RESEARCH ARTICLE

Perch diameter and branching patterns have interactive effects on the locomotion and path choice of anole lizards

Zachary M. Jones and Bruce C. Jayne*

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, USA

*Author for correspondence (bruce.jayne@uc.edu)

SUMMARY

Natural branches vary conspicuously in their diameter, density and orientation, but how these latter two factors affect animal locomotion is poorly understood. Thus, for three species of arboreal anole lizards found on different size branches and with different limb lengths, we tested sprinting performance on cylinders with five diameters (5–100 mm) and five patterns of pegs, which simulated different branch orientations and spacing. We also tested whether the lizards preferred surfaces that enhanced their performance. The overall responses to different surfaces were similar among the three species, although the magnitude of the effects differed. All species were faster on cylinders with larger diameter and no pegs along the top. The short-limbed species was the slowest on all surfaces. Much of the variation in performance resulted from variable amounts of pausing among different surfaces and species. Lizards preferred to run along the top of cylinders, but pegs along the top of the narrow cylinders interfered with this. Pegs on top of the 100-mm diameter cylinder, however, had little effect on speed as the lizards ran quite a straight path alongside pegs without bumping into them. All three species usually chose surfaces with greater diameters and fewer pegs, but very large diameters with pegs were preferred to much smaller diameter cylinders without pegs. Our results suggest that preferring larger diameters in natural vegetation has a direct benefit for speed and an added benefit of allowing detouring around branches with little adverse effect on speed.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/215/12/2096/DC1

INTRODUCTION

Unlike the conditions often used for laboratory studies of animal locomotion, animals in diverse natural habitats rarely travel straight paths on flat and unobstructed surfaces, and this is especially true for arboreal species. In arboreal habitats, some attributes of branches that are likely to affect arboreal locomotion include the cylindrical shape, diameter and length of the surfaces upon which animals move as well as the orientation and spacing of branches. Cylindrical surfaces with small diameter provide a limited width to accommodate the propulsive structures of animals; in addition, their surface steepness increases rapidly towards their sides, and both of these factors are likely to make balancing and propulsion of animals more difficult (Cartmill, 1985). If secondary branches emerge from the branch that an animal is moving on, they could create an obstacle that slows an animal by requiring it to maneuver, but the extent of such problems could vary depending on the amount of space beside the secondary branch, where the secondary branch is around the circumference of the primary surface, and how frequently secondary branches occur along the length of the primary surface. Despite the likely importance of all of these factors, few of them beyond branch diameter have been well studied.

Several studies have found that the diameter of cylindrical arboreal surfaces affects the locomotor performance of many species of animals, but these effects may differ with variation in the morphology of the animals, arising either from different body plans, such as those of snakes and lizards (Astley and Jayne, 2007), or from variation within a body plan, such as that found in different species of anole lizards, which vary in overall size and limb length (Irschick et al., 1996; Irschick and Losos, 1998). In addition to the direct importance of branch diameter for arboreal locomotion, the diameter of branches in natural habitats also has a significant positive correlation with the distance between nodes that give rise to additional branches, which also seem likely to affect performance (Mattingly and Jayne, 2004).

Many arboreal species of animals have distinct preferences for the location and attributes of the branches they use, and the arboreal anole lizards have been a model system for quantifying these preferences and their associations with morphology, ecology, behavior and locomotor performance (Irschick and Losos, 1998; Losos and Sinervo, 1989; Mattingly and Jayne, 2005; Pounds, 1988; Schoener, 1968). For example, several anole species (ecomorphs) have convergently evolved similar morphology and habitat preferences, such as longer limbs being positively correlated with the lizards occurring on branches with larger diameter (Moermond, 1979; Williams, 1983). This correlation between habitat preference and limb length may result from decreased cylinder diameter having more severe detrimental effects on the sprinting speeds of the longer limbed species compared with shorter limbed species (Irschick and Losos, 1999).

An issue that is distinct but related to habitat preference is what animals choose when confronted with two or more alternatives at a single location, and this occurs frequently as arboreal animals move along branches that diverge and create discrete choices. The only previous study of this issue used three anole ecomorphs with

different limb lengths and habitat preferences and found remarkably similar biases in choosing larger diameters when the different ecomorphs encountered diverging surfaces during their rapid escape locomotion, both in the field and in laboratory experiments (Mattingly and Jayne, 2005). These previous laboratory tests of perch choice by anoles used only one treatment with two different diameters, both of which were rather small. However, some of the nonlinear effects of perch diameter on the locomotion of anoles (Spezzano and Jayne, 2004) suggest that few changes may occur between different large-diameter perches. Furthermore, the apparent field preferences of anoles for increased diameter could have arisen in response to some other factors that were correlated with diameter and not controlled. Despite the considerable background information for anoles, no experimental data exist regarding how either branch spacing or the location of secondary branches affect either locomotor performance or the choice of different branches emerging from a single node.

In addition to its effects on the speeds of escape locomotion (locomotor performance), the diameter of cylindrical surfaces affects the limb posture and the space around a cylinder that is required for unimpeded movement. For example, the hind feet and legs of the long-limbed, trunk-ground ecomorph *Anolis sagrei* on cylinders require the space around the entire circumference of a perch with a diameter of 10 mm, but only the top 180 deg arc around a perch with a diameter of 30 mm (Spezzano and Jayne, 2004). Consequently, for this species, a secondary branch emerging anywhere on a surface with a diameter less than 10 mm could impede limb movements during locomotion, whereas a secondary branch emerging from the bottom of a cylinder with a diameter exceeding 30 mm should be of little consequence. Therefore, the diameter of the primary cylindrical surface, the dimensions of the limbs and the location where another branch emerges all may interact to affect locomotor performance and where animals choose to go. However, no previous study of a limbed vertebrate has manipulated branch spacing and position by themselves or in conjunction with branch diameter.

For three ecomorphs of *Anolis* with similar overall size but different limb lengths and habitat preference, we manipulated both perch diameter and branching structure to test how these factors affect locomotor performance, kinematics and the surfaces that animals choose to move on. We expected that both decreased perch diameter and the presence of secondary branches would decrease maximal running speeds and that the magnitude of these detrimental effects would increase with increased limb length. We also expected that very large perch diameters would reduce the expected detrimental effects of secondary branches on speed if the perches had sufficient space for the lizard to detour around secondary branches. We also expected that lizards encountering a pair of surfaces would choose the one that enhanced locomotor performance.

MATERIALS AND METHODS
Experimental subjects

We studied three species of anoles, *Anolis sagrei* Duméril and Bibron 1837, *A. carolinensis* Voigt 1832 and *A. angusticeps* Hallowell 1856, because they represent different ecomorphs (trunk-ground, trunk-crown and twig, respectively) with fairly similar overall size but different limb lengths (Fig. 1A) and microhabitat preferences (Williams, 1972). The rank order of these species from longest to shortest limbs and from largest to smallest preferred branch diameter in their natural habitat is *A. sagrei*, *A. carolinensis* and *A. angusticeps*. Previous studies correlating the morphology, ecology and performance of anoles have focused on adult males
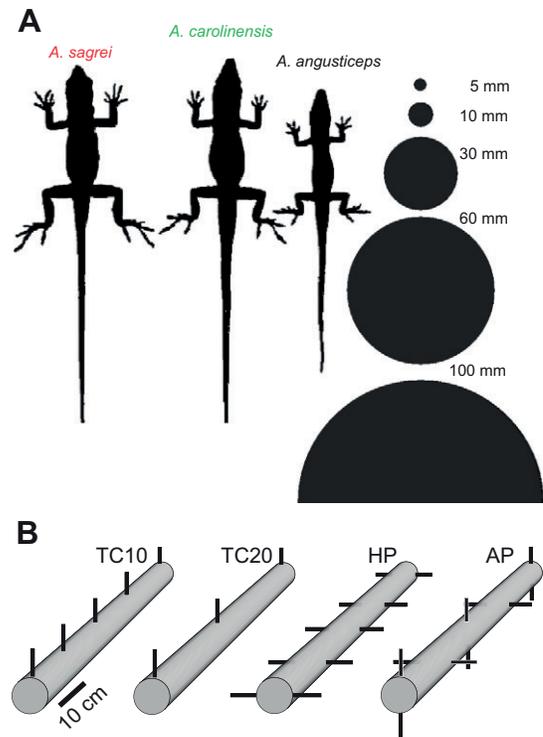

Fig. 1. (A) Dorsal view silhouettes of the three *Anolis* study species compared against the diameter of the running surfaces. The lizards and cross-sectional areas of the running surfaces are all shown to the same scale. All running surfaces were cylindrical, but only one-half of the largest diameter is shown. (B) Schematic diagram of the peg treatments (not to same scale as the lizards). Pegs along the top center were placed at 10 cm (TC10) or 20 cm (TC20), horizontal pairs of pegs (HP) were placed every 10 cm, and alternating pairs of pegs (AP) oriented vertically or horizontally were placed every 10 cm along the length of the primary running surface (gray). The cylinder with no pegs (NP) is not shown.

