

Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards

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Accepted 24 September 2001

Summary

Although the maximal speeds of straight-ahead running are well-documented for many species of *Anolis* and other lizards, no previous study has experimentally determined the effects of turning on the locomotor performance of a lizard. *Anolis* lizards are a diverse group of arboreal species, and the discrete paths created by networks of perches in arboreal environments often force animals to turn in their natural habitats. For three species of *Anolis* with similar overall body size but different shape, we quantified the escape locomotor performance for arboreal locomotion on 4.8 cm diameter perches that were straight (0°) or had turning angles of 30° and 90°. The turning angle had widespread significant effects that were often species-dependent. This was shown by measuring the average gross velocity (including the times while the lizards paused) of the three species covering the middle 30 cm of a racetrack with either 30° or 90° turns. The results were expressed as a percentage of the gross velocity over the same distance on a straight racetrack. The values obtained for *A. grahmi* (99% for 30° turns and 79% for 90° turns) showed a smaller effect of turning angle than

for *A. lineatopus* (79% for 30° turns and 50% for 90° turns) and *A. valencienni* (74% for 30° turns and 48% for 90° turns). Consequently, the rank order of species based on speed depended on the angle of the turn. Some of the magnitudes of decreased locomotor speed associated with turning exceeded those reported previously for the effects of decreasing perch diameter for these species. For all species, more pausing occurred with increased turning angle, with the twig ecomorph (*A. valencienni*) pausing the most. Approximately half the individuals of each species jumped to traverse the 90° turn, but some of the potential benefits of jumping for increasing speed were offset by pauses associated with preparing to jump or recovering balance immediately after a jump. The tail of *Anolis* lizards may facilitate the substantial rotation (>60°) of the body that often occurred in the airborne phase of the jumps.

Key words: arboreal, locomotion, intermittent, jumping, lizard, manoeuvring, *Anolis* spp.

Introduction

Different environments and habitat structure can affect the locomotion of animals substantially both by altering the transmission of forces and by imposing limits on where animals can move. Both within and among clades of animals, the functional demands of performing a particular locomotor task in similar habitats have presumably caused convergent similarities in quantitative features such as limb lengths (Garland and Janis, 1993; Hildebrand, 1985; Rewcastle, 1981), fin surface area (Weihs and Webb, 1983) and wing aspect ratio (Norberg, 1981). For example, animals that move in fluids and have low wing or fin aspect ratios are often highly maneuverable and occur in structurally complex habitats (Norberg, 1985). Morphological specializations for maneuverability often compromise other aspects of locomotion such as the ability to sustain high-speed locomotion (Norberg, 1981; Norberg and Rayner, 1987). Thus, understanding maneuvering locomotion is important for understanding the morphological variation and the locomotion of animals in

natural habitats, which are generally more complex than laboratory settings. However, maneuvering locomotion is not as well understood as straight-ahead locomotion, and this is especially the case for locomotion on solid surfaces.

For terrestrial vertebrates, lizards have been a model group for testing locomotor performance (for a review, see Garland and Losos, 1994), which is affected by attributes of the habitat such as the firmness of the substratum (Carothers, 1986), incline (Huey and Hertz, 1982; Irschick and Jayne, 1998) and perch diameter (Losos and Irschick, 1996; Losos and Sinervo, 1989). Data on the relationship between locomotor speed and turning (maneuvering) are only available from field studies of two species of terrestrial lizard, for which it was shown that the speeds during escapes (Irschick and Jayne, 1999; Jayne and Ellis, 1998) and undisturbed locomotion (Jayne and Irschick, 2000) decrease with increases in turning angle. In these studies, the lizards were on the surface of a sand dune with only sparse vegetation and, hence, they could move and turn in nearly any

direction. Unlike the nearly continuous surfaces that are commonly available for terrestrial habitats, the network of perches in arboreal habitats severely limits where the feet can be placed and, hence, constrains the choice of paths traveled by the animal (Cartmill, 1985). Consequently, arboreal habitats and animals are well suited for experimentally determining the relationship between habitat structure and maneuvering locomotion.

Many species of lizard are arboreal, and *Anolis* lizards are a particularly diverse clade of arboreal species (Williams, 1983) for which habitat choice and locomotor performance are well studied (Irschick and Losos, 1999), but information on maneuverability is lacking. Different ecomorphs of anoles have different preferences for perch height and diameter, which is often associated with body size and relative limb length (Losos, 1990a). Larger anoles or anoles with relatively long limbs commonly have greater running speeds and jumping distances (Losos, 1990b). For our study, we tested the maneuvering performance of three sympatric ecomorphs of *Anolis* (*A. grahami*, *A. lineatopus* and *A. valencienni*) with grossly similar overall size. From largest to smallest mean values per species for hindlimb length, perch diameter, maximal sprinting speeds, maximal jumping distances and the occurrence of jumping observed in the field, the rank order is always *A. lineatopus*, *A. grahami* and *A. valencienni*, and these values for the twig ecomorph *A. valencienni* are markedly smaller than those of the other species (Losos, 1990a). Furthermore, decreases in perch diameter significantly decrease the maximal sprinting speeds of both *A. grahami* and *A. lineatopus*, but not of *A. valencienni* (Losos and Sinervo, 1989).

As the diameters of plant branches decrease, the distance between branching points generally decreases. Consequently, if locomotion is confined to paths formed by the branches, then one would expect that turns would have to be made more frequently in those portions of vegetation with smaller branch diameters. The greater abundance of *A. valencienni* in natural habitats with small branches (Irschick and Losos, 1996; Losos, 1990a) led us to expect that *A. valencienni* would be the most specialized for maneuvering within our three study species and, hence, that the locomotor speed of this species would be least affected by turns imposed during our laboratory tests of maneuvering performance. Jumping provides one method of circumventing the limited choices resulting from paths that are formed by a network of branches. We expected that the probability of jumping during a turn would be proportional to the occurrence of jumping observed in the field for our three study species.

The purpose of this study was to address the following two questions regarding the effects of turning angle on the sprinting performance of three similarly sized sympatric ecomorphs of *Anolis* lizards (*A. grahami*, *A. lineatopus* and *A. valencienni*). (i) Does the turning angle of an arboreal path affect the sprinting speed? For all three *Anolis* species, we expected maximal running speed to decrease with increased turning angle, as has been found previously for some terrestrial species

of lizard. (2) Are the effects of turning angle on sprinting performance species-dependent? We expected that the speeds of *A. valencienni* would be least affected since it most frequently encounters turns in its natural habitat.

Materials and methods

Experimental subjects

We chose three closely related sympatric species of Jamaican lizards for which the phylogenetic relationships are well resolved (Irschick and Losos, 1999): the trunk/crown ecomorph *Anolis grahami*, the trunk/ground ecomorph *Anolis lineatopus* and the twig ecomorph *Anolis valencienni* (Losos, 1990a). All lizards were collected from the Discover Bay Marine Laboratory, St Ann Parish, Jamaica, during July 2000, and transported to the University of Cincinnati for experiments. Lizards were caged alone or in pairs and were fed crickets, which had been given a vitamin supplement, three times a week and given water *ad libitum*. Incandescent light bulbs above the cages provided a light and heat source for 12 h per day and allowed the lizards to thermoregulate behaviorally and attain their preferred field active temperature range of 29–31 °C (Irschick and Losos, 1999) (see also references therein).

Anolis grahami and *A. lineatopus* were abundant and easily collected in their natural habitat and thus, to minimize variation in size, we collected only adult males of these two species. *Anolis valencienni* was difficult to collect because it was both rare and cryptic; to obtain a reasonable number of individuals, we collected both males and females of the largest possible size. For *A. grahami* ($N=14$), *A. lineatopus* ($N=17$) and *A. valencienni* ($N=8$), the ranges for values of snout–vent length were 5.8–6.9, 5.4–6.5 and 4.7–6.5 cm, respectively, and the corresponding ranges of mass were 4.5–7.3, 4.0–7.0 and 1.3–4.8 g, respectively.

