



ARTICLES

The choice of arboreal escape paths and its consequences for the locomotor behaviour of four species of *Anolis* lizards

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The direction and speed of escape locomotion can affect the ability of an animal to evade a predator, and variation in habitat structure often affects speed. Consequently, the escape paths chosen by animals may affect their performance and subsequent survival. Arboreal locomotion is well suited for gaining insight into the choice of escape routes because of the discrete paths formed by branches. Decreased branch diameter and increased angles between branches can significantly decrease locomotor speeds, but no previous study has determined whether arboreal lizards selectively choose alternative paths. We quantified choice of escape paths and locomotor performance of four syntopic species of arboreal *Anolis* lizards in their natural habitat and in the laboratory. In the field, species with shorter limbs occurred more commonly on narrow perches than did long-limbed species, but all species favoured escape paths with larger-diameter perches and straighter interperch angles. Thus, short-limbed species used narrower perches than long-limbed species merely as a result of what they encountered, rather than as a result of a biased choice at branching points. In natural vegetation, choosing branches with the largest diameter often results in the straightest path. However, in the laboratory, most lizards preferred large-diameter perches with a sharp turn to continuing a straight path onto a small-diameter perch. Although an overriding preference for larger perch diameter may optimize escape speed within a single perch, a maladaptive side-effect could be a compromise of the overall rate of gaining distance from starting points in paths with turns.

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Locomotion of animals is often of central importance for escaping predators (Roeder 1963; Howland 1974; Webb 1986; Lima 1993), and many attributes of habitat structure affect maximal speeds of locomotion. Consequently, the escape routes chosen by animals may affect speed and the probability of successfully evading the threat. Although biomechanical studies facilitate predicting the theoretical optima possible for speed and direction of locomotion during escapes (Howland 1974; Weihs & Webb 1984), empirical data on the choice of escape routes are scarce, especially for animals in complex natural habitats. The locomotion of animals in structurally complex arboreal habitats is well suited for studying the choice of

escape routes, because many biomechanical effects of perch structure are well documented, and branching points present discrete choices for escape paths.

Diverse species face many similar environmental challenges during locomotion, and lizards, especially the diverse radiation of the arboreal anoles, have been a model system for quantifying the underlying general mechanical effects of habitat structure. For example, increased steepness of uphill inclines commonly decreases maximal locomotor speed and acceleration (Huey & Hertz 1982; Irschick & Jayne 1998). Locomotor speed usually decreases with increased turning (Jayne & Ellis 1998; Higham et al. 2001) and decreased diameter of arboreal perches (Losos & Sinervo 1989). Many arboreal species move their feet along the sides of perches (Higham & Jayne 2004; Spezzano & Jayne 2004), so perches with numerous, closely spaced side branches could impede foot placement and reduce speed. Thus, inclines, interperch angles, diameters and unobstructed lengths of perches all have demonstrated or expected effects on locomotor performance, and all

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of these attributes can be quantified readily in natural habitats and manipulated experimentally in the laboratory.

Many studies have documented striking interspecific correlations between behaviour, morphology, habitat use and locomotor performance of *Anolis* lizards (Schoener 1968; Williams 1972; Moermond 1979a; Pounds 1988; Losos 1990; Mattingly & Jayne 2004). For example, long-limbed species of *Anolis* generally use broader perches and have greater sprinting speeds than do short-limbed species, and the maximal speeds of long-limbed species are affected more severely than those of short-limbed species when perch diameter decreases (Losos & Sinervo 1989; Losos 1990; Losos & Irschick 1996). The different modal values of perch attributes used by syntopic species of anoles in the field confound determining and comparing the effects of habitat structure on behaviour and locomotor performance, but laboratory experiments can overcome this complication (Losos & Sinervo 1989; Losos 1990; Losos & Irschick 1996; Higham et al. 2001). Combined field and laboratory observations are thus a powerful approach for ensuring ecological realism as well as establishing biomechanical capacity (Irschick & Garland 2001).

Similar to the data on resource use of most other groups of animals, most data regarding perch use of anoles are based on observations only of outcomes after a choice has been made (Schoener 1968; Moermond 1979a; Pounds 1988; Losos 1990; Irschick & Losos 1999). Additional information on either resource availability or direct observations of the process of choosing is necessary to clarify the extent to which resource use reflects selectivity. For example, after quantifying the global availability of perches in the habitat, Mattingly & Jayne (2004) found that the primary use of very small-diameter perches by a short-limbed species of anole simply conforms to a random sample of available perch diameters, rather than reflecting selective use of resources. However, no laboratory or field study has directly determined whether anoles selectively choose a perch when crossing a branching point. Such a study is important to address the common situation where choices available in the immediate vicinity of animals differ considerably from those available within the entire habitat. Thus, one must disentangle the process of choosing from the constraints imposed on choice by local conditions.

For four syntopic species of *Anolis* lizards with different limb lengths and microhabitats, we quantified the choice of escape paths in the field and laboratory to test the following three alternative hypotheses. (1) Lizards within each species have no preference and thus choose randomly from the alternative perches encountered at a branching point. (2) Different species prefer different types of perches for escapes. The species found most frequently on large-diameter perches may have the strongest preference for escape routes with larger diameters. (3) All species show a similar bias in choosing among available perches for escape, which could result from similar mechanical factors that optimize locomotor performance. We also used multiple regression analyses to test whether the structural attributes of the natural arboreal habitat significantly affected escape speeds and whether these effects varied among species.

METHODS

Experimental Subjects

We studied only adult males to minimize the confounding effects of size. Furthermore, the effects of perch diameter and turning angle on locomotor behaviour are known only for adult male anoles (Losos & Sinervo 1989; Losos & Irschick 1996; Higham et al. 2001). From radiographs of anaesthetized specimens used for laboratory experiments, we observed the following mean \pm SE values of mass, snout-vent length and hindlimb span (between the tips of the fourth toes) for *Anolis sagrei* (4.6 ± 0.1 g, 5.3 ± 0.1 cm, 9.3 ± 0.1 cm, $N = 14$), *A. distichus* (3.3 ± 0.1 g, 4.8 ± 0.1 cm, 8.0 ± 0.1 cm, $N = 6$), *A. carolinensis* (4.6 ± 0.3 g, 6.1 ± 0.1 cm, 8.3 ± 0.1 cm, $N = 5$) and *A. angusticeps* (1.5 ± 0.1 g, 4.5 ± 0.1 cm, 5.4 ± 0.1 cm, $N = 11$), respectively. Hereafter, based on the mean ratio of hindlimb span to snout-vent length, we use 'long-limbed species' (L) to refer to both *A. sagrei* (1.75) and *A. distichus* (1.66) and 'short-limbed species' (S) to refer to both *A. carolinensis* (1.36) and *A. angusticeps* (1.20).