(Losos, 1990; Williams, 1972), and hence we also studied only adult males, which minimized the variation in size within each of the species. For *A. sagrei* (*N*=16), *A. carolinensis* (*N*=13) and *A. angusticeps* (*N*=17) in this study, the mean (±s.e.m.) values of snout–vent length and mass were 56±0.03, 60±0.05 and 49±0.34 mm and 4.6±0.11, 3.6±0.05 and 2.4±0.04 g, respectively.

Anolis sagrei and *A. carolinensis* were from a commercial supplier who captured the lizards in the same sites in Citrus County, FL, USA, in June, 2009; *A. angusticeps* were borrowed from other investigators who caught the lizards during February 2009 within their native range in the Bahamas. All of the animals were shipped to the University of Cincinnati, where the experiments were conducted. The lizards were housed individually in 38-liter cages, and they were maintained on a diet of crickets, which were fed a calcium-enriched food. Incandescent light bulbs above the cages provided light and heat for 12 h each day, and perches within the cages allowed the lizards to thermoregulate to their active field temperature, approximately 29–31°C (Irschick and Losos, 1999). The care and treatment of the lizards were approved by the Institutional Animal Care and Use Committee (protocol number 07-01-08-01) of the University of Cincinnati.

Performance tests

The primary surfaces of the racetracks were 1.2-m long cylinders with five diameters (5, 10, 30, 60 and 100 mm; Fig. 1A), and they

were inclined at a 30 deg angle relative to horizontal. The cylinders with the three smallest diameters were wooden dowels, and the two largest cylinders were polyvinyl chloride (PVC) pipes. All of these cylinders were covered with 1.5-mm fiberglass mesh to provide good traction, as in previous studies of locomotor performance of anoles (Irschick and Losos, 1999). The lower end of the cylinder was 1 m above the floor, and a mirror 35 cm above the cylinder provided a dorsal view of the middle 50 cm of the racetrack. In addition to using five cylinders with no pegs (NP), wooden pegs 5-cm long with a 4-mm diameter were placed perpendicular to the long axis of the primary surface and within the middle 60 cm of each perch diameter in four different orientations (Fig. 1B). The horizontal pairs (HP), alternating pairs (AP) oriented vertically or horizontally and one of the top center patterns (TC10) all were spaced at 10-cm intervals, whereas the remaining top center treatment (TC20) only had pegs every 20 cm along the primary surface (Fig. 1B). Consequently, each individual of each species experienced a total of 25 combinations of diameter and peg treatments. A 180-deg arc separated the two pegs within each pair at a given location along the length of the primary surface. Lines every 10 cm along the primary surface of each perch delineated the intervals from which speeds were determined.

Immediately prior to each trial, the lizards were placed individually into clear plastic bags, which were placed into a $33 \times 58 \times 36$-cm, insulated container and on top of containers holding water with a temperature of 30.5 to 31.0°C. After the temperature of the lizards within the containers equilibrated for 30 min, testing commenced. Preliminary experiments used a combination of a PE-1 infrared temperature gun (Pro Exotics, Littleton, CO, USA) and a Tegam 871A digital thermometer with an 8712 type K thermocouple (Tegam Inc., Geneva, OH, USA) to verify that these methods resulted in body temperatures of the lizards between 29.0 and 31.0°C for the duration of each treatment used to test performance.

For a single treatment, each lizard was tested three times in rapid succession (total time approximately 1 min). The 25 treatments were performed during 19 days in November and December of 2009 for *A. sagrei* and *A. carolinensis* and for 20 days in December 2010 for *A. angusticeps*. The lizards were tested by alternating between days of one or two treatments per day with one day per week with no testing. When two treatments were conducted for an individual within a single day, approximately 4 h of rest were provided between treatments. To minimize the effects of time and experience, the individuals within each species were divided into two batches, each of which had a different randomized order of the 25 combinations of diameters and peg treatments.

Immediately upon releasing each lizard, the researcher used his hand to chase it uphill. The lizards often ran so quickly that the researcher was unable to touch them while they were running. However, if a lizard paused then the distal tail was gently tapped as soon as possible to prompt the lizard to continue running.

We videotaped simultaneous dorsal and lateral views of lizards running on perches using a two-camera (Basler piA640, Ahrensburg, Schleswig-Holstein, Germany) high-speed video system (Innovision Systems, Inc., Columbiaville, MI, USA) operating at 200 images s^{-1}, and a single 500-W light provided illumination. A mirror 35 cm above the cylinder provided a dorsal view. A 3-mm diameter reflective marker on the dorsal surface of the occipital region of the head of the lizard facilitated using the auto-tracking feature of our motion analysis software (MaxTraq version 2.13 by Innovision Systems, Inc.), which determined the displacement of the lizard with sampling frequency of 200 Hz. For the fastest of the three trials for each individual per treatment, we quantified performance as the average velocity ($\mathbf{v}$) of the lizard along the long axis of the perch for the middle 40 cm of each racetrack. The values of $\mathbf{v}_{gross}$ indicated the total time taken to traverse this distance, whereas the values of $\mathbf{v}_{net}$ excluded all of the time that the lizard paused within the 40-cm interval.

Kinematics

For the four individuals from each species with the largest mean of $\mathbf{v}_{gross}$ across all 25 treatments, we used MaxTraq to manually digitize the location of the lizard at the time of each footfall of the right hind foot for every stride involved in traversing the 40-cm interval used to determine $\mathbf{v}_{gross}$. The following three variables described these strides: stride length (L) was the distance traveled along the long axis of the perch between successive footfalls; stride frequency (f) was the inverse of the elapsed time between successive footfalls (excluding pausing); and the average velocity per stride ($\mathbf{v}_{stride}$) was stride frequency times stride length. We used the two-dimensional coordinates of the head from the overhead view to reconstruct the paths traveled by the lizards.

Perch choice

To determine whether lizards had preferences for perches with different diameters and branching structure, we used a Y-shaped apparatus for which the two arms of the Y were destinations with different attributes. The test arena was 3.2 m high with a floor of 2.4×3.0 m, and white cloths covered all of the walls to provide a uniform visual background. The entire test apparatus was in a plane inclined 30 deg relative to the horizontal, and the lowest end of the apparatus was 30 cm above the floor. The 1.2-m-long arms of the Y, which were the uphill portion of the apparatus, created 45 deg turns relative to the base of the Y, which was 0.9 m long with a 60-mm diameter. All surfaces were covered with the same mesh as was used for testing performance. Monofilament fishing line 0.3 mm in diameter, attached to the ceiling and uphill ends of 1.2-m long cylinders, supported the test apparatus while minimizing potential visual distractions. At the beginning of a trial, each lizard was placed on the base of the Y 50 cm from the intersection of the three cylinders forming the apparatus. When pegs were present on a destination, the peg nearest the intersection of the three cylinders was 10 cm from this location.

Eleven pairs of destination perches with a variety of diameters and peg orientations were used in the choice tests. For each lizard and treatment, we obtained six replicates by performing three tests in rapid succession on one day and three additional tests in rapid succession on a different day in which the left/right position of the two destination perches was reversed. Thus, each individual experienced 22 bouts of testing. The individuals within each species were divided into two batches, for which different randomized orders of 22 bouts of testing treatments were used. We alternated between one and two bouts of testing per batch per day, and approximately 4 h of rest were provided between two bouts of testing within a single day. We also included 1 day per week without any testing. The choice tests for *A. sagrei* and *A. carolinensis* were completed between 9 February and 1 March 2010 and those for *A. angusticeps* between 3 January and 3 February 2011.

Statistical analysis

For the performance and kinematic data, we used SYSTAT (version 9; SYSTAT Software, Inc., Richmond, CA, USA) to perform four-way, mixed-model ANOVAs, in which species, diameter and peg placement were fixed and crossed factors and individual was a random factor nested within species.