Experimental protocol

We conducted all performance trials within 1 month of capturing the lizards. All three of the racetracks were 2 m long and consisted of 4.8 cm diameter polyvinylchloride pipe covered with a fiberglass screen (1.5 mm mesh) to enhance the traction of the lizards, as used previously (Irschick and Losos, 1998). All the perches comprising the racetracks were inclined by 30° relative to the horizontal plane, and the midpoint of each racetrack was approximately 1 m above the ground. We tested the performance of each lizard on racetracks with turning angles of 0° (straight) 30° or 90° at the midpoint of the track. The turning angles indicate the angles between the projection of the two halves of the racetrack onto a horizontal plane, and one should note that these turning angles differ slightly from the three-dimensional angle between the two halves of the racetrack. To provide fixed points of reference, we drew lines at 5 cm intervals along the length of the racetracks.

We tested the performance of each lizard on only one racetrack per day. Within each of the 3 days of performance

testing, we conducted testing sessions in both the morning and afternoon, and we chased each lizard three times in rapid succession within each testing session. Thus, for each individual, we obtained a total of six trials per racetrack, from which we selected the fastest trial for detailed analysis. We provided 1 day of rest between successive days of testing and, hence, the tests of performance on all three racetracks were completed over a span of 5 days. We tested all lizards on the straight racetrack on the first day. The logistical difficulties of setting up different racetracks and aligning cameras prohibited randomizing turning angle completely with respect to time. However, to minimize the confounding effects of time, we tested half the individuals of each species on the 30° and 90° turns on the third and fifth days of the experiments, respectively, whereas the remaining individuals had 30° and 90° trials on the fifth and third days, respectively. We also randomized the order of testing individuals among different testing sessions.

To control the body temperature of the lizards during all trials, we placed them in a heated chamber and, immediately prior to testing, we used a thermocouple and a Tegam model 871A digital thermometer to verify that body temperatures conformed closely to previously reported field active body temperatures (29–31 °C) (Irschick and Losos, 1999). We only used lizards that had complete tails with a round cross section, which implied that they were healthy. One investigator attempted to elicit maximal speeds of running by startling the lizard from behind and using a hand to continue chasing the lizard while it ran. Rather than excluding any individuals on the basis of a subjective rating of performance (see Losos, 1990b), we analyzed the results from all lizards that ran on each of the three racetracks and did not autotomize any portion of their tail during the entire course of the experiment.

For all the performance trials, we obtained two simultaneous lateral images of the lizards using a two-camera NAC HSV-500 high-speed video system operating at 250 images s⁻¹. To obtain direct lateral views of both perches comprising each racetrack, the two cameras were at the same height and pointed perpendicularly to the middle of a 50 cm portion on either side of the midpoint of the racetrack. Each of the two cameras was also tilted sideways at the same angle as the perch incline (30° relative to a horizontal plane). Consequently, in the resulting video images of performance trials, the long axis of each perch was parallel to the bottom edge of the video image. Four 500 W lights were positioned approximately 1 m above the track to provide illumination.

After the completion of the performance trials, we conducted supplementary trials of all individuals running on a 90° turn to clarify some of the details involved in turning. For this video footage, we used stroboscopic lights for illumination and obtained simultaneous lateral and overhead views of approximately 25 cm on either side of the turn. The overhead view was *via* a mirror with its long axis parallel to the plane containing the perches that formed the racetrack. Each of the pipes that formed the 90° turn was inclined by 30° relative to the horizontal plane and, hence, the normals relative to the path

along the top of each pipe were different. Consequently, the mirror view was only an approximate overhead view of the path along the top of the racetrack.

For each of the lizards for which the performance data were analyzed, we made several morphological measurements. We used a ruler to measure snout–vent and tail lengths to the nearest millimeter. We used life-size dorsal-view radiographs of anesthetized or preserved specimens and digital calipers (± 0.05 mm) to measure a total of 11 skeletal distances from the left side of each lizard (see Table 1). Intergirdle distance was the longitudinal distance between the centers of the glenoid fossa and the acetabulum. The widths of the pelvic and pectoral girdles were the lateral distances between the left and right glenoid fossae and acetabula, respectively. The lengths of the femur, tibia, humerus and ulna were measured from their most proximal to their most distal portion. The lengths of the hindfoot and forefoot were measured from the heel to the base of the fourth metatarsal and from the wrist joint to the base of the fourth metacarpal, respectively. The lengths of the fourth toe of the forefoot and hindfoot were measured from the base of the claw on the fourth digit to the base of the fourth metacarpal and metatarsal, respectively.

Data analysis

We used frame-by-frame playbacks from videotapes of the performance trials to determine the total elapsed time (± 4 ms) taken to travel the middle 30 cm of the racetrack for each trial. The net elapsed time equaled the total elapsed time minus the total duration of all pauses (no forward progression) within the 30 cm interval. We calculated the average gross (V_{g30}) and average net (V_{n30}) velocities by dividing 30 cm by the total and net elapsed times, respectively. For each lizard and turning angle, we selected the trial with the greatest value of V_{g30} for a further kinematic analysis of five successive strides (numbered -2, -1, 0, 1 and 2, respectively), for which stride 0 straddled the midpoint and turn within the racetrack.

We used custom-designed video-analysis software (Measurement TV, written by Garr Undergraff, San Clemente, CA, USA; garru@uci.edu, garru@fea.net) to determine x, y coordinates from the views of each of the two cameras. The x -axis of each video image from each camera was parallel to the portion of the racetrack that was within the field of view of a particular camera during performance trials. The y -axis was perpendicular to the racetrack and within a vertical plane passing through the long axis of each part of the racetrack, and $y=0$ for the uppermost portion of the pipe along its entire length. At the moment of each footfall, we digitized the x and y coordinates of the point at which the fourth and fifth metatarsal diverged on the right hindfoot.

We used the digitized coordinates of the performance trials to calculate the length, speed and position for each of the five strides per lizard. The lengths of the first two and last two strides equaled the difference between the x -coordinate of the foot at the times of successive footfalls, but the length of stride 0 for racetracks with turns was calculated using different

methods with some of the additional quantities explained below.

The gross duration of each stride was the total time between successive footfalls, whereas the net duration of each stride equaled the gross duration minus the duration of pauses within that stride. Consequently, the average gross (V_g) and net (V_n) velocities per stride equaled stride length divided by gross stride duration and net stride duration, respectively. Stride frequency equaled the inverse of net stride duration. Step length equaled the forward distance traveled by the lizard while the right hind foot remained in contact with the racetrack (stance), and the net step duration equaled the duration of stance minus the duration of any intervening pause. The duty factor of each stride equaled net step duration expressed as a percentage of net stride duration. For each stride, we used the y -coordinate of the footfall at the beginning of the stride to indicate foot position relative to the top of the pipe (Y_{foot}).