Field Experiments

All field observations were conducted during July 2002 in blackland forest ($25^{\circ}42'7''N$, $79^{\circ}18'5''W$) on South Bimini, Bahamas, using the same 50×50 -m plot as in Mattingly & Jayne (2004). We haphazardly distributed the focal observations of each species throughout the relatively homogeneous habitat, which is quantified in Mattingly & Jayne (2004). We elicited escape responses from individuals of each focal species and videotaped their responses to quantify choice of escape paths for each species. The initial heights (cm) of the lizards from which we elicited escapes (mean \pm SE values and ranges: *A. sagrei*: 133 ± 10 , 19–226; *A. distichus*: 177 ± 11 , 32–272; *A. carolinensis*: 161 ± 14 , 69–266; *A. angusticeps*: 173 ± 9 , 68–242) are typical for the vast majority of habitat used by these species on South Bimini (Schoener 1968; Mattingly & Jayne 2004). The four syntopic study species partition this habitat on a fine scale in part by using perches with different diameters and heights (Schoener 1968). We frequently observed more than one *Anolis* species on a single tree.

We elicited escape responses from focal individuals when the long axes of the lizards and initial perches were parallel to each other, thus forcing the lizards to cross at least one branching point (node) and choose between alternative paths. The initial head orientation could be either uphill or downhill, but this orientation did not affect our choice of animals for eliciting escapes. To elicit an escape, from an initial distance of 2 m we lunged at each lizard with a 1-m pole pointed towards the middle of the lizard's body, dorsal and perpendicular to its long axis. To avoid observing an individual more than once, we used indelible ink to mark the ventral surface of lizards captured after the focal observations. Furthermore, male anoles are territorial, and we did not elicit escapes from more than one individual per species per tree. For those individuals that we were able to capture and measure after

escapes, we observed the following mean \pm SE values of snout-vent length (cm): *A. sagrei*: 5.2 ± 0.1 ($N = 11$); *A. distichus*: 4.9 ± 0.2 ($N = 2$); *A. carolinensis*: 4.9 ± 0.2 ($N = 5$); and *A. angusticeps*: 4.3 ± 0.1 ($N = 17$). The size of the individuals that eluded capture appeared to be within the size range of the captured individuals.

We defined a perch as the portion of a branch between two successive branching points. For every perch upon which movement occurred and every perch emanating from each node crossed (within a $\pm 90^\circ$ arc from the lizard along the circumference of the previous perch) during an escape, we recorded the diameter (± 1 mm), length (± 1 mm) and rise (sine of the angle of inclination measured $\pm 1^\circ$) as in Mattingly & Jayne (2004). We also measured the three-dimensional interperch angle ($\pm 5^\circ$) between each initial perch and every perch emanating from a crossed node ($0^\circ =$ straight path).

Anoles commonly pause very briefly even during high-speed escape locomotion (Higham et al. 2001). Thus, we used a long pause (> 3 s) to delineate the end of an entire escape, within which we quantified the duration (± 0.03 s) and distance (± 1 mm) of each of the continuous movements separated by short pauses (< 3 s). Within-perch speed equalled distance divided by the elapsed time of continuous movement along one perch, and the average speed per continuous movement equalled the sum of the distances divided by the sum of elapsed times of movement on each perch. For the entire escape response, we determined the average speed, total distance and total duration of short pauses (± 0.03 s). Lizards use the hindlimbs alternately during striding locomotion, but simultaneously retract both hindlimbs when jumping.

We analysed one escape per individual of *A. sagrei* ($N = 30$), *A. distichus* ($N = 30$), *A. carolinensis* ($N = 21$) and *A. angusticeps* ($N = 30$), which involved a total of 41, 62, 30 and 80 continuous movements for each species, respectively. For continuous movements that crossed a node during escapes, we quantified the perches taken and the perches not taken, respectively, by *A. sagrei* ($N = 62$ and $N = 71$), *A. distichus* ($N = 48$ and $N = 66$), *A. carolinensis* ($N = 60$ and $N = 78$) and *A. angusticeps* ($N = 48$ and $N = 58$).

Laboratory Experiments

We collected adult males from the study site (Bahamas permit no. 02/31) to make detailed measurements of anatomy in the laboratory and to use in laboratory performance and path choice trials. Animal husbandry and care were in accordance with Institutional Animal Care Use Committee of the University of Cincinnati (protocol number 01-01-30-02) and as described in Higham et al. (2001). The lizards used in the laboratory studies either died of natural causes in captivity or were ultimately euthanized with an overdose of anaesthetic (sodium pentobarbital) after the performance and path choice trials.

Performance trials

Within 2 weeks of collecting the anoles, we videotaped (250 images/s, NAC HSV-500 high-speed video camera)

and tested the sprinting performance (as in Higham et al. 2001) of all lizards within their preferred active body temperature range of $29\text{--}31^\circ\text{C}$ (Irschick & Losos 1999) on courses that were straight and with a 90° turn. Both race courses were within planes inclined 30° relative to the horizontal, with a total path length of 2 m, and were made of 4.8-cm diameter polyvinyl chloride (PVC) pipe covered with fibreglass screen (1.5-mm mesh) to enhance traction (as in Irschick & Losos 1998).

We completed all performance trials within two successive days and tested each individual on only one race course per day. On each day, we conducted both morning and afternoon testing sessions in which every individual ran approximately four times in rapid succession. We selected the single fastest trial per individual for a detailed stride-by-stride analysis. To minimize the confounding effects of time, we divided individuals of each species into two groups for which the order of testing on the different race courses was reversed, and we randomized the order in which the individuals were tested within each session.

Path choice trials

To assess path choice in the laboratory, we constructed four perch networks covered with fibreglass screen (1.5-mm mesh) and with different combinations of 1.0- and 4.8-cm perch diameters and interperch angles of 0° , 45° and 90° (Fig. 1). We designed perch network 1 in the laboratory specifically to decouple perch diameter from interperch angle, because these quantities usually covary in natural vegetation. All perches within a network were coplanar. We used a combination of two NAC HSV-500 high-speed video cameras (250 images/s) and a JVC GR-DVL9800 digital camcorder (120 images/s) to videotape the lizards. The visual background was similar for all available pathways. For all observations of perch network 1, 82–100% of the individuals for each of the four species turned both left and right. Thus, no obvious bias in turning direction was evident.