Table 1. *F*-values from four-way, mixed-model ANOVAs performed separately for seven dependent variables describing performance, pausing and modulation of strides for *Anolis sagrei*, *A. carolinensis* and *A. angusticeps* running on all combinations of perch diameter and peg orientation

ANOVA effect	Dependent variable					Dependent variable			
	v_{gross}	v_{net}	Pause duration	Pauses	d.f.	v_{stride}	L	f	d.f.
Species	13.2**	12.8**	5.9**	16.8**	2, 43	119.8**	1369.2**	306.5**	2, 9
Diameter	278.9**	394.0**	70.8**	237.7**	4, 172	1311.3**	1129.0**	292.6**	4, 36
Peg	44.2**	65.7**	29.0**	3.4*	4, 172	122.5**	97.5**	18.4**	4, 36
Species × Diameter	11.1**	7.5**	1.7	0.9	8, 172	9.8**	53.7**	9.4**	8, 36
Species × Peg	6.3**	4.3**	1.1	0.2	8, 172	14.3**	12.3**	3.4**	8, 36
Diameter × Peg	4.1**	4.5**	9.3**	4.8**	16, 688	5.2**	2.8**	2.7**	16, 144

v_{gross}, average forward speed for 40 cm including pauses; v_{net}, average forward speed for 40 cm excluding pauses; v_{stride}, average forward speed per stride; L, stride length; f, stride frequency.

*$P<0.05$; **$P<0.001$. The *F*-values for v_{gross}, v_{net} and pause duration are for all individuals, whereas the remaining *F*-values are only for the four fastest individuals of each species.

To clarify where lizards ran on the perches for each treatment and each species, we generated cumulative frequency distributions of the *y*-coordinates of the head during the fastest trial of each individual. The fastest trial had only 44 values of the *y*-coordinate within the 40-cm interval used to determine performance. Thus, to obtain identical replication per individual, we obtained a random sample of 44 points for each individual per treatment after excluding all of the points when an individual paused. The resulting total samples sizes were 704, 572 and 748 for each cumulative frequency distribution of each treatment of *A. sagrei*, *A. carolinensis* and *A. angusticeps*, respectively.

For the results of the tests of perch choice, we calculated the proportion of the six trials per individual per treatment in which a particular perch was chosen, and we used a two-tailed *t*-test to determine whether the mean of these values for each species and treatment (where *N* is the number of individuals) differed significantly from 50% (random behavior with no preference). All mean values are reported ±s.e.m., and for all tests we used $P<0.05$ as the criterion for statistical significance.

RESULTS
Performance
Perch diameter, peg orientation, species and all of their two-way interaction terms had highly significant effects on v_{gross} (Table 1). For cylinders lacking pegs, the values of v_{gross} increased rapidly with increased perch diameter up to some intermediate diameter, after which further increases in diameter had little effect (Fig. 2A). For all three species on cylinders without pegs, the greatest amount of pausing occurred on the perch with the smallest (5 mm) diameter, but little change in the total duration of pausing occurred with further increases in perch diameter (Fig. 2B). For a given perch diameter without pegs, the rank order of species from greatest to smallest values of v_{gross} was *A. sagrei*, *A. carolinensis* and *A. angusticeps* (Fig. 2A).

The TC10 treatment resulted in the slowest speeds for all three species on each of the perches with the two smallest diameters (Fig. 3A,B). However, the peg treatments also had interactive effects with perch diameter, partly as a result of the addition of pegs having less effect on v_{gross} for lizards on smaller compared with larger diameter perches (Fig. 3). The values of v_{gross} often differed little for the lizards on the perches with no pegs (NP) and horizontal pairs of pegs (HP), and both of these treatments were often substantially faster than all remaining treatments with pegs (Fig. 3C,D). For all combinations of perch diameter and pegs, *A. angusticeps* was usually the slowest species, and the effects of the

peg treatments on this species were usually smaller than those for the other two species (Fig. 3). *Anolis sagrei* was usually the fastest species for a given treatment, even though the effects of both pegs and perch diameter were often larger for this species than for the other species (Fig. 3).

The total duration of pausing and the number of pauses per 40 cm also differed significantly with variation in perch diameter and peg placement and between species (Table 1). The greatest duration of pausing usually occurred on the smaller diameter perches and when pegs were placed along the top of the perches (Fig. 4). For a given treatment, the rank order of species from greatest to least total time
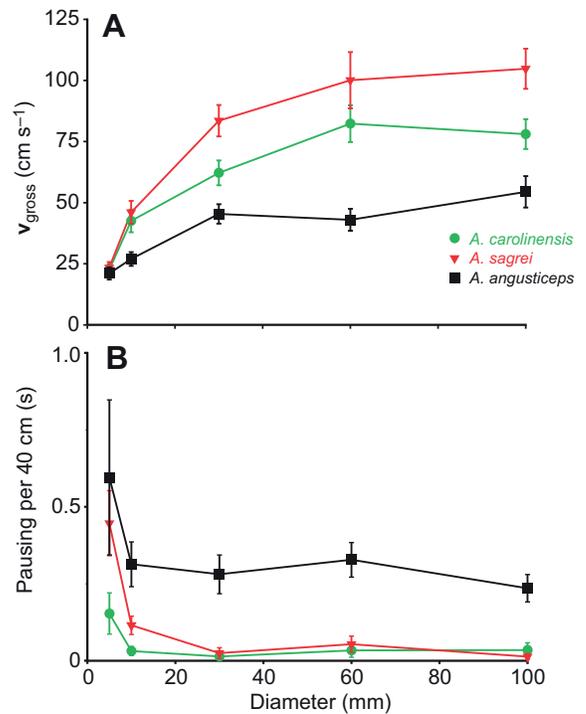

Fig. 2. Mean values of performance and pausing for lizards running on cylinders lacking pegs. (A) The average sprinting velocity for 40 cm calculated from the elapsed time, which included pausing. (B) The total duration of pausing that occurred while traversing 40 cm. The effects of perch diameter on both performance and the amount of pausing were not linear and were greatest among the perches with the smaller diameter. The magnitude of the effects of diameter also differed among species.

spent pausing was usually *A. angusticeps*, *A. sagrei* and *A. carolinensis* (Fig. 4).

The mean number of pauses per 40 cm (not shown) had a pattern of change with treatments very similar to that for the total duration of pausing (Fig. 4). The greatest value of mean number of pauses (10.9±2.3) was on the AP 5-mm diameter perch for *A. angusticeps*, whereas 44 of the 45 mean values of the number of pauses for all three species running on the three largest perch diameters were less

than two. For the smallest perch diameter, 14 of the 15 values exceeded two pauses, and 10 of these values exceeded four pauses.

Although the duration of pausing explained much of the variation in the values of v_{gross}, the velocities of the lizards when they were running (v_{net}) were also significantly affected by all of the same factors that affected v_{gross} (Table 1). Consequently, the pattern of variation in v_{net} (cm s^{-1}) with the perch structure was very similar to that of v_{gross}. In a few cases, the values of v_{net} were 50% greater than those of v_{gross}, but most of the increases in v_{net} compared with v_{gross} were between 10 and 20% (Fig. 5). The rank order of species from fastest to slowest based on v_{net} was similar to that based on v_{gross}.

Kinematics

All of the fixed factors and their two-way interaction terms had highly significant effects on the net speed per stride (v_{stride}), stride length (L) and stride frequency (f) (Table 1). The overall trends in v_{stride} among species and different perches closely resembled those of v_{gross} (Fig. 6 *vs* Fig. 3). However, an interesting exception was that v_{stride} of *A. carolinensis* exceeded that of *A. sagrei* on the two
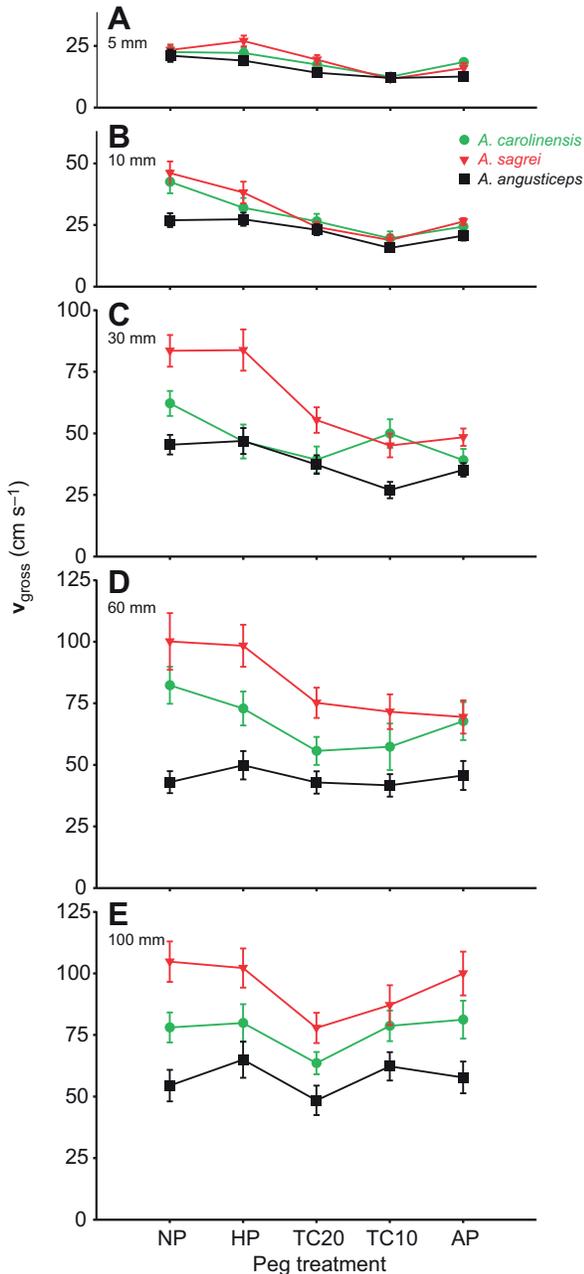