Quantifying the locomotion that spanned the turn (stride 0) required more complex calculations than the strides of locomotion that were along the long axis of the perches on either side of the turn. The general convention for calculating stride length for locomotion without turns is simply a straight-line distance along a reference axis of forward progression, even though the trajectory of the center of mass of most limbed animals actually follows an arc. Applying similar logic, we used the two perches to define a plane of reference that we felt was most relevant for quantifying the stride length and trajectory of the locomotion of lizards that spanned the turn. We used the long axis of the perch preceding the turn as our first reference axis with an origin at the center of the turn along the tops of the perches. Our second reference axis was perpendicular to the first axis and within the plane defined by the tops of the two perches. At the time of the footfall preceding stride 0, we estimated the lateral distance (perpendicular to the long axis of a perch and within a horizontal plane) of the foot as $r \cos\{\arcsin[(Y_{\text{foot}}-r)/r]\}$, where r is the radius of the perch (2.44 cm). We determined the coordinate of the foot along the second reference axis by multiplying the lateral distance of the foot relative to the top of the perch by $\cos\theta$, where θ is the three-dimensional angle between a horizontal plane and the plane defined by the tops of the two perches. We used similar procedures to determine the two-dimensional coordinates along the first and second reference axes for the footfall at the end of stride 0 with additional correction factors that accounted for the angle of the second perch relative to the first perch. We subsequently calculated the length of stride 0 from a two-dimensional distance formula that used the coordinates along the first and second reference axes for the two footfalls that defined stride 0. Thus, the lengths of all strides were two-dimensional quantities within the plane defined by the long axes of the perches.

We also calculated the angle of the jump as a two-dimensional angle within the plane defined by the long axes of the two perches. We calculated the angle of the jump relative to the long axis of the perch used for take-off from the

arctangent of the ratio of the differences between the coordinates of the two stride 0 footfall positions along the second and first reference axes. We conducted preliminary three-dimensional calculations of jump angles relative to the perches and, because of the details of the specific geometry, the three-dimensional jump angles generally (20 of 24 jump angles) differed by less than 2° from our two-dimensional jump angles. However, a single three-dimensional angle calculated between the take-off perch and the trajectory of the jump is not sufficient to indicate whether a jump is above, below or to the side of the perch. Thus, we decided to use the two-dimensional values of jump angles as the best descriptor of the direction of movement in the plane in which most of the locomotion occurred.

We calculated three variables to characterize the extent to which locomotion was intermittent. The mean number of pauses per trial equaled the total number of pauses for each racetrack and species divided by the number of individuals per species. We also calculated the mean value of the number of pauses per trial for each species and racetrack only for trials with a pause. For each trial with one or more pauses, we also calculated the mean pause duration, which was then used to calculate the mean pause duration for each species and racetrack. Thus, the sample sizes of the latter two variables equaled the number of individuals per species that paused on a particular racetrack rather than the total number of individuals per species.

After viewing all the footage from the supplementary trials, we performed a frame-by-frame analysis of the two trials for each of the three species that most closely matched the mean values of speed and jumping distance from the performance tests of each species on the 90° turn. We defined take-off as the earliest time when none of the feet touched the racetrack and landing as when a hindfoot touched the racetrack. We digitized two-dimensional coordinates of the center of the pectoral and pelvic girdles and the tip of the tail from the overhead view every 8 ms during the jump and at intervals ranging from 8 to 20 ms before take-off and after landing. The 90° racetrack formed two sides of an isosceles triangle, the base of which was used to define a reference angle of 0° , and the first and second portions of the racetrack had angles of approximately -45° and 45° , respectively. We then calculated the angles of the body (pectoral to pelvic girdle) and tail (pelvic girdle to tail tip) relative to the reference axis such that positive values indicate that the anterior point of a pair was to the right of the more posterior point. The angle between the tail and body was positive when the lizard was concave to the right.

We used SAS version 8.0 for all statistical analyses, and $P < 0.05$ was the criterion for statistical significance. We performed four-way mixed-model analyses of variance (ANOVAs) when analyzing the stride-by-stride data. One of the four independent categorical variables, individual, was a random factor nested within species ($N=3$), whereas species, turning angle ($N=3$) and stride number ($N=5$) were all fixed and crossed. To determine the appropriate mean squares to use for the F -tests in this mixed model four-way ANOVA, we used

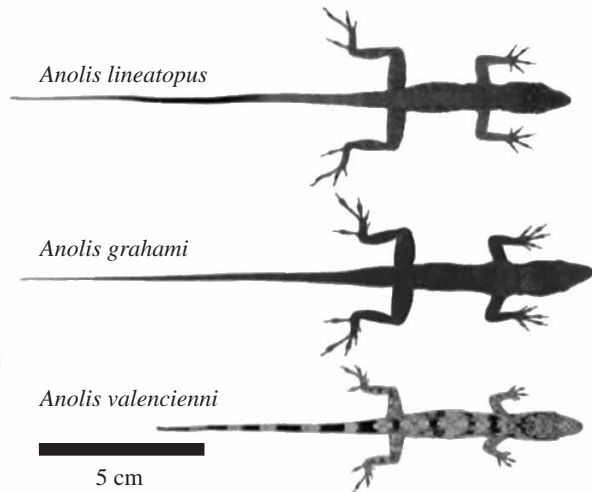


Fig. 1. Dorsal views of anesthetized specimens from each of the three *Anolis* species. Note that the overall body size is similar, whereas tail length and limb dimensions are much smaller in *Anolis valencienni* than in the other two species. All specimens are shown at the same magnification.

Scheffe (1959). We performed three-way ANOVAs for the data over the 30 cm interval, using the categorical variables above except stride number.

Results are presented as means ± S.E.M., unless stated otherwise. In Figs 2–5, *N*=17 for *A. lineatopus*, *N*=14 for *A. grahami* and *N*=8 for *A. valencienni*.

Results

Morphology

The overall body size of the individuals used in the experiments was grossly similar (Fig. 1, Table 1). The mean snout–vent lengths (SVLs) showed statistically significant variation among the three species (one-way ANOVA, $F_{2,36}=5.9, P=0.006$). The mean SVL of both *A. grahami* was significantly greater than that of both *A. lineatopus* and *A. valencienni* (Tukey’s honestly significant difference); however, the values for *A. valencienni* and *A. lineatopus* did not differ significantly. Furthermore, the smallest mean value of SVL (for *A. valencienni*) was at least 90 % greater than those of the other two species (Table 1). The morphological differences among our sample conformed to the average differences calculated for several species of each ecomorph as described in more detail by Beuttell and Losos (1999). For a similar SVL, *A. valencienni* was less massive and had a substantially smaller tail length, girdle widths and lengths of elements within the fore- and hindlimbs, which were often only approximately 70 % of the values of the other two species.

Performance

The gross velocity over the 30 cm interval differed significantly both among turning angles and among species (Table 2). On the straight racetrack, the rank order of the

Table 1. Descriptive statistics of morphological measurements for the three species of *Anolis*

Variable	<i>A. lineatopus</i> , N=17	<i>A. grahami</i> , N=14	<i>A. valencienni</i> , N=8
Mass (g)	5.2±0.2	6.6±0.2	2.9±0.4
Snout–vent length (mm)	60±0.7	64±0.7	58±2.0
Tail length (mm)	100±3.5	100±4.0	70±3.5
Intergirdle distance (mm)	27.5±0.6	31.6±0.7	29.6±1.1
Pelvic width (mm)	5.0±0.1	5.7±0.2	4.0±0.2
Femur length (mm)	13.4±0.2	13.6±0.1	9.9±0.2
Tibia length (mm)	12.4±0.2	12.0±0.1	7.9±0.3
Hindfoot length (mm)	8.1±0.2	7.9±0.2	5.0±0.2
Hindfoot fourth toe length (mm)	10.0±0.3	10.6±0.2	6.5±0.2
Pectoral width (mm)	5.5±0.3	6.6±0.2	4.4±0.1
Humerus length (mm)	9.9±0.1	10.8±0.1	8.2±0.2
Ulna length (mm)	7.6±0.3	8.4±0.1	6.0±0.1
Forefoot length (mm)	2.7±0.1	3.0±0.1	1.8±0.1
Forefoot fourth toe length (mm)	5.5±0.2	6.2±0.2	3.5±0.3

Values are means ± S.E.M.

species from fastest to slowest was *A. lineatopus*, *A. grahami* and *A. valencienni* (Table 3). The gross velocities of all three species decreased substantially for the 90° compared with the 0° turn. For example, *A. lineatopus* and *A. valencienni* ran approximately twice as fast on the 0° as on the 90° turn (Table 3). The gross velocities of both *A. lineatopus* and *A. valencienni* for 30° turn were also substantially lower than those for the straight racetrack, whereas *A. grahami* had nearly identical values for the 0° and 30° turns. Consequently, the species by turn interaction term was highly significant (Table 2).