Within 4 weeks of collecting the anoles, we assessed the path choice of each individual on each of the four perch networks inclined at both 30° and 60° relative to a horizontal plane. During 2 weeks of testing, we conducted trials on two consecutive days followed by a single

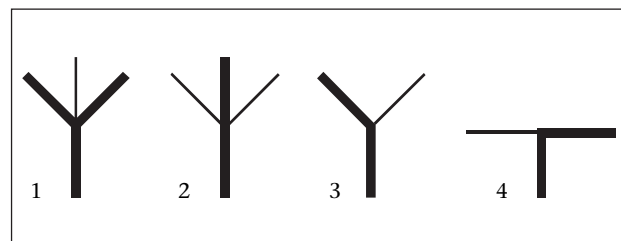


Figure 1. Schematic illustrations of the four perch networks used in the laboratory path choice trials. For each perch network, thin lines represent diameters of 1.0 and thick lines represent diameters of 4.8 cm. Perch networks 1 and 2 provided both 0° and 45° interperch angles, and perch networks 3 and 4 provided 45° and 90° interperch angles, respectively. Each length of perch emanating from the central node was 1 m. The top of each diagram represents the uphill end of the perch network.

resting day. We tested each individual on only one combination of perch network and incline per testing day. The temperature, replication, timing of tests within a day and randomization with respect to time were similar to those of the performance tests.

Data Analysis

Field experiments

Accounting for repeated measures within individuals is desirable, and conceptually our data for individuals were nested within species, nodes were nested within individuals, and two groups of perches occurred at each node (taken and not taken). However, our data were not appropriate for a nested analysis of variance (ANOVA) for the following reasons. Some individuals crossed only a single node, and the resulting lack of replication within an individual precludes performing a nested ANOVA. Furthermore, some data had distributions for which no transformation could yield an approximate normal distribution. Sometimes taking paired differences is useful for collapsing the number of observations so that the degrees of freedom will not be inflated from repeated measures, but some nodes crossed by lizards had more than two perches, which precludes such a strategy.

Furthermore, important biological information can be lost when calculating paired differences. For example, the absolute diameter of a perch affects locomotor function by determining how the lizards we studied will fit onto a perch, and the functional difference between 19- and 20-cm diameters is trivial compared to that between 1- and 2-cm diameters (Spezzano & Jayne 2004), even though the paired differences are equal. Similarly, collapsing multiple values to a single mean for each individual can obscure biological meaning, as in the case of equal-magnitude uphill and downhill perch inclines, which would have a mean value of zero, indicating a nonexistent choice of a horizontal perch. We also think that an entire escape path is biologically most relevant, because this determines total distance moved from a threat.

However, a statistical drawback of analysing an entire escape path is that repeated observations are present within individuals. A choice of a conservative P value as the criterion for a significant result can help to compensate for some of the complications arising from the inflated degrees of freedom associated with multiple observations within individuals. We therefore used this approach, along with additional methods described below, to minimize some of the complications arising from the repeated observations within individuals.

For all nodes crossed and for only the first node crossed by each individual, we determined the frequency with which the perch with the most extreme attribute was chosen. For each species, we calculated a mean expected frequency of choosing a particular perch by calculating the mean of the inverses of the numbers of perches per node. For example, if all nodes had three perches and if lizards randomly selected perches, then the expected frequency for a particular perch being taken would be 0.33. We calculated Z scores to test whether the observed and expected proportions of perches taken differed significantly (Zar 1999). Despite the benefit

of retaining some information by comparing perches within a node, a drawback of only using such frequencies is that they are not sufficient either to establish resource availability or to allow complete comparisons of resource use among species, which are best accomplished with frequency distributions of absolute measures of both resources available and resources used.

We used SYSTAT version 5.0 (Wilkinson 1992) to perform two-sample Kolmogorov–Smirnov tests for pairwise comparisons of the cumulative frequency distributions of perch attributes taken and not taken within each species. For our data, which were not normal, one attraction of the Kolmogorov–Smirnov test is that it requires no assumptions regarding the nature of the distribution. Furthermore, the Kolmogorov–Smirnov test could be applied uniformly to all of our variables to directly test our key hypothesis of whether the perches used were chosen randomly. A disadvantage of this approach is losing the association between perches taken and not taken within a node. However, for multiple nodes crossed by multiple individuals, a consistent bias in choosing perch attributes will result ultimately in two different populations, and the Kolmogorov–Smirnov test specifically tests whether two samples are from the same population without collapsing the variation of a population to a single parameter, such as a mean. To alleviate concerns regarding pseudoreplication, we performed the Kolmogorov–Smirnov tests on perches only from the first node encountered by each individual as well as on all perches. To correct for multiple comparisons in these analyses, we emphasize results for which $P < 0.005$, but we provide the relevant (uncorrected) exact P values for individual tests to facilitate evaluating the effects of multiple comparisons.

We used SYSTAT version 5.0 to perform forced-fit multiple regressions that related the effects of habitat structure to both the within-perch movement distances and within-perch speeds of each species during escape locomotion. 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 within-perch speed). For the average speed per escape, we also performed forced-fit multiple regressions to assess the effects of total movement distance, cumulative amount of turning and the number of nodes crossed per entire escape. Our final choice of a model was the multiple regression with the greatest value of R^2 and for which each partial regression coefficient was significant ($P < 0.05$).

Laboratory trials

From videotapes of all performance trials, we determined the total elapsed time (± 4 ms) for traversing the middle 50 cm of each perch network as well as for each stride. Net elapsed times of events excluded the total duration of all pauses within the interval of interest. Thus, we calculated gross and net speeds as distance divided by the total and net elapsed times, respectively. For each combination of individual and perch network with the greatest value of gross speed, we used the same methods as Higham et al. (2001) to conduct a kinematic analysis of

five successive strides (numbered -2, -1, 0, 1 and 2, respectively, where stride 0 straddled the midpoint of the perch network). For each stride, we determined its length (straight-line distance between positions of the right ankle at successive footfalls) and gross and net speeds.

We used SAS version 8.0 to perform four-way (for stride-by-stride variables) and three-way (gross speeds, net speeds, and number of pauses over the entire 5-stride interval) ANOVAs. For the independent categorical variables, individual was a random factor nested within species, and species ($N = 4$), turning angle ($N = 2$) and stride number ($N = 5$) were all fixed and crossed. We performed F tests according to the guidelines of Scheffé (1959) for mixed models. For the path choice trials, we used only the fastest (gross speed over the middle 50 cm) trial for each combination of perch network and incline per individual to determine the frequency of particular paths taken.

RESULTS

Field Experiments

Escape locomotion

For escapes in the field, all species strongly preferred straight paths with large diameters. Most of the escape paths chosen by each species involved perches with either the greatest diameter (83%) or the straightest interperch angle (73%; Table 1). Furthermore, for each species, the cumulative frequency distributions of both diameter and interperch angle of perches taken differed significantly from those of the perches not taken (Figs 2, 3). The inclines of perches taken and not taken differed significantly only for *A. sagrei*, and most escape paths of all species were uphill on nearly vertical surfaces (Fig. 4). For each species, the lengths of the perches taken and not taken were statistically similar (Kolmogorov–Smirnov tests: all $P > 0.05$ using either all nodes or only the first node crossed).