Fig. 3. Mean values of performance illustrating the combined effects of perch diameter and different locations of pegs. NP, no pegs were present; HP and AP, pairs of pegs were present every 10 cm and were oriented only in a horizontal plane or alternately in a horizontal plane and then a vertical plane, respectively; TC10 and TC20, pegs were present along the top center of the cylinder spaced at 10 or 20 cm intervals, respectively. The most conspicuous effects of pegs on performance usually occurred for the intermediate cylinder diameters, but magnitude of the effects of pegs also depended upon the species.
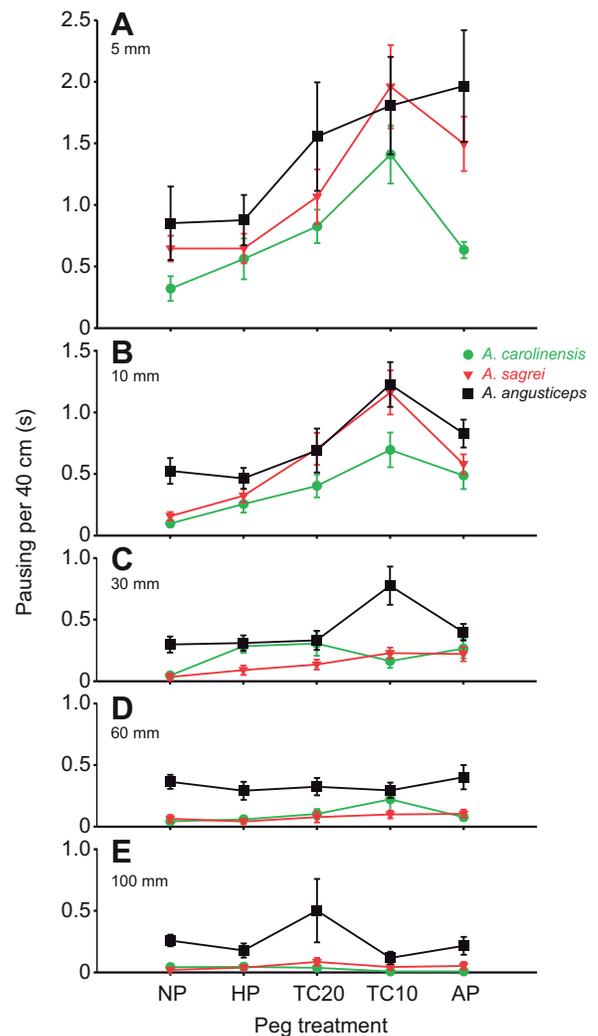

Fig. 4. Mean values of total pause duration per 40 cm, illustrating the combined effects of perch diameter and different patterns of peg placement. Abbreviations are as in Fig. 3. The addition of any pegs along the top of the perch (TC20, TC10 and AP) was most likely to increase the amount of pausing on the smaller diameters.
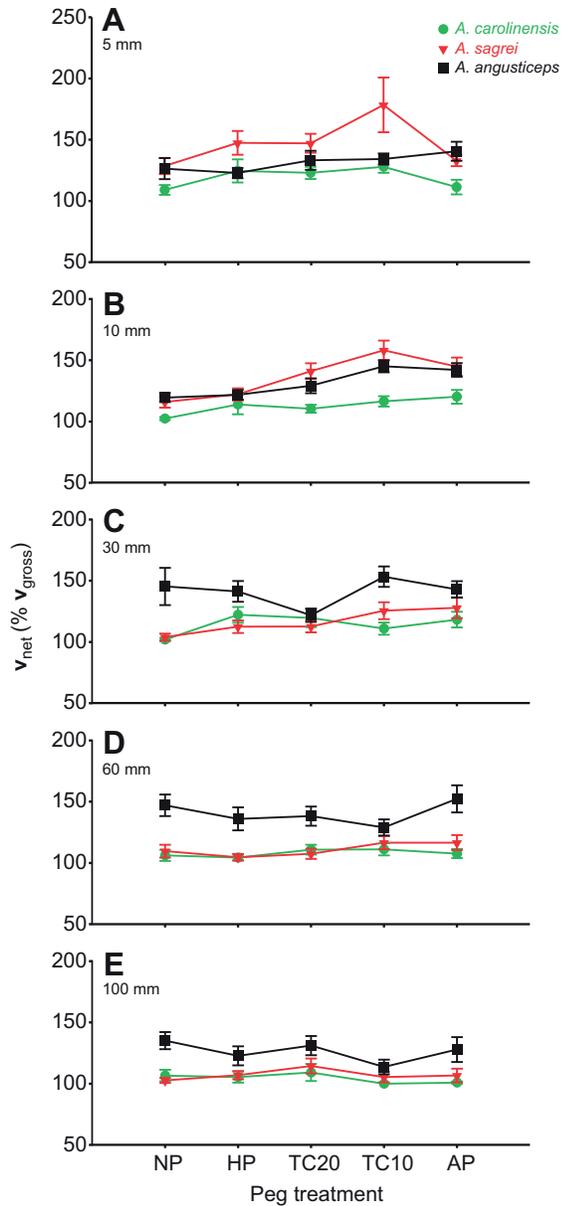
Fig. 5. Mean values of velocity while running relative to those calculated from elapsed times that included pausing. Abbreviations are as in Fig. 3. For the three largest perch diameters (C–E), the minimal amounts of pausing by both *Anolis carolinensis* and *A. sagrei* and resulted in smaller disparities between $\mathbf{v}_{net}$ and $\mathbf{v}_{gross}$ compared with *A. angusticeps.*

Fig. 6. Mean values of net velocity per stride for all species and surfaces. Abbreviations are as in Fig. 3.

largest diameters for some of the treatments with pegs on the top of the perch (Fig. 6D,E). For a given peg treatment, the stride length of each species usually increased with increased perch diameter (Fig. 7). The most conspicuous detrimental effects of adding pegs on stride length were often more apparent for the larger diameter perches (Fig. 7) and the treatments that had any pegs on the top of the perch (TC20, TC10 and AP). Stride frequency was often enhanced by both increased perch diameter and the absence of pegs (Fig. 8). For a given treatment, *A. angusticeps* usually had both the shortest strides and highest stride frequencies, whereas *A. sagrei* usually had the longest strides and lowest frequencies (Figs 7, 8).