For all three species, as turning angle increased, the number of pauses increased significantly (Table 2) and, hence, the difference between gross and net velocity for each species increased with increased turning angle (Table 3). With only one exception, the significant differences in net velocity over a 30 cm interval among species and turning angles were similar to the pattern for gross velocity (Tables 2, 3). Namely, for *A. grahami*, net velocity was effectively constant over all three

Table 2. F-values from three-way ANOVAs performed separately for variables for a 30 cm interval

Dependent variable	Species, d.f.=2,36	Turn, d.f.=2,32	Species × Turn, d.f.=4,32
V_{g30}	11.1**	53.5**	6.1**
V_{n30}	12.8**	19.5**	5.8**
Number of pauses	4.6*	54.8**	1.8

* $P<0.05$, ** $P<0.001$.
Main effects and interaction terms are listed above each column. d.f., degrees of freedom; V_{g30} , average gross velocity; V_{n30} , average net velocity.

Table 3. Descriptive statistics for gross and net velocities over a 30 cm interval

Velocity (m s ⁻¹)	Turn angle (degrees)	<i>A. lineatopus</i> , N=17	<i>A. grahami</i> , N=14	<i>A. valencienni</i> , N=8
V_{g30}	0	1.46±0.06	1.21±0.06	1.00±0.06
V_{g30}	30	1.16±0.06 (79%)	1.20±0.06 (99%)	0.74±0.08 (74%)
V_{g30}	90	0.73±0.04 (50%)	0.96±0.08 (79%)	0.48±0.01 (48%)
V_{n30}	0	1.46±0.06	1.22±0.06	1.01±0.06
V_{n30}	30	1.17±0.05 (80%)	1.24±0.05 (102%)	0.80±0.06 (79%)
V_{n30}	90	1.00±0.06 (54%)	1.19±0.09 (98%)	0.68±0.04 (67%)

V_{g30} , gross velocity; V_{n30} , net velocity.

Values are means ± S.E.M.

Values as a percentage of straight perch running speed are given in parentheses.

See Table 2 for tests of significant effects.

turning angles and, hence, the decrease in gross velocity on the 90° turn for *A. grahami* was almost entirely a result of pauses taken rather than a decreased speed of running.

Stride-by-stride variables

All seven variables describing the velocity and kinematics of each stride changed significantly with both turning angle and stride number and had a significant turning angle by stride number interaction term (Table 4). For all three species, net (Fig. 2) and gross velocity per stride decreased significantly with increasing turning angle (Table 4). For the 90° turn, stride 1 had the slowest net velocity per stride for all three species, and stride 0 had the fastest net velocity for *A. grahami* and *A. valencienni*. The remaining trends in net and gross velocity per stride among species and turning angles were similar to those of net and gross velocity over the 30 cm interval.

Anolis grahami (9.7±0.4, 4.8±0.2 cm, N=14) and *A. lineatopus* (10.7±0.3, 4.9±0.1 cm, N=17) had similar stride and step lengths, as indicated by the means of the averages for stride -2 of each individual across all three turns, whereas the stride and step lengths of *A. valencienni* (6.9±0.4, 3.6±0.4 cm, N=8) were significantly shorter (Fig. 3, Table 4). For all three species, stride length usually decreased with increasing turning angle, except for the length of stride 0 on the 90° turning angle, which was longest for *A. grahami* and *A. valencienni* as a result of some individuals jumping. The shortest stride length of *A. grahami* and *A. lineatopus* occurred for stride 1 on the 90° turning angle. These differences in the lengths of strides 0 and 1 on the 90° turn contributed to the highly significant turning angle by stride number interaction term (Table 4). The overall pattern of change in step length among species, turning angle and stride number was similar to that of stride length except that the magnitude of the differences was much smaller.

Duty factor and stride frequency did not differ significantly among the three species (Table 4). The means of the averages for duty factor and of stride -2 of each individual across all three turns were 49±1% for *A. lineatopus*, 52±1% for *A. grahami* and 51±3% for *A. valencienni*, and the means of the averages for stride frequency were 11.8±0.3 Hz for *A. lineatopus*, 11.5±0.3 Hz for *A. grahami* and 12.0±0.5 Hz for *A.*

valencienni (Fig. 4). The vast majority (36 of 45) of the mean values of duty factor for each species, turning angle by stride number were between 45 and 55%. Duty factor varied

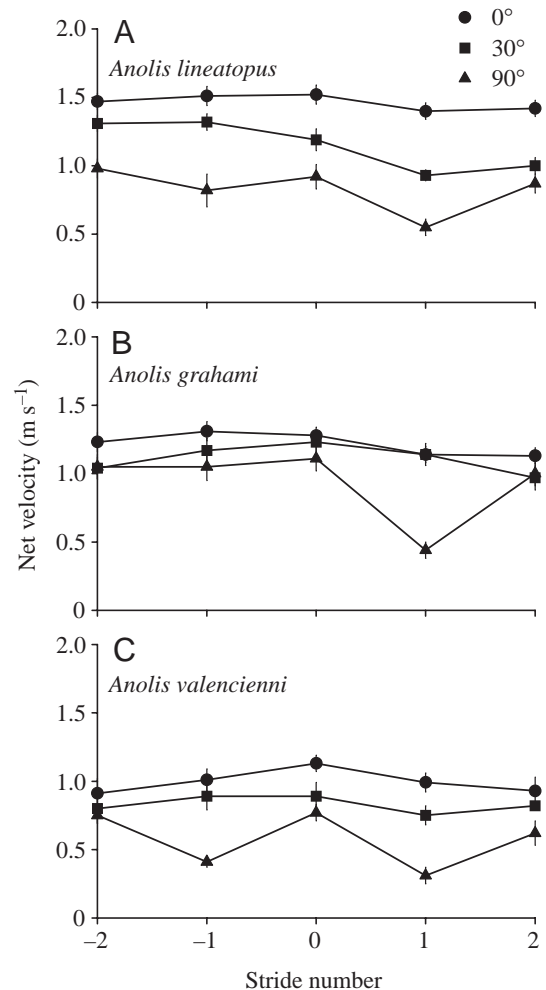


Fig. 2. Net velocity versus stride number for *Anolis lineatopus* (A), *A. grahami* (B) and *A. valencienni* (C). The circles, squares and triangles represent turning angles of 0°, 30° and 90°, respectively. Values are means ± S.E.M. Some error bars are not visible because they are smaller than the size of the symbols.

Table 4. F-values from four-way ANOVAs performed separately on each variable

Dependent variable	Species, d.f.=2,20	Turning angle, d.f.=2,32	Stride number, d.f.=4,64	Species × Turning, d.f.=4,32	Species × Stride, d.f.=8,64	Turn × Stride number, d.f.=8,128
V_g	16.4**	83.7**	13.9**	6.5**	2.3*	5.5**
V_n	15.0**	81.7**	18.2**	6.7**	1.4	5.1**
L	32.2**	28.3**	17.1**	4.5**	2.8**	6.6**
SL	30.2**	13.8**	6.0**	2.3	0.9	3.1**
Y_{foot}	3.4	5.4**	24.3**	0.5	1.7	13.8**
DF	1.6	7.4**	5.5**	3.2*	0.4	3.4**
f	1.2	13.8**	2.7*	3.2*	0.9	2.4*

* $P < 0.05$, ** $P < 0.001$.

Main effects and interaction terms are listed above each column.

d.f., degrees of freedom.