Interspecific differences in the attributes of perches taken were more widespread for perch diameter than for any other perch attribute (Table 2). The long-limbed

species (i.e. *A. sagrei* and *A. distichus*) had the greatest and second-greatest median values, respectively, of perch diameters taken (Fig. 2). In contrast to perch diameter, none of the distributions of interperch angles taken differed significantly between species, and most species lacked highly significant differences in the inclines of perches taken (Table 2, Figs 3, 4). The most conspicuous interspecific differences in the lengths of perches taken involved *A. carolinensis* versus the long-limbed species (Table 2), as indicated in part by the following mean and median values: *A. sagrei* (mean = 39.5 cm, median = 23.8 cm); *A. distichus* (44.2 cm, 23.3 cm); *A. carolinensis* (10.4 cm, 7.5 cm); *A. angusticeps* (20.2 cm, 11.8 cm).

Most individuals of *A. sagrei* (67%) were oriented head downward before being startled, whereas the remaining species usually had an uphill orientation (*A. distichus*, 60%; *A. carolinensis*, 71%; *A. angusticeps*, 67%). For all species, none of the lizards with an initial uphill orientation reversed orientation after being startled, but lizards with an initial downhill orientation commonly began their escape with a rapid turn to orient and run uphill (*A. sagrei*, 85%; *A. distichus*, 83%; *A. carolinensis*, 50%; *A. angusticeps*, 50%).

None of the straight (less than 5°) escape paths taken across a node in the field included a jump. However, for paths with a turn greater than 5°, jumps were used in 16%, 0%, 27% and 23% of the escapes of *A. sagrei* ($N = 19$), *A. distichus* ($N = 12$), *A. carolinensis* ($N = 11$) and *A. angusticeps* ($N = 13$), respectively.

Both the distance and speed of continuous movements differed significantly in most of the species comparisons (Fig. 5). Although Kolmogorov–Smirnov tests showed that the distances travelled per continuous movement did not differ significantly between *A. sagrei* and *A. distichus* ($P = 0.052$) or between *A. carolinensis* and *A. angusticeps* ($P = 0.197$), all remaining pairwise comparisons between species had P values below 0.001. Except for *A. carolinensis* versus *A. angusticeps* ($P = 0.011$), all pairwise species comparisons of the cumulative frequency distributions of the average speed per movement had highly significant differences (all P values < 0.0001; Fig. 5). The field escapes of

Table 1. Percentages of extreme perch attributes chosen by each *Anolis* species upon crossing nodes during bouts of escape locomotion in the field

Perch attribute	<i>A. sagrei</i> (L) $N=62$ (30)		<i>A. distichus</i> (L) $N=48$ (30)		<i>A. carolinensis</i> (S) $N=60$ (21)		<i>A. angusticeps</i> (S) $N=48$ (30)	
	%	P	%	P	%	P	%	P
Broadest diameter	95 (93)	<0.0001 0.0001	94 (90)	<0.0001 0.0003	90 (95)	<0.0001 0.0015	83 (87)	0.0002 0.0013
Longest length	39 (53)	0.20 0.43	38 (50)	0.32 0.456	25 (24)	0.016 0.082	40 (37)	0.31 0.29
Shallowest incline	31 (33)	0.040 0.18	46 (40)	0.46 0.42	38 (38)	0.026 0.33	52 (57)	0.37 0.30
Straightest angle	84 (80)	<0.0001 0.0095	90 (87)	<0.0001 0.0008	87 (91)	<0.0001 0.0042	73 (80)	0.0078 0.0085

Values of N indicate the numbers of perches taken. Values in parentheses represent data for only the first node crossed and values not in parentheses represent data for all nodes crossed. P values are for the comparison of observed and randomly expected frequencies. L: long-limbed species; S: short-limbed species.

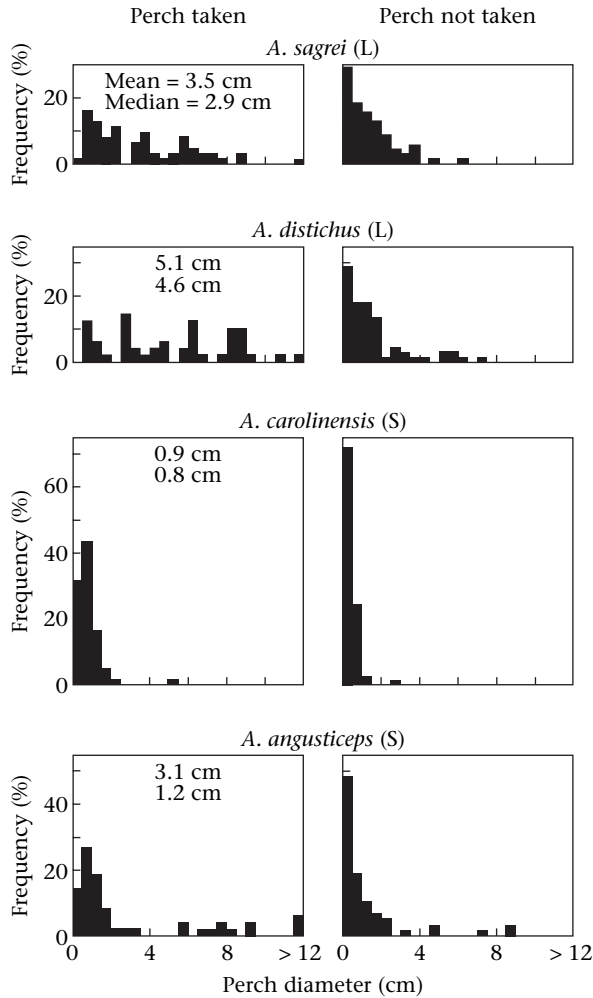


Figure 2. Frequency distributions of the diameters of all perches taken (left) and all perches not taken (right) by each *Anolis* species during escape locomotion in the field. Mean and median values are also shown. Using all nodes and only the first node yielded the following *P* values for Kolmogorov–Smirnov tests comparing the cumulative frequency distributions of perches taken and not taken by *A. sagrei* (<0.0001 , 0.0005), *A. distichus* (<0.0001 , 0.0002), *A. carolinensis* (<0.0001 , 0.0132) and *A. angusticeps* (<0.0001 , 0.0045), respectively. L: long-limbed species; S: short-limbed species.

A. sagrei and *A. distichus* had the greatest and second-greatest mean and median values, respectively, of both distance and speed per continuous movement (Fig. 5).