When no pegs were present, the lizards of all species usually ran near the top of the cylindrical perch (Fig. 9). For the smallest
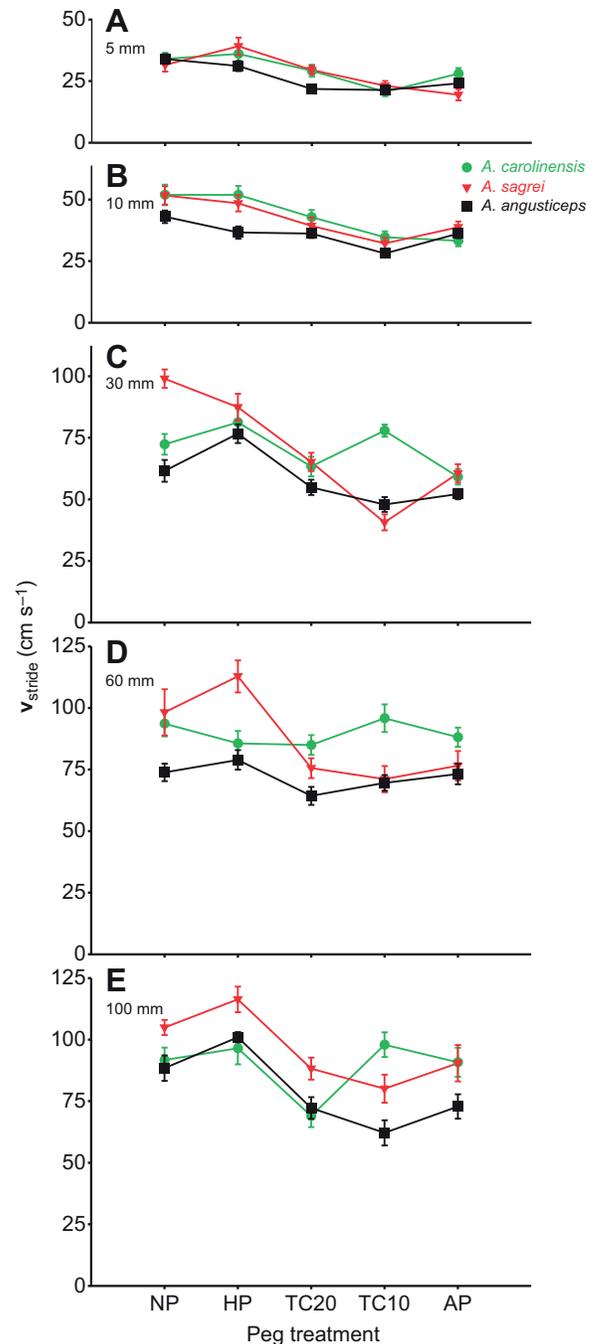
diameter perches, the paths of some lizards deviated markedly from the center of the perch, and they occasionally used a horizontal peg as a foot-hold (Fig. 9, 5 mm diameter, AP). The 30-mm diameter was sufficiently large to allow the lizards to run reasonably straight and avoid the pegs on top of the perch by running along the side of the perch (Fig. 9). However, interspersing vertical pegs with horizontal pegs on intermediate diameter perches often caused a more convoluted path as a result of alternately moving to the left and the right of vertically oriented pegs (Fig. 9, 30 mm diameter, AP). Some sinusoidal trajectories also occurred when some lizards
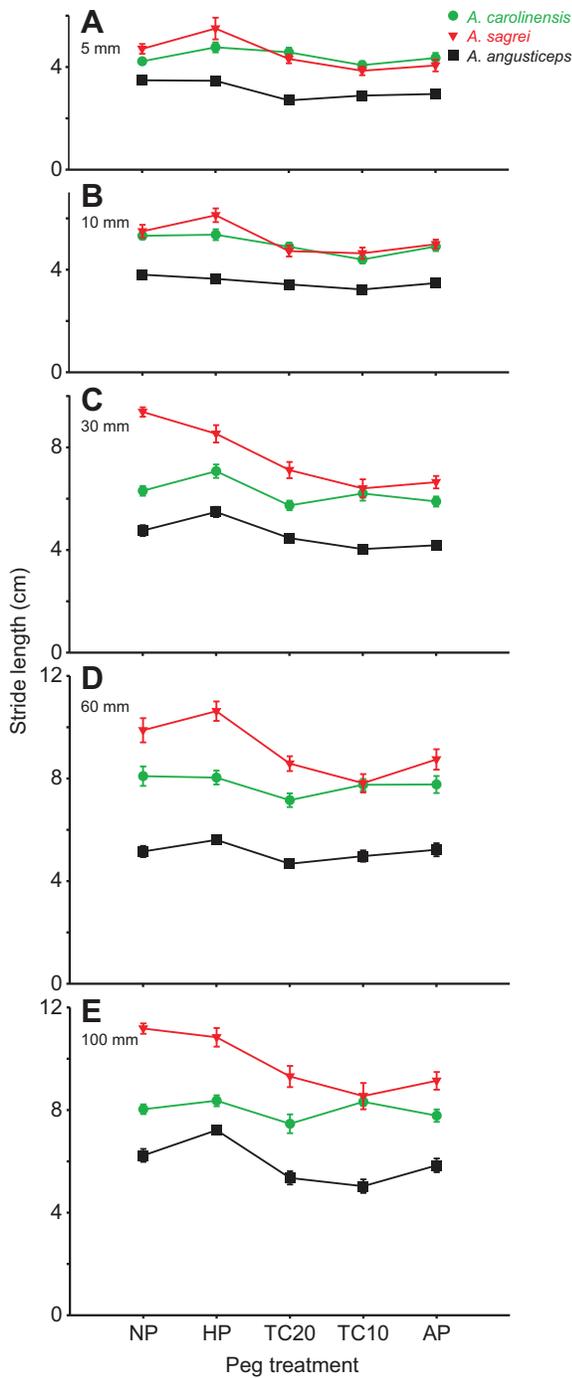
Fig. 7. Mean values of stride length for all species and surfaces. Abbreviations are as in Fig. 3. The stride lengths of all species were often greater for larger diameter perches lacking pegs along their top surface.
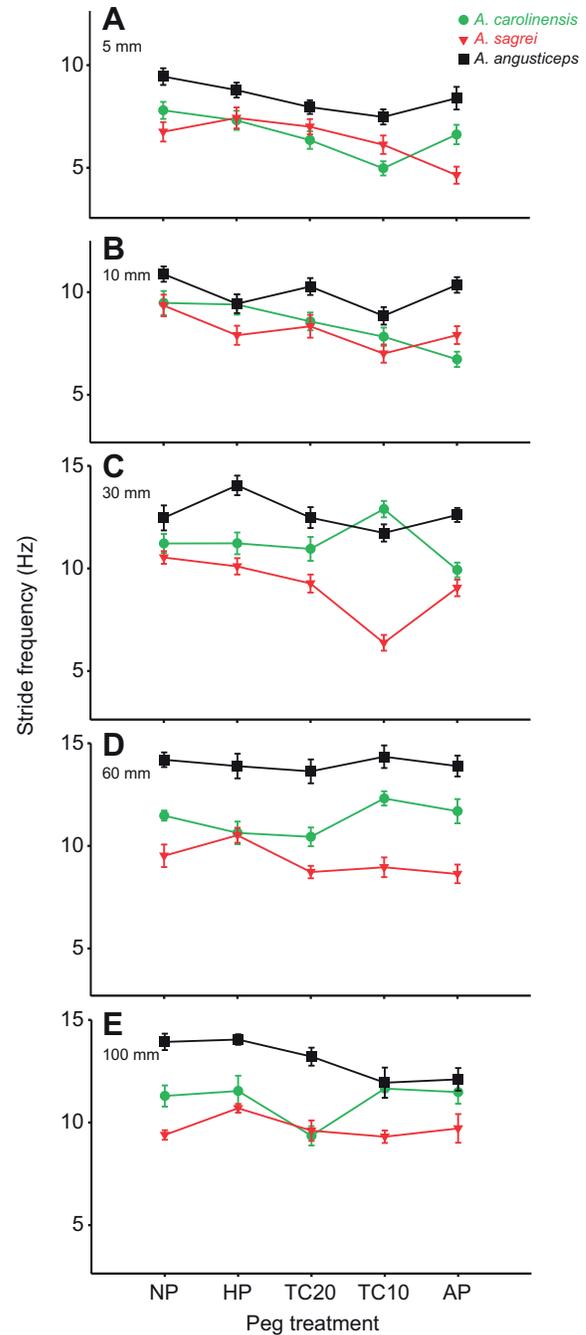

Fig. 8. Mean values of stride frequency for all species and surfaces. Abbreviations are as in Fig. 3. The slowest species with the shortest limbs, *A. angusticeps*, had larger values of stride frequency for most surfaces compared with the other two species.

ran along only one side of the vertically oriented pegs (not shown). The perches with the largest diameter (100 mm) had sufficient space so that the lizards were often able to run a straight path between the alternating vertical and horizontal pegs (Fig. 9).