V_g and V_n are the gross and net velocities, respectively.

L and SL are the stride and step lengths, respectively.

Y_{foot} is the vertical position of the hindfoot, relative to the top of the perch, at footfall.

DF is the duty factor per stride.

f is the stride frequency.

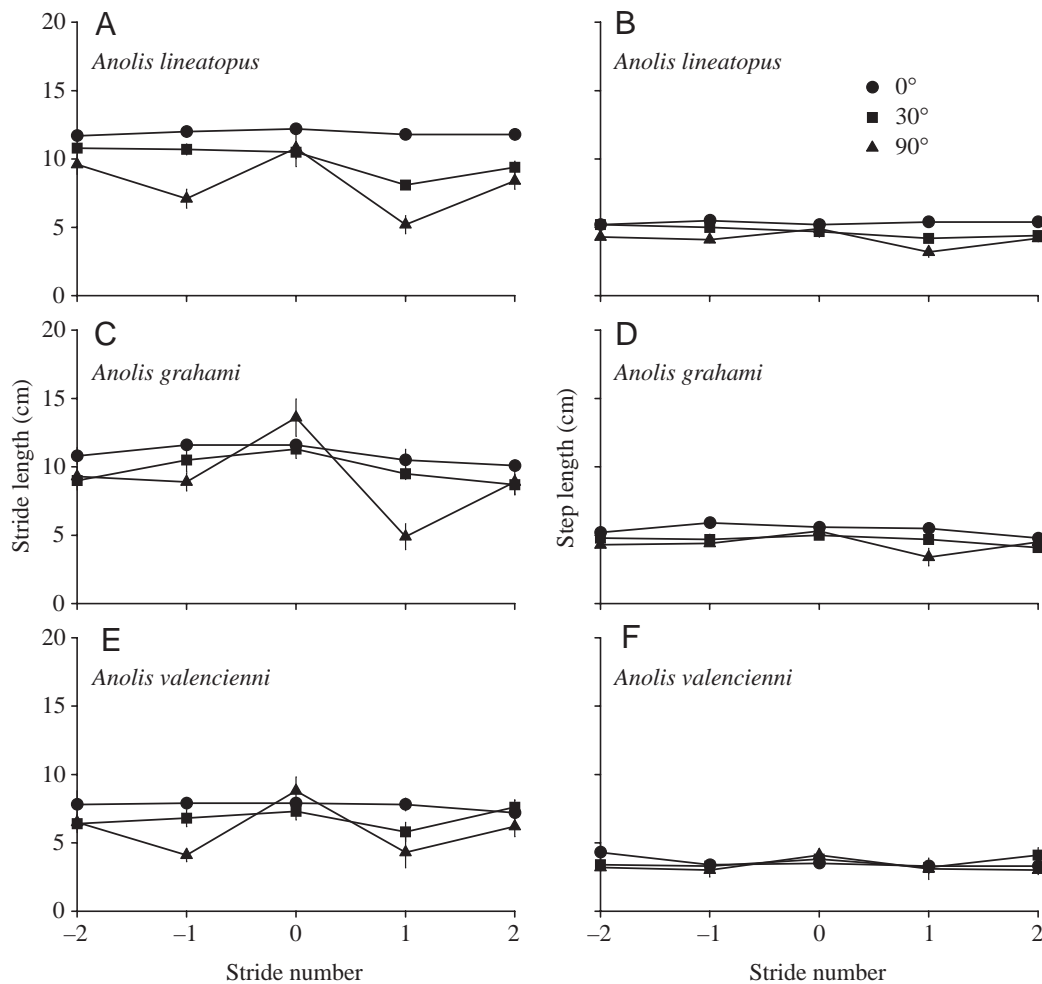


Fig. 3. Stride length (A,C,E) and step length (B,D,F) versus stride number for *Anolis lineatopus* (A,B), *A. grahamsi* (C,D) and *A. valencienni* (E,F). The circles, squares and triangles represent turning angles of 0°, 30° and 90°, respectively. For stride 0 on the 90° turn, stride and step lengths included jumps. Values are means ± S.E.M. Some error bars are not visible because they are smaller than the size of the symbols.

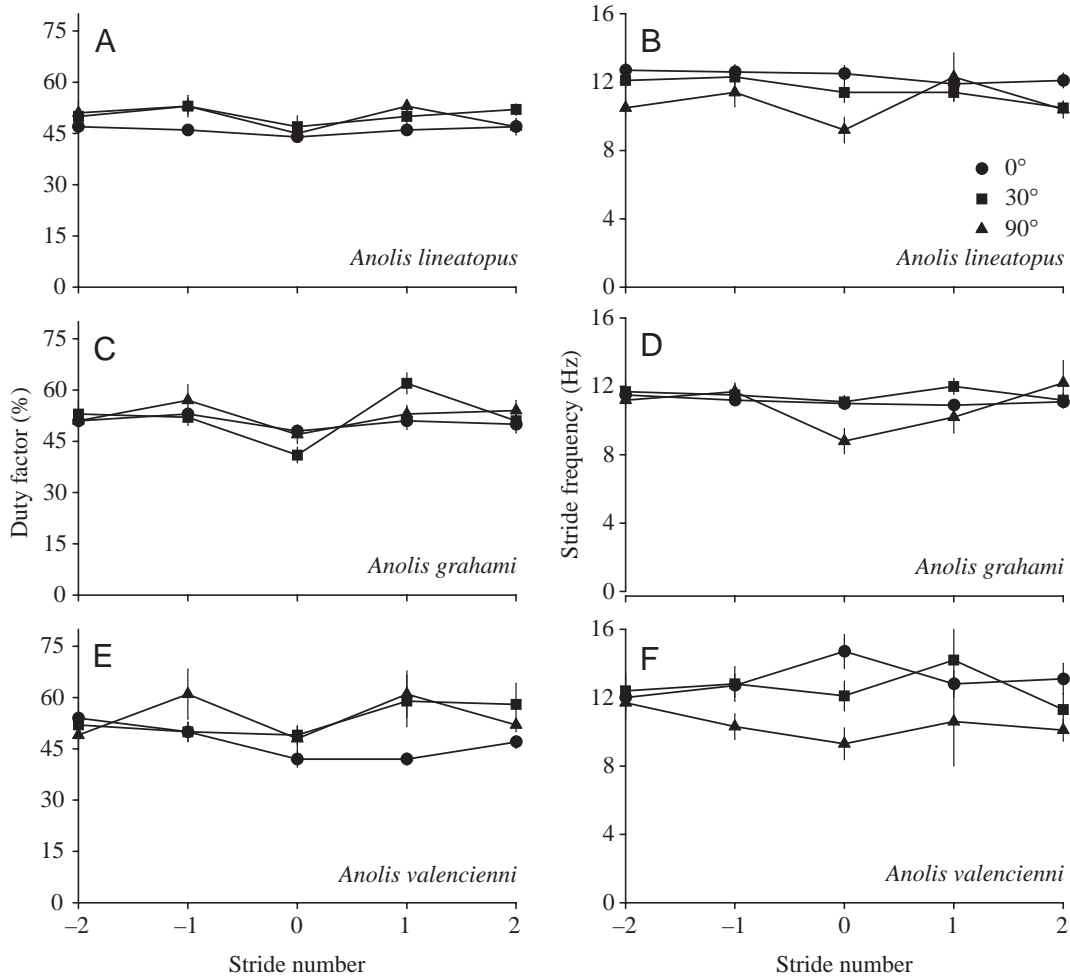


Fig. 4. Duty factor (A,C,E) and stride frequency (B,D,F) versus stride number for *Anolis lineatopus* (A,B), *A. grahami* (C,D) and *A. valencienni* (E,F). The circles, squares and triangles represent turning angles of 0°, 30° and 90°, respectively. Values are means \pm S.E.M. Some error bars are not visible because they are smaller than the size of the symbols.

conspicuously among strides for locomotion on the 90° turn, but not for the 0° and 30° turns (Fig. 4), resulting in a significant turning angle by stride number interaction term (Table 4). The significant variation in stride frequency with turning angle was primarily a result of low values for the 90° turn.