Effects of habitat on escape locomotion

Multiple regressions revealed that the effects of habitat structure on within-perch speed, within-perch movement distance and whole-escape speed differed considerably between the four species. For example, the within-perch speeds of both short-limbed species increased significantly with perch diameter, but within-perch speeds of both long-limbed species were unaffected by diameter (Table 3). The within-perch movement distances of both *A. sagrei* ($R^2 = 0.19$, $P < 0.001$) and *A. angusticeps* ($R^2 = 0.20$, $P < 0.001$) increased significantly only with perch length, but in *A. carolinensis*, this variable increased significantly

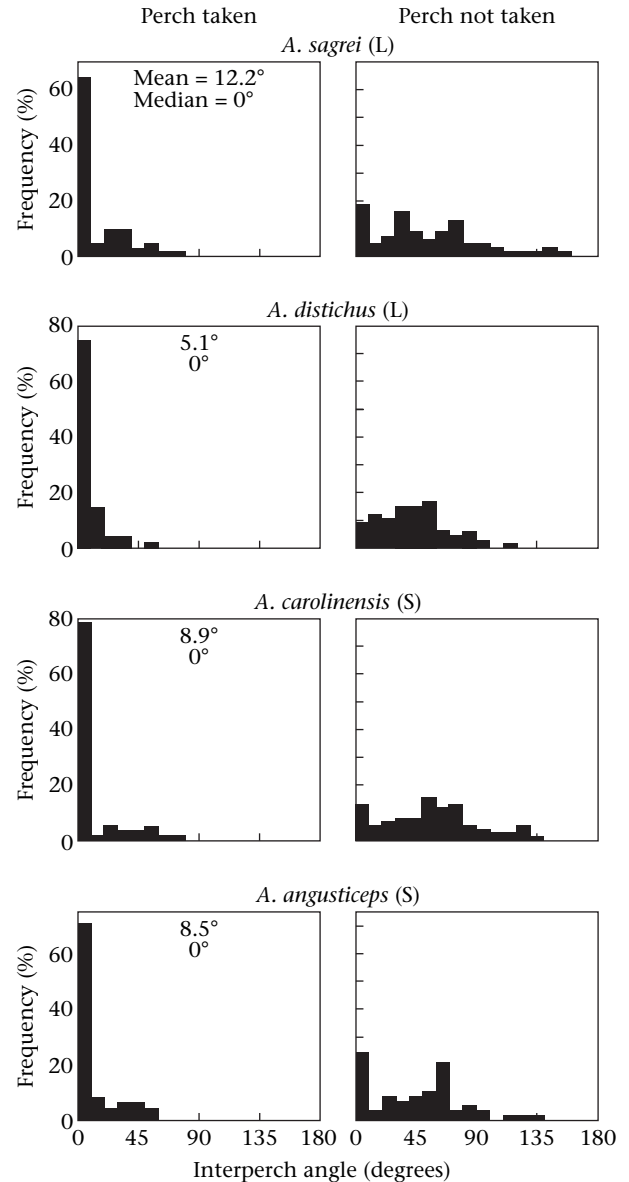


Figure 3. Frequency distributions of the interperch angles of all perches taken (left) and all perches not taken (right) by each *Anolis* species during escape locomotion in the field. Mean and median values of interperch angles traversed are also shown. Using all nodes and only the first node yielded the following *P* values for Kolmogorov–Smirnov tests comparing the cumulative frequency distributions of perches taken and not taken by *A. sagrei* (<0.0001 , 0.0016), *A. distichus* (<0.0001 , <0.0001), *A. carolinensis* (<0.0001 , <0.0001) and *A. angusticeps* (<0.0001 , 0.0002), respectively. L: long-limbed species; S: short-limbed species.

with both perch diameter ($R^2 = 0.49$, $P = 0.003$) and length ($P < 0.001$). Whole-escape speeds decreased significantly only with increased number of nodes crossed for *A. sagrei* ($R^2 = 0.32$, $P = 0.001$) and only with increased amounts of turning for *A. distichus* ($R^2 = 0.14$, $P = 0.040$). No measured attribute of habitat structure significantly affected either the within-perch movement distances of *A. distichus* or the whole-escape speeds of *A. carolinensis* and *A. angusticeps*.

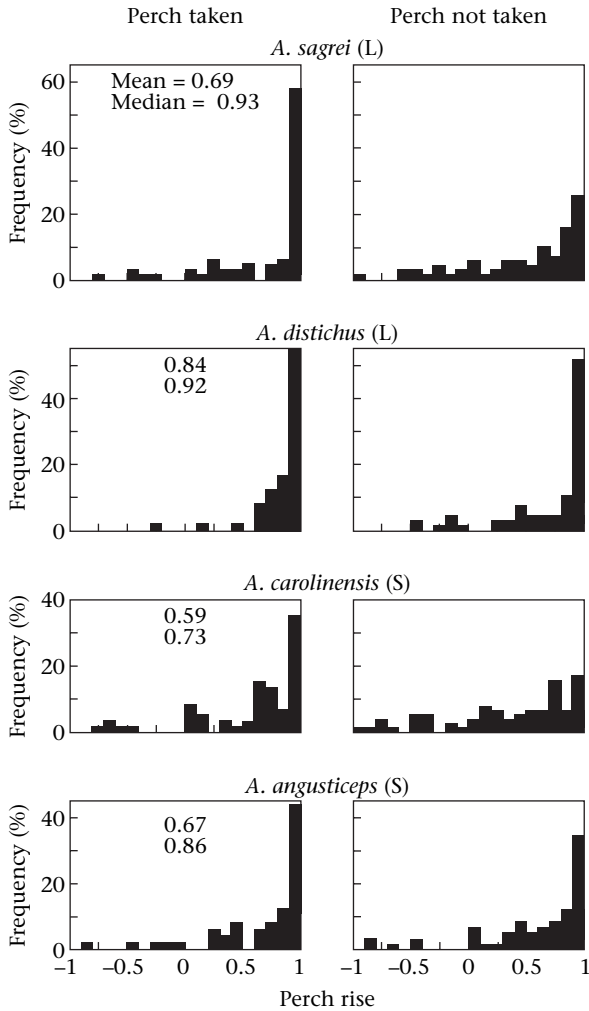


Figure 4. Frequency distributions of the values of rise of all perches taken (left) and all perches not taken (right) by each *Anolis* species during escape locomotion in the field. Mean and median values of perch rise taken by each species are also shown. Using all nodes and only the first node yielded the following *P* values for Kolmogorov–Smirnov tests comparing the cumulative frequency distributions of perches taken and not taken by *A. sagrei* (0.0008, 0.0112), *A. distichus* (0.33, 0.52), *A. carolinensis* (0.028, 0.172), and *A. angusticeps* (0.14, 0.99), respectively. L: long-limbed species; S: short-limbed species.