All three species had extremely similar variation in head position associated with different diameters and peg placement (supplementary material Figs S1–S3). When the lizards were on perches without vertical pegs, the modal position of the head usually approximated the top center location relative to the running surface

(Fig. 10A,D,J). As perch diameter increased, variance in the *y*-coordinate of the head increased markedly, but the mode remained near the top center of the perch (Fig. 10D). For the smallest diameter perch, pegs along the top of the perch also increased the variation in the locations of the head, but the frequency distributions still appeared unimodal and centered near the top position (Fig. 10C,L). By contrast, distinctly bimodal frequency distributions of head position occurred for the two largest diameters whenever at least some pegs were along the top of the perch (TC10, TC20 and AP)

Diameter=5 mm
NP
HP
TC20
TC10
AP

Diameter=30 mm
NP
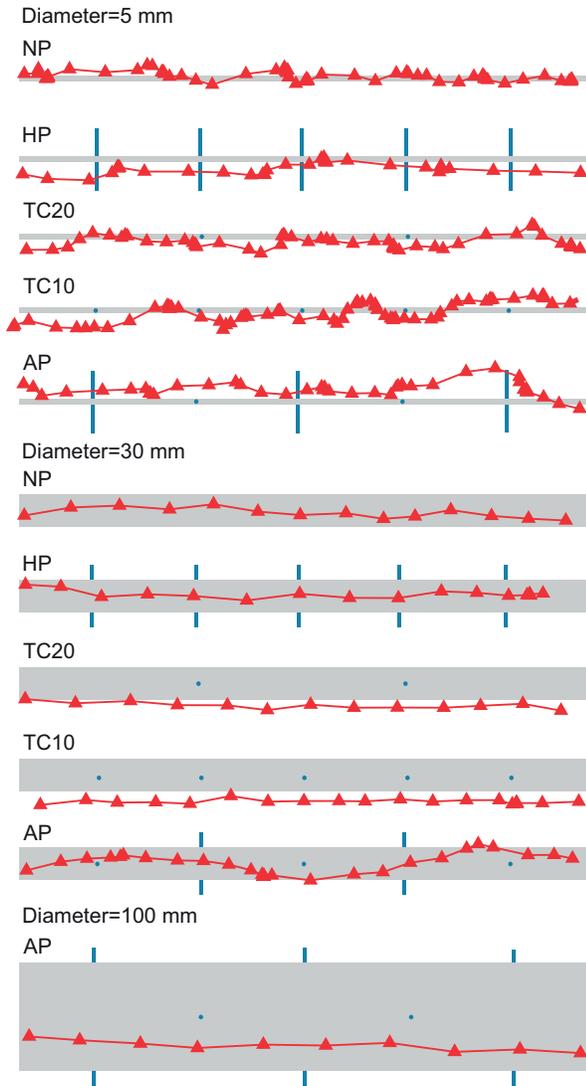HP
TC20
TC10
AP

Diameter=100 mm
AP

Fig. 9. Dorsal views of the position of the head of a single individual of *A. sagrei* running on a variety of perch diameters with different peg arrangements. Abbreviations are as in Fig. 3. The time between successive points within each panel is 40 ms. The less even spacing of points illustrates the more unsteady and intermittent movement that was common on narrower surfaces, especially when pegs were present along the top surface of the cylinder. Note the detouring behavior on the 30 mm diameter perches with pegs along the top (TC20, TC10), whereas the lizard wove its way through the pegs along the top of the 30 mm diameter perch with alternating pegs (AP).

as well as for the 30-mm diameter perch with the TC10 peg arrangement (Fig. 10E,F,H,I, supplementary material Figs S1–S3). For *A. sagrei* on the 100-mm diameter perch with pegs located every 10 cm, a swath nearly 4 cm wide centered on the top of the cylindrical perch was almost entirely avoided (Fig. 10F), but the extent to which this area was avoided diminished when the pegs were spaced farther apart (Fig. 10E).

Perch choice

In all but one case, when more than one species had significant preferences for a particular perch within a pair, the significant preferences were for the same option (Table 2). Significant bias in perch choice was widespread (17 of 33 combinations of species and

treatment), and all but two of these *P*-values were extremely low (<0.005; Table 2). Highly significant bias in choice occurred in all of the 11 cases in which the ratio of v_{gross} of the preferred perch to that of the perch not chosen was greater than 1.7 (Table 2). Thus, much of the bias in choosing a perch was associated with substantial benefits for performance.

For perches lacking pegs, the strength of the bias for choosing a larger diameter depended somewhat on how large the diameters were. For example, all three species strongly preferred the 30-mm diameter to the 5-mm diameter perch, but for both *A. sagrei* and *A. angusticeps*, the preference for a larger perch diameter decreased as the diameters of both the options increased (Table 2, rows 1–3).

The following three trends involving at least one destination with pegs were consistent for all three species. No bias in choice occurred for different spacing of top-center pegs (Table 2, rows 10–11). The 100-mm diameter cylinder with no pegs was strongly preferred to the 5-mm diameter cylinder with horizontal pegs (Table 2). The TC10 100-mm diameter perch was strongly preferred to the 10-mm diameter perch lacking pegs.

Some of the additional patterns of preferences varied among the species. For example, collectively, for all of the treatments involving at least some pegs along the top of the perch (Table 2, rows 6–11), *A. sagrei* had the most and *A. angusticeps* had the least treatments with biased choice. For the 10-mm diameter perches, the preference for the perch lacking pegs compared with the TC20 treatment was highly significant for *A. sagrei*, marginally significant for *A. carolinensis* and not significant for *A. angusticeps* (Table 2).

DISCUSSION

The size, orientation and spacing of branches all vary in natural habitats, and some of these aspects of habitat structure are correlated with each other. In particular, the spacing between branches is positively correlated with branch diameter (Mattingly and Jayne, 2004), and our study is the first for any limbed vertebrate wherein both of these variables were manipulated to test their effects on locomotor performance and perch choice. The magnitude of our treatment effects often varied among the three ecomorphs that we studied, but the overall nature of these effects were very similar despite the different habitat preferences of these species. Consequently, the rank order of our three study species on different surfaces was often similar for many of the variables describing performance and kinematics.

Performance

The effects of perch structure on the performance of the anoles in our study were widespread and substantial. Similar to several other studies (Losos and Irschick, 1996; Losos and Sinervo, 1989), increased perch diameter increased performance, but this benefit was greatest for the longest limbed species. The mean values of v_{gross} were approximately 25 cm s^{-1} for all three species on the smallest diameter, but on the largest diameter these values increased to 105, 78 and 54 cm s^{-1} for *A. sagrei*, *A. carolinensis* and *A. angusticeps*, respectively (Fig. 2A). The effects of pegs on performance were also highly significant, but the magnitude of the change in the values was usually much less than that which was associated with increased perch diameter. Pegs along the top of surfaces caused the greatest decrement in performance, but the magnitude of this effect was highly dependent on perch diameter. For example, one of the largest changes associated with pegs was for *A. sagrei* running on the 30-mm diameter perch without pegs and with pegs along the top, for which the mean values of v_{gross} were 84 and 45 cm s^{-1}, respectively.
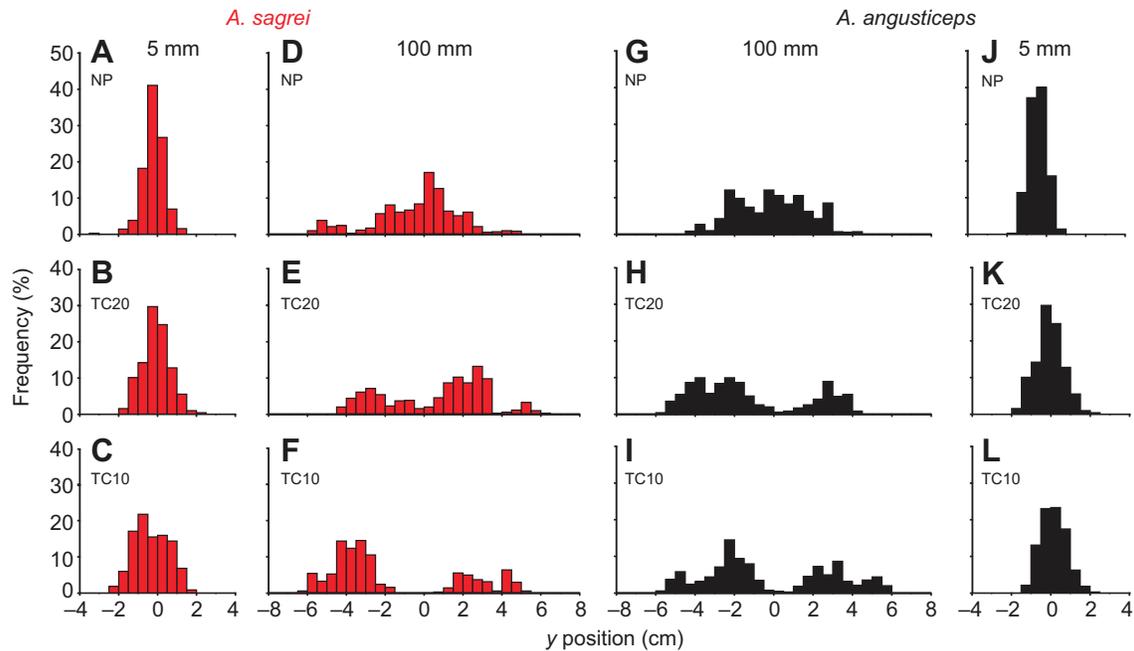
Fig. 10. Cumulative frequency distributions of the lateral location of the head during escape locomotion on perches with diameters of 5 mm (left) and 100 mm (right) of *A. sagrei* and 100 mm (left) and 5 mm (right) of *A. angusticeps*. Abbreviations are as in Fig. 3. For each *A. sagrei* histogram, *N*=704, and for each *A. angusticeps* histogram, *N*=748. Regardless of perch diameter, in the absence of pegs along the top center of the perch (A,D,J), the modal lateral position of the head of the lizard was near the center (*y*=0) of the perch. As perch diameter increased, pegs along the top of perches (TC10, TC20) increased the avoidance of the center of the perch to the extent that the frequency distribution changed from unimodal (B,C,K,L) to bimodal (E,F,H,I). For the sake of brevity, data are only shown for select treatments and the longest and shortest limbed species, but the patterns were general for all of the species (see supplementary material Figs S1–S3).