The most conspicuous variation in the placement of the right hindfoot relative to the top of the perch (Y_{foot}) resulted from very low values occurring for the stride immediately after turning on the 90° racetrack (Fig. 5). Consequently, Y_{foot} had a highly significant variation among strides as well as a highly significant turning angle by stride number interaction term (Table 4). For the straight and 30° racetracks, the body of the lizard was usually directly above the tops of the perches, whereas the lower values of Y_{foot} on the 90° racetrack indicate that the body of the lizard was off-center and towards the inner surface of the perches comprising the turn (Fig. 6).

The percentage of strides with a pause increased substantially with increased turning angle for all three species (Fig. 7). Pausing occurred most frequently at stride 1 for *A.*

grahami and at stride 0 for *A. lineatopus*, whereas *A. valencienni* paused with equal frequencies at strides -1, 0 and 1. *A. lineatopus* never paused on the straight racetrack. The duration of individual pauses showed little regular variation either with increases in turning angle or among the three species, whereas *A. valencienni* had the greatest number of pauses per trial on all three turning angles (Table 5). For all species on the 90° turn, two or more pauses commonly occurred within the five strides that were measured.

For the fastest trials for each individual, jumping occurred only at stride 0 on the 90° turning angle, but not all individuals jumped on the 90° turning angle. A pause immediately preceded most of the jumps of *A. lineatopus* (8 of 9) and *A. valencienni* (4 of 6), whereas running preceded jumping for most *A. grahami* (7 of 9). Pauses immediately followed the jumps of *A. grahami* (7 of 9) and *A. valencienni* (5 of 6), whereas most *A. lineatopus* (8 of 9) ran immediately after landing rather than pausing. The durations of pauses immediately after a jump were commonly longer than those immediately preceding a jump, as indicated by the mean values

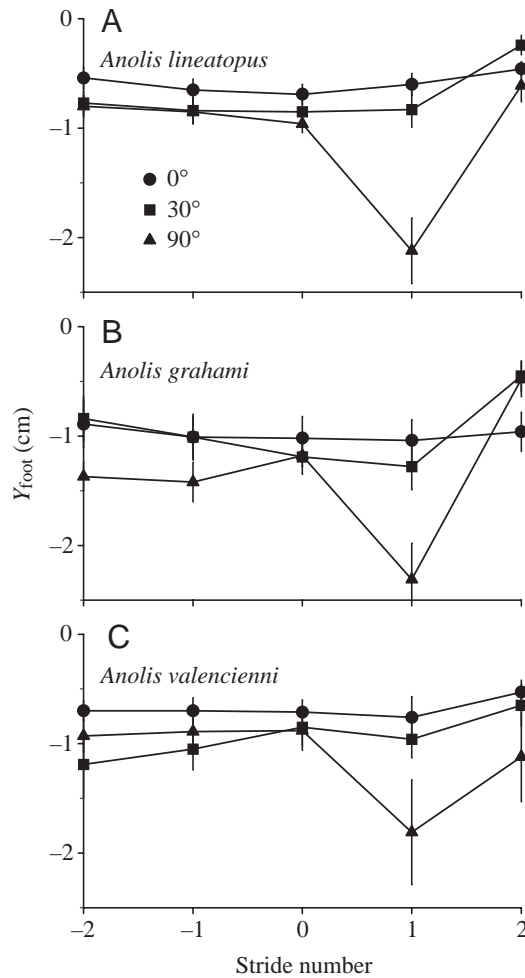


Fig. 5. Vertical position of the foot relative to the top of the perch (Y_{foot}) versus stride number for *Anolis lineatopus* (A), *A. grahami* (B) and *A. valencienni* (C). The circles, squares and triangles represent turning angles of 0° , 30° and 90° , respectively. Values are means \pm S.E.M. Some error bars are not visible because they are smaller than the size of the symbols.

for *A. grahami* (101 ± 42 ms versus 82 ± 17 ms), *A. lineatopus* (144 ms, $N=1$, versus 98 ± 21 ms) and *A. valencienni* (123 ± 16 ms versus 58 ± 30 ms).

For all three species during performance trials on the 90° racetrack, the mean values of jump length were substantially larger than the corresponding lengths of stride 0 (Table 6). For all three species, no differences were apparent in the lengths of jumps occurring immediately after a pause compared with those that were not preceded by a pause. The mean values of net velocity for jumps were greater than those of strides spanning the 90° turn for *A. grahami* and *A. lineatopus*, whereas the corresponding values for *A. valencienni* were very similar (Table 6). The mean values of gross velocity for jumps exceeded those of strides for all species. The mean values of the angle indicating the overall trajectory of the jumps varied only slightly among the three species (Table 6).

The overhead views from the supplementary trials revealed that the trajectory of the body of the lizards changed

Table 5. Descriptive statistics summarizing intermittent locomotion for the three *Anolis* species on each of the three turn angles

Turning angle (degrees)	<i>A. lineatopus</i>	<i>A. grahami</i>	<i>A. valencienni</i>
Duration of pauses when present (ms)			
0	–	54 ± 9 (3)	88 ± 38 (4)
30	127 ± 19 (2)	72 ± 8 (7)	111 ± 32 (5)
90	84 ± 13 (14)	101 ± 23 (12)	84 ± 14 (7)
Number of pauses per trial per individual when present			
0	–	1.3 ± 0.3 (3)	1.3 ± 0.3 (4)
30	1.5 ± 0.5 (2)	1.4 ± 0.3 (7)	1.4 ± 0.2 (5)
90	1.9 ± 0.2 (14)	2.0 ± 0.3 (12)	2.7 ± 0.2 (7)
Number of pauses per trial per individual			
0	0 ± 0 (17)	0.3 ± 0.2 (14)	0.6 ± 0.3 (8)
30	0.2 ± 0.1 (17)	0.7 ± 0.2 (14)	0.9 ± 0.3 (8)
90	1.6 ± 0.2 (17)	1.7 ± 0.3 (14)	2.4 ± 0.4 (8)

Values are means + S.E.M. (N).

substantially while the lizard was airborne (Fig. 6). At take-off, the tail was nearly parallel to the take-off perch (-45°), whereas the body was pointed to the right of the perch (Fig. 6). While airborne, the angle of the body always increased and approached the orientation of the landing perch (45°). During the airborne phase, the tail and body were initially concave to the right and then often became nearly straight. The rapid initial increase in the angle of the tail relative to the body was correlated with turning the body in some sequences (Fig. 6A,C) but not others (Fig. 6B).

Discussion

Performance

Although maximal running speeds have been determined for several species of *Anolis* and other lizards (for a review, see

Table 6. Descriptive statistics summarizing the strides and jumps that straddled the 90° turn

Variable	<i>A. lineatopus</i>	<i>A. grahami</i>	<i>A. valencienni</i>
Jump length (cm)	14.0 ± 1.6 (9)	16.8 ± 1.1 (9)	9.9 ± 1.0 (6)
Stride length (cm)	7.1 ± 1.4 (8)	7.9 ± 0.6 (5)	5.6 ± 1.3 (2)
Jump V_n (cm s^{-1})	113 ± 6 (9)	126 ± 9 (9)	79 ± 8 (6)
Stride V_n (cm s^{-1})	68 ± 14 (8)	85 ± 13 (5)	70 ± 9 (2)
Jump V_g (cm s^{-1})	70 ± 7 (9)	111 ± 14 (9)	63 ± 7 (6)
Stride V_g (cm s^{-1})	54 ± 13 (8)	85 ± 13 (5)	49 ± 29 (2)
Jump angle (degrees)	31 ± 3.7 (9)	29 ± 3.1 (9)	35 ± 4.9 (6)
Path length minus jump length (cm)	5.9 ± 0.5 (9)	6.7 ± 0.3 (9)	4.8 ± 0.4 (6)
Path length minus stride length (cm)	3.9 ± 0.3 (8)	4.2 ± 0.3 (5)	4.0 ± 0.4 (2)

V_g and V_n are the gross and net velocities, respectively.