Laboratory Experiments

Performance trials

For the 5-stride interval during performance trials, average gross and net speeds differed significantly between species (gross: $F_{3,32} = 5.6$, $P < 0.005$; net: $F_{3,32} = 8.6$, $P < 0.001$) and turning angles (gross: $F_{1,32} = 34.0$, $P < 0.001$; net: $F_{1,32} = 14.8$, $P < 0.001$). Compared to the short-limbed species, the two long-limbed species had greater values of net speed and greater decreases (nearly 50%) in gross speed associated with turning 90° (Table 4). Variation in the total duration of pausing rather than running speed explained much of the species-dependent decline in performance associated with turning, as indicated by the significant interaction

between species and turning angle for gross ($F_{3,32} = 4.9$, $P < 0.05$) but not net ($F_{3,32} = 1.7$, $P = 0.20$) speed. The number of pauses during five strides for the 90° turn also significantly exceeded that for the straight perch ($F_{1,32} = 29.1$, $P < 0.001$) and was greater for the long-limbed than for the short-limbed species (species by turning angle: $F_{3,32} = 5.0$, $P < 0.05$). For the speeds per stride, a significant decrease occurred for stride 1 immediately after the 90° turn, but strides on the straight perch had relatively uniform speed (turning angle by stride number: gross: $F_{4,128} = 6.3$; net: $F_{4,128} = 8.6$, $P < 0.001$; Table 4). Pausing was most frequent (60–100%) in the stride immediately after crossing the node of the 90° turn and infrequent in all remaining strides (0–25%). Most pause durations were between 100 and 150 ms.

Path choice trials

All species preferred the larger-diameter path after the node, and the frequencies of taking the larger-diameter perches did not vary between species (two-way contingency table: perch network 1: at 30°: $P = 0.51$; at 60°: $P = 0.36$; perch network 2: at 30°: $P = 0.51$; at 60°: $P = 1.0$; perch network 3: at 30°: $P = 1.0$; at 60°: $P = 0.81$; perch network 4: at 30°: $P = 0.59$; at 60°: $P = 0.64$). For 27 of 32 combinations of perch network, incline and species, more than 90% of the individuals per species chose the larger-diameter path, and the remaining percentages all exceeded 70%. Based on mean values of average gross speeds, the rank order of species from slowest to fastest was *A. angusticeps*, *A. carolinensis*, *A. sagrei* and *A. distichus* for nearly every combination of perch network and incline. For all species, the slowest gross speeds occurred on perch network 4.

DISCUSSION

The uniform choice of largest perch diameter and straightest interperch angle did not support our first two alternative hypotheses, that the choice of escape routes of anoles would either be random or would differ among species. We hypothesized species differences in choice of escape paths partly because of the well documented occurrence of long-limbed species of anoles on perches of larger diameter and of short-limbed species on perches of smaller diameter (Schoener 1968; Williams 1972; Moermond 1979a; Pounds 1988; Losos 1990; Mattingly & Jayne 2004). Furthermore, three of our study species used larger-diameter perches more frequently than predicted from the global availability in the habitat, although diameters used by a short-limbed study species (*A. carolinensis*) conformed to a random sample (Mattingly & Jayne 2004). Consequently, both of these methods for quantifying habitat use were insufficient to predict the lizards' uniformly high bias in choosing thicker perches both in the field and the laboratory. Unlike the laboratory trials, which offered identical alternatives for all species, in the field, the thickest perches available in the immediate vicinity of the short-limbed species were usually narrower than those encountered during escapes of long-limbed species. Thus, differences in the availability of perch types altered the

Table 2. *P* values from Kolmogorov–Smirnov tests comparing the cumulative frequency distributions of the attributes of perches taken during field escapes between pairs of species

Comparison	<i>A. sagrei</i> (L) <i>N</i> =62 (30)	<i>A. distichus</i> (L) <i>N</i> =48 (30)	<i>A. carolinensis</i> (S) <i>N</i> =60 (21)
Perch diameter			
<i>A. angusticeps</i> (S) <i>N</i> =48 (30)	0.0153 (0.0045)	<0.0001 (0.0030)	0.0011 (0.32)
<i>A. carolinensis</i> (S) <i>N</i> =60 (21)	<0.0001 (<0.0001)	<0.0001 (<0.0001)	—
<i>A. distichus</i> (L) <i>N</i> =48 (30)	0.020 (0.43)	—	—
Interperch angle			
<i>A. angusticeps</i> (S) <i>N</i> =48 (30)	0.87 (0.52)	0.93 (0.99)	0.99 (0.99)
<i>A. carolinensis</i> (S) <i>N</i> =60 (21)	0.62 (0.35)	0.96 (0.55)	—
<i>A. distichus</i> (L) <i>N</i> =48 (30)	0.22 (0.39)	—	—
Perch incline			
<i>A. angusticeps</i> (S) <i>N</i> =48 (30)	0.50 (0.52)	0.14 (0.074)	0.23 (0.97)
<i>A. carolinensis</i> (S) <i>N</i> =60 (21)	0.028 (0.23)	0.0029 (0.082)	—
<i>A. distichus</i> (L) <i>N</i> =48 (30)	0.080 (0.78)	—	—
Perch length			
<i>A. angusticeps</i> (S) <i>N</i> =48 (30)	0.0028 (0.0112)	0.0070 (0.0075)	0.096 (0.80)
<i>A. carolinensis</i> (S) <i>N</i> =60 (21)	<0.0001 (0.0011)	<0.0001 (<0.0001)	—
<i>A. distichus</i> (L) <i>N</i> =48 (30)	0.98 (0.18)	—	—

Values of *N* indicate the numbers of perches taken. Values in parentheses represent data for only the first node crossed and values not in parentheses represent data for all nodes crossed. L: long-limbed species; S: short-limbed species.

outcome of a similar tendency to choose the largest available perch when crossing a node. The interspecific similarity of preference for type of escape path supports our third hypothesis and suggests some common underlying biomechanical factors.

When using locomotion to escape, several of the following biomechanical factors could influence the outcome. Maximal speed is the locomotor capacity most commonly measured by workers interested in escape behaviour (Garland & Losos 1994), but maximal acceleration (Huey & Hertz 1984; Domenici & Blake 1997) and turning ability, which are more difficult to quantify, may be even more important (Howland 1974). Minimizing the time needed to get out of the perceptual range of a predator predicts very different escape routes than those for maximizing the rate of gaining distance from a predator (Weihs & Webb 1984). Furthermore, reaching a refuge permits some prey to evade predators with superior locomotor capacities. Besides creating potential refuges, physical attributes of the habitat may affect all of the locomotor capacities mentioned above and thus influence escape tactics. We use our results to choose from this wealth of possibilities by integrating information regarding preference for type of escape path with its functional consequences.