As occurs commonly for diverse species of limbed animals (Garland and Losos, 1994), the slower speeds of the anoles in our study were closely associated with shorter stride lengths both for different surfaces within a species and between different species for the same surface. Even though the shortest-limbed species, *A. angusticeps*, had extremely high stride frequencies compared with the longer-limbed species in our study, this was not sufficient to compensate for its much shorter strides. In addition to the variation in the speed of running that contributed to decreased values of performance, much of the decreased performance was associated with increased pausing, which, in turn, was associated with narrow

surfaces and maneuvering past pegs. Hence, this system is useful for gaining insights into some of the causes and consequences of intermittent and maneuvering locomotion.

Intermittent and unsteady locomotion

The occurrence of intermittent (occasional stopping) or unsteady (variable speed) locomotion is common in natural settings, but it has been studied minimally compared with continuous bouts of steady movement (Kramer and McLaughlin, 2001). Intermittent locomotion is especially common in a variety of lizards (Avery et al., 1987), and for anoles short bouts of continuous movement are

Table 2. Mean percentage of trials in which perch 1 was chosen by *Anolis sagrei*, *A. carolinensis* and *A. angusticeps*

Diameter (mm); Pegs		Choice of perch 1 (*P*); Performance ratio		
Perch 1	Perch 2	*A. sagrei* (*N*=16)	*A. carolinensis* (*N*=13)	*A. angusticeps* (*N*=17)
30; NP	5; NP	86±4 (<0.001); 3.57	67±5 (0.004); 2.76	83±2 (<0.001); 2.16
60; NP	30; NP	69±5 (0.002); 1.20	55±6 (0.393); 1.32	67±6 (0.012); 0.95
100; NP	60; NP	56±4 (0.164); 1.05	74±6 (0.001); 0.95	58±4 (0.089); 1.03
100; NP	5; HP	78±6 (<0.001); 3.88	76±5 (<0.001); 3.52	94±2 (<0.001); 2.86
5; NP	5; HP	69±5 (0.001); 0.87	67±8 (0.072); 1.02	26±5 (<0.001); 1.10
100; TC10	10; NP	85±4 (<0.001); 1.89	82±5 (<0.001) 1.85	95±2 (<0.001); 2.31
10; NP	10; TC20	63±3 (0.002); 1.90	59±4 (0.047); 1.60	55±7 (0.473); 1.17
30; AP	30; TC20	60±6 (0.106); 0.87	58±6 (0.254); 0.99	55±6 (0.248); 0.94
30; HP	30; AP	66±4 (<0.001); 1.73	56±5 (0.209); 1.19	47±5 (0.548); 1.33
5; TC20	5; TC10	47±4 (0.485); 1.67	51±5 (0.808); 1.39	47±4 (0.484); 1.17
60; TC20	60; TC10	50±5 (0.808); 1.05	51±4 (1.00); 0.97	45±5 (0.332); 1.03

Values are means ± s.e.m.

P-values are from a two-tailed *t*-test comparing the mean percentage of perch 1 chosen with 50%.

NP, no pegs; HP, horizontal pairs of pegs every 10 cm; AP, alternating vertical and horizontal pairs of pegs every 10 cm; TC10 and TC20, single pegs every 10 or 20 cm along the top center of the primary surface, respectively; Performance ratio, v_{gross} of perch 1 divided by that of perch 2.

not unique to our laboratory experiments (Irschick, 2000). In their natural habitat, the mean distances traveled between pauses during the undisturbed locomotion of *A. sagrei*, *A. carolinensis* and *A. angusticeps* are 11, 10 and 7 cm (Mattingly and Jayne, 2004), respectively, and these values are approximately one-half of those traveled before stopping during an escape (44, 22 and 13 cm, respectively) (Mattingly and Jayne, 2005). In this habitat, the mean length of branches (distance between successive nodes) is 27 cm, but the branch lengths vary considerably (>20% of the branches had a length <15 or >270 cm) (Mattingly and Jayne, 2004).

In natural vegetation, the positive correlation between branch length and diameter (Mattingly and Jayne, 2004) contributes to arboreal animals on larger diameter branches usually having more unobstructed space for moving straight and more space available to detour around secondary branches. Reductions in unobstructed space could explain some of the increased pausing and decreased performance for the anoles in our study running on perches with pegs on their top surface. Some terrestrial lizards also are more likely to pause when moving on a coarser surface (gravel *vs* sand) or when approaching larger obstacles (Hofling and Renous, 2004; Kohlsdorf and Biewener, 2006). Expansive open spaces also may contribute to the longer (>10 m) continuous bouts of escape locomotion of some lizards that occur on sand dunes (Irschick and Jayne, 1999; Jayne and Ellis, 1998) and to some patterns in different sprint speeds among other different species of terrestrial lizards (Goodman, 2009).

Pauses decrease values of v_{gross} by increasing the total transit time between two points; in addition, extra time is needed re-accelerate after each pause. Some anoles sprinting on cylinders require more than 0.2 s to attain maximal speed (Vanhooydonck et al., 2006), which corresponds to one or two strides for the species in our study (Fig. 8). In an extreme case, even if a lizard accelerated to maximal speed (with a constant acceleration) within a single stride and paused just an instant after each stride, it could not exceed an overall average speed equal to one-half its maximal speed. Considering that the anoles in our study often paused more than five times within 40 cm on some of narrow surfaces with pegs, the time needed just to re-accelerate probably decreased v_{gross} substantially.

Pausing may have some additional consequences beyond those for the time required to traverse a given distance. For example, pausing facilitates stabilizing the visual fields of diverse animals (Frost, 1982; Gibson, 1986), which may be correlated with enhanced predatory success (Avery, 1993; Getty and Pulliam, 1991), increased vigilance for detecting threats (McAdam and Kramer, 1998; Trouillod et al., 2004) and route planning (Stojan-Dolar and Heymann, 2010). The possible benefit of pausing for a sensory function in facilitating route choice may also be supported further by the common occurence of pausing by the lizards in our study before they selected one of the alternative destinations.

Much of the pausing that we observed for the anoles when they were on narrow perches or had to negotiate obstacles could also be consistent with a loss of balance and the need to hold onto the perch to prevent falling. In some cases, maintaining balance on narrow or cluttered perches could be a greater constraint on the maximal speed of some arboreal animals than the physiological capacities of their locomotor muscles (Jayne and Herrmann, 2011). Similarly, a previous study suggested that short-limbed anoles on small diameters benefited from having greater 'sure-footedness' than long-limbed ecomorphs (Losos and Sinervo, 1989). However, in the present study, the different amounts of pausing among the three anole ecomorphs for a given surface does not seem to be explained solely by biomechanical factors

related to loss of balance. The short limbs of *A. angusticeps* seem well suited for enhancing its stability by lowering its center of mass, and yet this species paused more than the longer limbed species in our study. In addition, *A. angusticeps* moves very slowly, and low speeds appear to be a common strategy of diverse arboreal animals, such as chameleons, lorises and snakes, to avoid a loss of balance (Jayne and Herrmann, 2011; Peterson, 1984). The color, behavior and limb posture of twig ecomorphs are consistent with the use of crypsis to avoid threats (Irschick and Losos, 1996), and for other animals, pausing may also enhance the ability to evade a predator (Martel and Dill, 1995).