Values are means \pm S.E.M. (N).

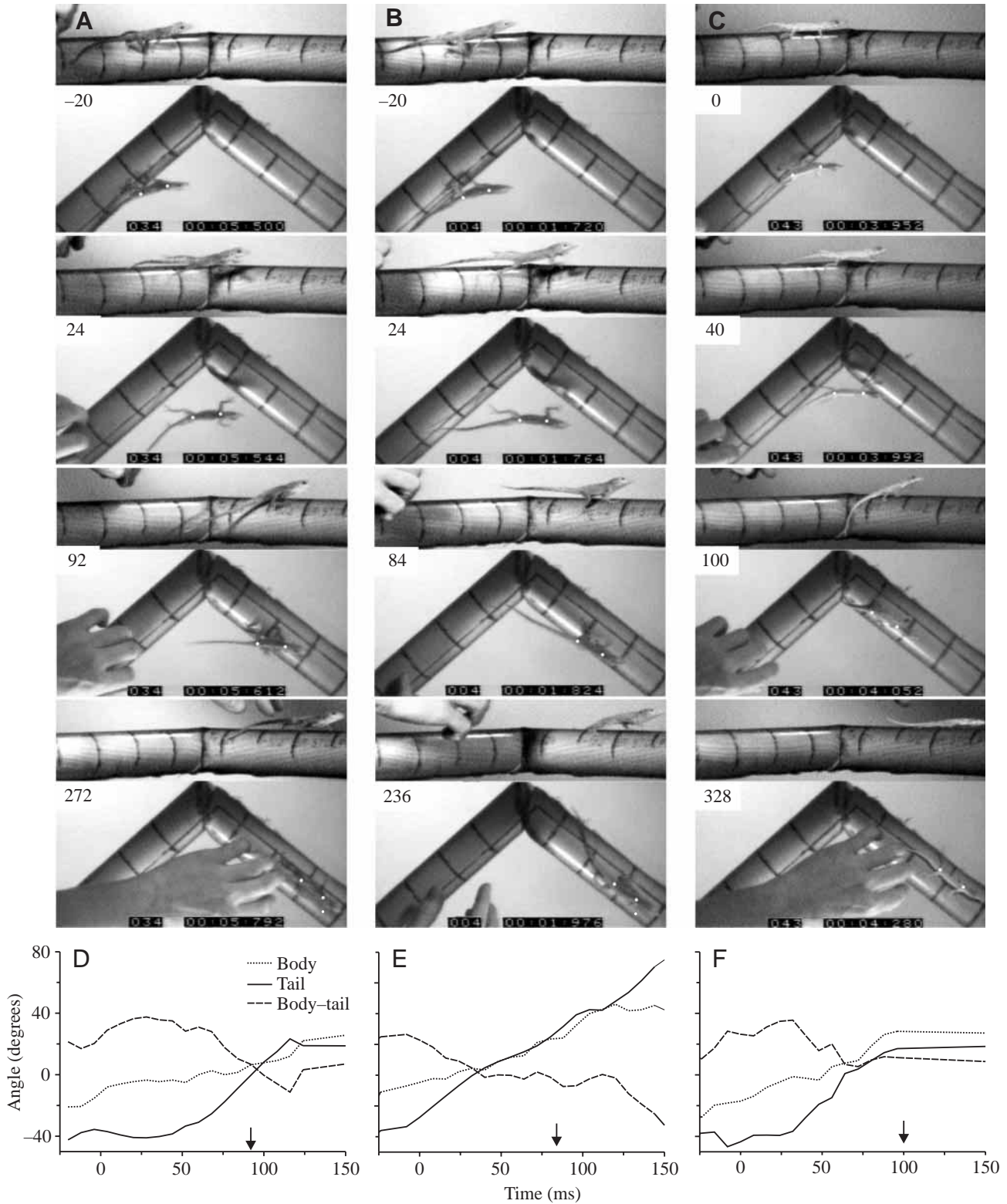


Fig. 6. Overhead and lateral views and tail and body orientation of *Anolis lineatopus* (A,D), *A. grahmi* (B,E) and *A. valencienni* (C,F) during (from top to bottom) take-off, mid-jump, landing and post landing on the 90° turning angle. The value to the left of each video image is the elapsed time (in ms); 0 ms indicates the time of take-off. The two white dots on the lizards indicate the midpoints of the pectoral (anterior dot) and pelvic (posterior dot) girdles. The line parallel to the long axis of the pipe on the top of the perch in the dorsal view represents the top of the perch. Note that all three species land on the inner side of the perch. Although the original overhead video images were inverted because they were obtained *via* a mirror, for the sake of clarity in these figures we edited the overhead view so that it resembled a simple dorsal view. The orientations of the perches prior to and after the turn are -45° and 45°, respectively. The downward-pointing arrows in D-F indicate the time of landing.

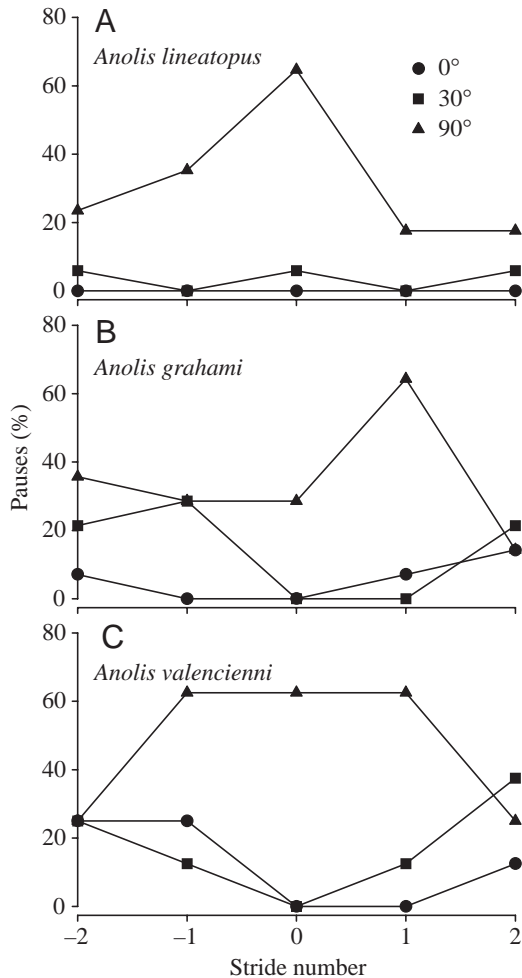


Fig. 7. The percentage of strides that contained a pause for *Anolis lineatopus* (A), *A. grahami* (B) and *A. valencienni* (C) for a particular stride number. The circles, squares and triangles represent turning angles of 0°, 30° and 90°, respectively.

Garland and Losos, 1994), our study is the first to manipulate turning angle experimentally and to quantify its effects on the locomotion of lizards. Increased angles of turning had widespread effects on the escape locomotion observed in our study including decreased running speed, decreased stride length, increased amounts of pausing, increased amounts of jumping and changes in the position of the footfalls relative to the circumference of the perch.

The locomotor speeds of *A. grahami* were contrary to our expectations for two reasons. First, the net speeds of *A. grahami* were virtually unaffected by increased turning angle (Table 3), whereas we expected that the speed of all species would decline with increased turning angle. Second, although the gross speeds of *A. grahami* declined for the 90° turn compared with the values for straight and 30° turns, the magnitude of this decline in performance was substantially less than that of *A. valencienni*, which we had expected would be least affected by turning.