Escape Route Choice and Effects of Habitat Structure

For all four species that we studied, the biased choice of the largest available diameter in both our field and laboratory experiments agrees well with the detrimental effect of decreased perch diameter on the sprinting speeds of anoles (Losos & Sinervo 1989; Losos & Irschick 1996; Irschick & Losos 1999). Thus, the results of our field and laboratory experiments suggest that all four *Anolis* species tend to optimize within-perch escape speeds by choosing perches with greater diameters.

The lack of diameter effects in regressions of escape speeds in the field for the long-limbed species and the significant diameter effects for the short-limbed species were unexpected, because in the laboratory, decreased perch diameter decreases escape speeds relatively more for longer-limbed species (Losos & Sinervo 1989; Irschick & Losos 1999). Changes in the limb movements of *A. sagrei* with decreased perch diameter are most evident among diameters below 3 cm, and perch diameter may have a non-linear effect on sprinting speeds of some *Anolis* species (Spezzano & Jayne 2004). Long-limbed species had more locomotion on perches with diameters of 3 or more cm than did short-limbed species. Consequently, different ranges of what animals choose from can obscure the ability to detect functional consequences of environmental variation in an uncontrolled, natural setting.

The bias of all species of *Anolis* for choosing the straightest interperch angle was expected, because the sprinting speeds of anoles decrease with increased turning angles in laboratory trials (Higham et al. 2001). Furthermore, mechanical analyses of turning reveal trade-offs between speed and turning radius for nearly all types of animal locomotion (Howland 1974). In our laboratory experiments, the effects of turn angle on speed of the short-limbed species were small compared to those for the long-limbed species. This difference could result because short-limb species have such slow speeds that the detrimental effects of turning on speed are trivial over a range of biologically meaningful values. The strong preferences for straight paths that we observed in the field also suggest that these species are unlikely to use the theoretically possible escape tactics of out-turning a larger organism (Howland 1974) or manoeuvring to escape the visual field of the animal posing the threat (Weihs & Webb 1984).

The preferences in the field for the straightest path also could be correlated with choosing the largest diameter, because the thickest tree branches often form the

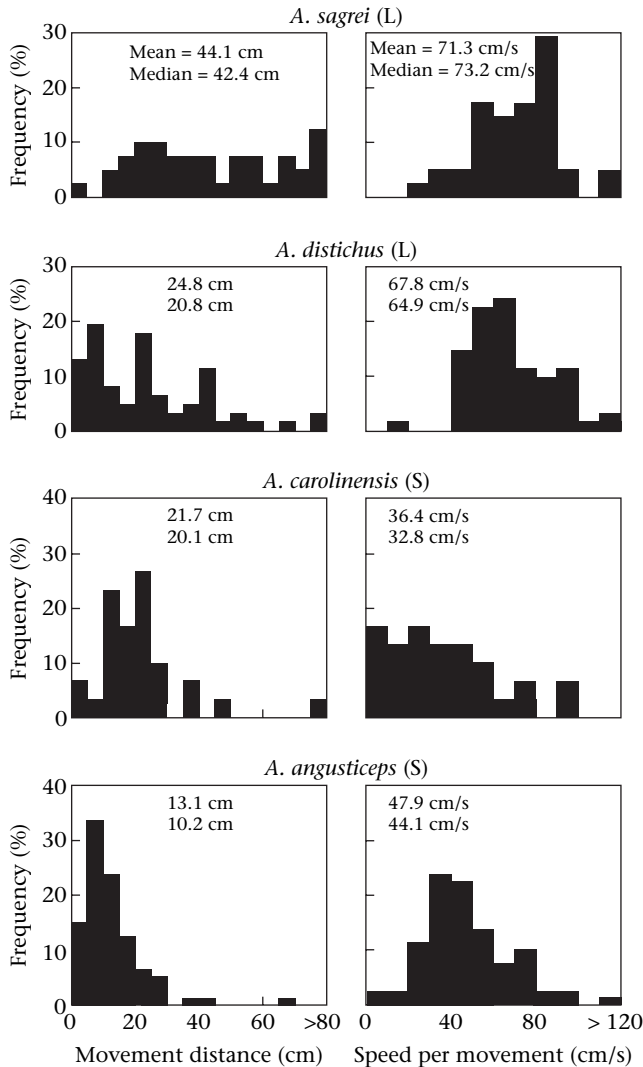


Figure 5. Frequency distributions of movement distance (left) and average speed (right) per continuous movement for each *Anolis* species during escape locomotion in the field. Mean and median values of movement distances and average speed per continuous movement are also shown. L: long-limbed species; S: short-limbed species.

straightest paths. Of the 218 perches with the largest diameter within each node measured during field escapes, 91% had the smallest interperch angle, 61% had the steepest incline, but only 35% had greatest length. In laboratory path choice trials, most individuals chose the greatest available diameter (4.8 cm) and turned 45° rather than travelling straight on a smaller (1.0 cm) diameter. Thus, the preference for a larger diameter may override a preference for minimizing turning angle.

When an escape path has a turn, optimizing speed within a single perch may not optimize the rate at which the distance from a starting point increases. The difference between a straight-line distance and the total distance travelled on the two perches on either side of the turn increases with increased turning angle. Furthermore, the detrimental effect of turning on within-perch speeds would

exacerbate the adverse effects of increased turning angle on the rate of increasing distance from a starting point.

Although all *Anolis* species studied chose perch lengths randomly after crossing a node in the field, some field data do suggest that short perches compromise escape speed. For example, regressions revealed that escape speeds of *A. sagrei* decreased significantly with an increased number of nodes crossed, and decreased lengths of individual perches increased the number of nodes crossed for a given distance travelled. Only a minority of the perches encountered with the largest diameter also had the greatest unobstructed length, however, so optimizing both perch diameter and perch length can occur only rarely.

Three of the four species randomly chose perch incline, but most escapes by all *Anolis* species were up nearly vertical surfaces, because most surfaces encountered by the lizards were nearly vertical (Fig. 4). Running up natural vegetation has several consequences for path choice and the ability to evade a predator. First, animals running uphill usually encounter smaller interperch angles, which are less detrimental to locomotor speed. Animals running down trees encounter more interperch angles exceeding 90°, which, if taken, would decrease the distance from the starting point. Second, running up a tree usually increases the amount of vegetative cover, which could facilitate evading both nonaerial and aerial predators, either by hiding from visually oriented species or by physically impeding the progress of larger species. Third, the number of alternative paths usually increases when running up trees, but the strong preferences of *Anolis* for travelling straight may reduce the relevance of this theoretical advantage. Individuals running from proximal to distal portions of a tree will usually encounter the same advantages as above for running uphill. Finally, the adverse effects of running up steep slopes on speed and acceleration are much smaller for small animals than for large animals (Huey & Hertz 1982). Thus, the lightweight (<5 g) species of *Anolis* in our study may be able to evade larger (nonaerial) predators by running up steep inclines.

