly pause both before and after a jump as the limbs are repositioned to facilitate the next locomotor movement (Higham et al. 2001). Despite *A. distichus* occurring most frequently on large perches with long unobstructed pathways, the short distances moved may simply result from the biomechanical constraints involved in preparing for and recovering from moving with bilateral rather than alternating use of the limbs.

Of all the attributes of habitat that we measured, the mechanical consequences for locomotion are best understood for inclines. Uphill inclines commonly decrease maximal speed and acceleration, and increase energetic cost of locomotion; and these effects are often more pronounced for relatively large organisms (Taylor et al. 1972, Huey and Hertz 1982, Farley and Emshwiller 1996, Irschick and Jayne 1998). The fastest undisturbed speeds of *U. scoparia* are most likely to occur on shallow downhill slopes (rise = 0.06), and for humans and other large mammals, the energetic cost of locomotion is minimal on a shallow downhill slope and increases with increased steepness (Dailey and Hobbs 1989). Thus, a highly significant positive quadratic effect predicting faster speeds of *A. distichus* on both the steep uphill and downhill surfaces was contrary to expectations based on the mechanical effects of incline on locomotion. In addition, incline had no effect on the undisturbed speeds predicted for *A. carolinensis* and *A. angusticeps*, but the extremely slow speeds of these species may have such low physiological demands that the effects of incline were not apparent. These cumulative results emphasize how the actual use of physiological capacities by animals in their natural setting may depart considerably from expectations of environmental effects based on laboratory tests of maximal capacities.

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