Escape path choice and maneuvering

Despite the severe constraints that a single narrow branch imposes on the overall movement trajectories of an arboreal animal, diverse directions of movement in three dimensions are possible if a bout of movement includes several branches. The orientation of surfaces that animals move on affects the amount of work done against gravity (Farley and Emshwiller, 1996; Full and Tullis, 1990), the tendency to slip downward (Clark and Higham, 2011) as well as the tendency of an animal to roll about its long axis (Cartmill, 1985; Spezzano and Jayne, 2004). Increased diameter of cylindrical surfaces also increases the variety of three-dimensional trajectories that are possible for the locomotion of an animal moving on them as well as increasing the amount of space available to avoid secondary branches. Consequently, it is useful to examine the factors that influence the paths traveled by arboreal animals, both on a single branch and when multiple branches are used.

Despite increased branch diameter increasing the possibilities for an animal to move in different directions or move with a more convoluted path, the lizards in our study usually ran very straight when cylinders lacked pegs (Fig. 9). Relatively straight escape trajectories are also a common feature for diverse animals such as fish (Webb, 1986) and terrestrial lizards, especially those in open habitats such as sparsely vegetated sand dunes (Irschick and Jayne, 1999), but some terrestrial species such as kangaroo rats in open habitats may use very erratic trajectories to evade a threat (Djawdan and Garland, 1988). Fleeing from predators and averse stimuli by moving as directly away from the threat as the environment permits maximizes the rate of increasing the distance between the animal and the original location of the stimulus (Howland, 1974), and the convoluted paths that we observed for anoles within a single perch seem more consistent with losing balance or deliberate maneuvering around obstacles rather than using maneuvering within a single branch as a tactic for evading a threat.

Different straight trajectories along a horizontal cylinder could result in an animal being right-side-up, upside-down or tilted sideways. However, effectively all of the locomotion of the lizards in our study was on the top half of the perch, even though this was the side of the perch on which the stimulus was located and the specialized scales on their toes should allow the anoles to run upside down (Irschick et al., 1996). Unlike our results with surfaces with a 30 deg incline, anoles on vertical tree trunks are often difficult to capture because they frequently change their circumferential location to stay out of view (Regelado, 1998). Unlike a vertical cylinder, different locations around the circumference of a non-vertical cylinder can profoundly change the extent to which the supporting surface is normal to the weight of the animal.

The increased variation in the location of the anoles running on the largest diameter cylinders (Fig. 10D,F,G,I) resulted mainly from different individuals running straight trajectories at different circumferential locations on the cylinder rather than individual

lizards running convoluted paths. When many of the lizards ran along the sides of the 60- and 100-mm diameter perches with their feet nearly in a vertical plane, they had sufficient space so that their feet did not collide with the pegs. Thus, some of the low net speeds per stride for these conditions (Fig. 6E) may indicate that running with the body tilted sideways can impede performance. Anoles have an impressive capacity to move in any three-dimensional orientation, and similar capacities exist in geckos and a wide variety of other arboreal animals with claws or adhering structures (Autumn et al., 2002; Gillet and Wigglesworth, 1932). However, for these and other animals, much remains to be learned about the consequences of being tilted sideways while running.

Compared with the options for moving along a single branch, the networks of branches in natural habitats create a plethora of potential pathways with a variety of orientations, sizes and obstacles. Thus, experimental manipulations of the attributes of perches are very helpful for gaining insight into the predictive value of habitat structure regarding where these animals go and some of the cues that may be used when choices are made. A previous study of the same three species of anoles as in our study found that, in laboratory tests, they all strongly preferred the larger of two perch diameters (10 and 48 mm), and in their natural habitat, they preferred the largest diameter perch and the straightest path during escape locomotion (Mattingly and Jayne, 2005). Some of these uniform preferences for larger diameter among the three species in both of our studies may arise from the positive effects of increased diameter for the performance of all three species, but they contrast sharply with the habitat preference of shorter limbed ecomorphs for smaller diameter perches in their natural environment (Losos, 1990; Pounds, 1988). When they are crossing gaps, some arboreal species of snakes also prefer perches with greater width (Mansfield and Jayne, 2011) even though the larger diameters chosen decrease their maximum crawling speed (Astley and Jayne, 2007). Consequently, some preferences for larger perches may occur simply from a bias towards favoring objects either that are visually more conspicuous or that create a larger target, requiring less precise motor control (Mansfield and Jayne, 2011).

The preferences of anoles that we observed with different perch diameters add some interesting caveats to these general trends in perch preferences. The majority of significant preferences that we observed corresponded to perches that enhanced locomotor performance (Table 2). However, the nonlinear relationships between perch diameter and the sprinting speeds of anoles (Fig. 2) result in a wide range of different diameters that have little, if any, effect on performance, which corresponds well with our finding that the anoles had diminished or no significant preferences among the larger diameter perches lacking pegs (Table 2). These large diameters were not included in the only previous study of perch choice in anoles (Mattingly and Jayne, 2005). The variable preference of anoles for different diameters also argues against them relying only on the relatively simple strategy of 'bigger is better'.

A greater overall width (either from greater diameter or pegs pointed sideways) of a destination may be sufficient to elicit a preference when rat snakes cross a gap (Mansfield and Jayne, 2011), whereas the width of the primary surface used for running appeared to be the most important cue that was correlated with the preferences we observed for the anoles in our study. This difference between rat snakes and anoles may result from pegs on the sides of the primary surface having little consequence for the locomotion of anoles, whereas they are probably useful for supporting snakes after they cross a gap.

Pegs along the top of perches were often detrimental to the locomotor performance of anoles, but this effect depended on the diameter of the perch (Fig. 3). The longest-limbed species of anole (*A. sagrei*) had a strong preference for a lack of pegs on top of the 10-mm diameter perches, and the different degrees of preference among the three species for this treatment corresponded well to the different ratios of performance on these surfaces (Table 2, row 7). However, the strong preferences of all species of anoles for the largest diameter perch with pegs along the top compared with a perch of small diameter lacking pegs (Table 2, row 6) suggest that adequate clearance to the side of secondary branches may override a possible aversion to potential obstacles along the top where the lizards would otherwise prefer to run. Rather than creating obstacles, as for anoles and probably most other limbed animals, pegs on top of cylinders greatly enhance the speeds of snakes in a manner that is nearly independent of perch diameter (Astley and Jayne, 2009; Jayne and Herrmann, 2011), and rat snakes slightly prefer surfaces with pegs along the top compared with ones lacking pegs (Mansfield and Jayne, 2011). These differences further illustrate how different morphologies may alter the effects of perch structure on both performance and preference.

Presently, information regarding the effects of branch structure on both performance and perch choice of arboreal animals is extremely limited considering the large number of animal species that are arboreal. However, both rat snakes and anoles have demonstrated the ability to discriminate between many types of surfaces. Compared with rat snakes, the overall preferences of anoles seem to be more closely aligned with benefiting locomotion. Secondary branches seem likely to hinder the locomotion of diverse limbed animals, but the ability of anoles to cling may greatly moderate some of these potential consequences. The ability to further isolate the effects of limbed *versus* limbless body plans on locomotor performance and perch choice of arboreal animals would be facilitated greatly by studying limbed species without specialized adhering structures.

LIST OF SYMBOLS AND ABBREVIATIONS

AP	alternating pairs of pegs in a horizontal and vertical plane spaced every 10 cm along the primary surface
f	stride frequency; inverse of the elapsed time between successive footfalls excluding pauses
HP	pairs of pegs in a horizontal plane spaced every 10 cm along the primary surface
L	stride length; distance traveled along the long axis of the perch between successive footfalls
NP	no pegs
TC10	pegs in a vertical plane spaced every 10 cm along the top of the primary surface
TC20	pegs in a vertical plane spaced every 20 cm along the top of the primary surface
v_{gross}	gross speed; =40 cm divided by the total time taken to traverse this distance
v_{net}	net speed; =40 cm divided by the time taken to traverse this distance excluding pausing
v_{stride}	average speed per stride; $=fL$

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