Several factors besides mechanical considerations may also affect path choice. For example, choosing larger perch diameters can better conceal arboreal animals from both visually oriented predators (Scott et al. 1976) and prey (Shine & Li-Xin 2002). Many species of *Anolis* actively defend territories (Stamps 1977), and individuals familiar with the habitat structure of a territory may learn locomotor patterns that enhance performance (reviewed in Stamps 1995). Thus, anoles may traverse preplanned escape routes. Similarly, during the escapes of a terrestrial lizard, *Uma scoparia*, individuals often run past many suitable refuges in favour of more distant burrows along heavily used paths (Jayne & Ellis 1998). The use of familiar paths within cluttered habitats occurs in diverse animal lineages (Reese 1989; Clarke et al. 1993).

Modes of Locomotor Behaviour

We assumed that lizards would run faster when escaping a threat than during undisturbed activities. Indeed, the mean values of undisturbed speeds of locomotion in the

Table 3. 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 (cm/s) of each *Anolis* species during bouts of escape locomotion in the field

Species	N	Overall		Coefficients of independent variables				
		R ²	P	Constant (cm/s)	Diameter (cm)	Length (cm)	Rise ²	Distance (cm)
<i>A. sagrei</i> (L)	104	0.302	<0.001	57.9***			-11.72*	1.10***
<i>A. distichus</i> (L)	111	0.161	<0.001	64.7***		-0.06*		0.66***
<i>A. carolinensis</i> (S)	90	0.137	0.002	36.6***	12.36***		-17.65*	
<i>A. angusticeps</i> (S)	135	0.176	<0.001	33.2***	1.63***			1.05**

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$. Empty cells indicate nonsignificant results. L: long-limbed species; S: short-limbed species.

field (Mattingly & Jayne 2004) are so slow (*A. sagrei*, 19% of escape speed; *A. distichus*, 48%; *A. carolinensis*, 7%; *A. angusticeps*, 10%) that we expected that the physiological factors and mechanical constraints associated with habitat structure would be less important overall. For all four of the *Anolis* species, habitat structure better predicted locomotor speeds during escapes ($R^2 = 14\text{--}30\%$; Table 3) than for undisturbed activities (Mattingly & Jayne 2004: $R^2 = 5\text{--}16\%$). Contrary to the uniformity of response predicted from mechanical and physiological considerations, the features of habitat that predicted speed differed both between modes (escape versus voluntary locomotion) within a species and between species within a mode. For example, different species commonly had different significant independent variables in the regressions predicting speed from habitat structure. Consequently, the effects of habitat structure on speed were mediated by both behavioural modes (escape versus undisturbed activities) and the species of *Anolis*.

Jumping is a behaviour that may allow animals to circumvent some of the constraints imposed by the discrete pathways formed by networks of perches in arboreal habitats. For example, compared to travelling on connected perches, jumping across a node can decrease the turning angle and the distance between the initial and final points of the path. However, Higham et al. (2001) found that the speed of jumping strides rarely exceeds the speed of striding locomotion on a perch, and the duration of pauses increases as lizards reposition their limbs after they have landed from a jump. The undisturbed locomotion of *A. distichus* is a unique pattern of short (< 6 cm) and rapid jumps on the unobstructed pathways of large tree trunks (Moermond 1979a; Mattingly & Jayne 2004),

but during escapes, this species used striding locomotion similar to that of all other species. Thus, some theoretical benefits of jumping are not realized because of the behaviour of the lizards, and striding locomotion appears to be the preferred mode for maximizing speed.

The frequent pausing during the escape locomotion of *Anolis* in the field was unexpected, because of its detrimental effect on overall speed, and because the pauses seem too brief (all median values < 0.7 s) to provide substantial physiological benefits of recovery (Gleeson & Hancock 2001). Pausing facilitates stabilizing the visual field, which may explain its widespread occurrence during foraging (Kramer & McLaughlin 2001). As speed increases, the difficulty of stabilizing the visual field increases (Gilbert 1997), and during escapes, the difficulty of determining the speed of an approaching threat increases (Kramer & McLaughlin 2001). Scanning complex, three-dimensional habitats, such as those occupied by anoles, may be particularly demanding (Moermond 1979b; Tarsitano & Andrew 1999). Besides complicating foot placement, smaller perches can be more difficult to see, and the more cluttered visual background for small perches in natural vegetation poses further sensory challenges. Many effects of visual background on the motor output of flying insects are well documented (Srinivasan & Zhang 1997). Thus, similar studies manipulating the visual environment of arboreal animals could prove useful for distinguishing mechanical effects from those resulting from different sensory input.

In summary, the vast majority of previous data for the model system of perch use by anoles describe only what is used by different species, without accompanying data regarding what is available or the proximate choices that

Table 4. Average gross and net speeds (cm/s) for each *Anolis* species over a 5-stride interval during laboratory performance trials on a 4.8-cm diameter perch

Speed	Turning angle	<i>A. sagrei</i> (L) N=14	<i>A. distichus</i> (L) N=6	<i>A. carolinensis</i> (S) N=5	<i>A. angusticeps</i> (S) N=11
5-stride gross	0°	94 ± 9.4	98 ± 8.8	66 ± 12.3	49 ± 6.1
5-stride gross	90°	50 ± 4.0	49 ± 4.5	45 ± 3.6	44 ± 5.5
5-stride net	0°	99 ± 7.9	102 ± 6.0	69 ± 11.7	63 ± 5.8
5-stride net	90°	74 ± 3.7	75 ± 3.1	58 ± 7.3	58 ± 4.2
Stride 1 gross	0°	100 ± 12	101 ± 7.0	57 ± 10	55 ± 8.0
Stride 1 gross	90°	28 ± 3.0	19 ± 1.0	34 ± 2.0	25 ± 4.0
Stride 1 net	0°	106 ± 9.0	101 ± 7	57 ± 10	55 ± 8.0
Stride 1 net	90°	58 ± 6.0	68 ± 4	52 ± 5.0	56 ± 4.0

Values are means ± SE. L: long-limbed species; S: short-limbed species.

are made, and this is also the case for many other studies in behavioural ecology. The notion that interspecific differences in microhabitat would predict proximate choices made by different species seems plausible. However, accounting for resource availability in our study revealed a contradictory conclusion, that the preferences for choosing some perch attributes were remarkably uniform between species occurring in different microhabitats. Such uniformity of preference may imply more evolutionary conservatism in the mechanisms for choosing perches for paths than those for choosing microhabitat. Perhaps this uniformity of choice of perches for paths is associated with some of the uniformity in the mechanical and sensory factors that enhance escape performance. This decoupling of microhabitat preference from proximate path choices provides an important caution against drawing similar inferences regarding choice in other systems that lack direct information on resource availability or choice tests.

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