This expectation for *A. valencienni* was based primarily on

the habitat in which the species is found rather than its morphology. Compared with swimming and flying organisms (Fish, 1997; Norberg and Rayner, 1987; Schrank et al., 1999), the morphological specializations that facilitate maneuvering of limbed animals on solid surfaces are poorly understood. The habitat of the short-limbed twig ecomorph, *A. valencienni* (Fig. 1), has numerous, closely spaced turns and small-diameter branches that form dense networks where large unobstructed spaces are rare. Shorter limbs could benefit species occupying small branches as a result of requiring less unobstructed space. To isolate the effects of turning on performance, we did not vary either perch diameter or the amount of unobstructed space. Consequently, the benefits of the morphology of *A. valencienni* may be apparent in a more naturalistic setting where the occurrence of turns covaries with perch diameter and the amount of unobstructed space.

The effects of perch diameter on the running speeds of *Anolis* lizards, like the effects of turning on speed, are also species-dependent. For example, the ratio of sprinting speeds on 1.2 cm compared with 4.6 cm diameter perches are 77% for *A. grahami*, 68% for *A. lineatopus* and 87% for *A. valencienni* (Losos and Sinervo, 1989). The diameter of the perches that we used (4.8 cm) closely approximated the maximal diameter of perches used by Losos and Sinervo (1989) and, hence, both studies used similar conditions to obtain maximal speeds. Thus, the decrement in maximal speed associated with turning on a perch (Table 3) can exceed that associated with decreased perch diameter.

The only previously quantified effects of turning on the escape speeds of lizards are for two terrestrial species running on the surface of a sand dune. Between successive meters of the escape paths of *Uma scoparia* (Jayne and Ellis, 1998) and *Callisaurus draconoides* (Irschick and Jayne, 1999), turning angles greater than 45° are extremely rare (<7% of the total number of turns). Turning angle significantly affects the sprinting speed of *U. scoparia* but not of *C. draconoides*, and *C. draconoides* runs significantly faster than *U. scoparia*. For 30° and 90° turns of *U. scoparia*, a regression model predicts values of sprinting speeds that are 92% and 75%, respectively, of the maximal values predicted for running straight. Hence, despite having fewer constraints on foot placement, the magnitude of the decrease in speed for large turns of *U. scoparia* is as large as some of the detrimental effects of turning on speed that we observed for the arboreal locomotion of *Anolis* species. The percentage of escape locomotion that is bipedal in *C. draconoides* is approximately four times that of *U. scoparia*. Bipedality is common in terrestrial lizards and may enhance the maneuverability of *C. draconoides* compared with that of *U. scoparia*. None of the *Anolis* species in our study ran with striding (alternating hindlimb movements) bipedal locomotion, and no previous studies have documented bipedal running of arboreal species on perches.

Three quantities commonly used to describe maneuvering performance are the speed with which an animal can rotate about a fixed point, the radius of curvature of the path traveled by the animal and the centripetal acceleration, which is the

square of the tangential velocity divided by the turning radius times the gravitational constant (Drucker and Lauder, 2001; Fish, 1997; Norberg, 1994; Walker, 2000). The bodies of the lizards in our study were often nearly parallel to the perches immediately before and after turning. Consequently, average rotational velocities can be estimated by dividing the turning angle by the mean value of gross duration for the stride that spanned the turn. The average rotational velocities for the 30° turns were 328° s⁻¹ for *A. grahami*, 307° s⁻¹ for *A. lineatopus* and 349° s⁻¹ for *A. valencienni*, and the average rotational velocities for the 90° turns were 609° s⁻¹ for *A. grahami*, 499° s⁻¹ for *A. lineatopus* and 550° s⁻¹ *A. valencienni*.

Assuming that stride 0 was centered across the angle between the two perches comprising the turn, the average radius of curvature (r_{path}) can be estimated by calculating the point of intersection of the normals relative to each perch at the point of footfall and in the plane defined by the two perches. Using the average length of stride 0 excluding jumps for *A. grahami*, *A. lineatopus* and *A. valencienni*, the estimates of mean r_{path} for the 30° and 90° turns were 21.1, 19.6 and 13.6 cm, respectively, and 4.0, 3.6 and 2.8 cm, respectively, and for jumps on the 90° turn the corresponding values were 8.4, 7.0 and 5.0 cm, respectively. Using the average values of gross velocity (V_g) and r_{path} of stride 0, excluding jumps for *A. grahami*, *A. lineatopus* and *A. valencienni*, the estimates of centripetal acceleration were 0.7, 0.7 and 0.6g, respectively, for the 30° turns and 1.9, 0.8 and 0.9g, respectively, for the 90° turns. Estimates for jumps on the 90° turns were 1.5, 0.7 and 0.8g, respectively. Thus, *A. valencienni* was maneuverable primarily as a result of making a tight turn, whereas *A. grahami* was maneuverable primarily as a result of negotiating turns rapidly.

Intermittent locomotion

Intermittent locomotion is common for lizards, but previous quantitative data on pausing are limited to those of Avery et al. (1987), who manipulated both the environment and the behavioral state of the lizards. Avery et al. (1987) recorded the amounts of pausing during voluntary locomotion of lacertid lizards in variations of a standard arena with a central open area with shelters and obstacles at each end. Pauses accounted for 51% of total time that adults spent moving in the standard arena. Changes in the conditions in the arena had varying effects on this value. For example, the addition of wooden cubes had less effect (46%) than the addition of grass (78%). Similarly, when lizards searched for crickets in the open area of the standard arena, time spent pausing was greater (67%) than when they chased crickets (48%). The percentage of time spent pausing during escape locomotion in the open area of the arena was only 28% (Avery et al., 1987). Although the addition of wooden cubes increases the complexity of the environment, no significant effect on the amount of pausing was apparent. Another surprising result was that similar amounts of pausing occurred when the lizards were chasing prey compared with the standard conditions. The large amount of pausing during searching for prey suggests that pausing and

processing sensory information may be inter-related (Avery et al., 1987).

For our study of *Anolis* lizards, pausing varied considerably as we manipulated the environment, although we attempted to keep behavioral state constant by eliciting escape locomotion. For all three species of *Anolis* in our study, the amount of pausing increased with increased turning angle and, hence, we observed quite regular effects of environmental variation on pausing compared with Avery et al. (1987). Furthermore, we observed some very consistent patterns of interspecific variation. For example, the rank order from least to greatest amount of pausing, pooled across all five strides within a trial, was *A. lineatopus*, *A. grahami* and *A. valencienni* for each of the three turning angles (Table 5). The mean percentages of time spent pausing over a five-stride interval were 0±0, 3±2 and 19±3% for *A. lineatopus*, 3±2, 9±3 and 21±5% for *A. grahami* and 9±4, 15±6 and 25±4% for *A. valencienni* on the 0°, 30° and 90° turning angles, respectively.

The available data suggest that the endurance capacity of *Anolis* species is limited, as is the case for most species of lizard (Garland, 1994). For a particular net velocity and duration of movement, pausing can enhance distance capacity compared with the value for continuous locomotion, but pausing appears unlikely to affect endurance when the durations of pauses are short (Weinstein and Full, 1992). The extremely brief duration of most pauses (<150 ms) that we observed during the escape locomotion of *Anolis* thus seems unlikely to provide a physiological benefit.

A potential cost of pausing during high-speed locomotion is the rapid acceleration that must occur after the pause. For example, for *A. grahami*, *A. lineatopus* and *A. valencienni*, the mean values of net velocity of all strides after pauses were 106±7 cm s⁻¹ ($N=31$), 79±9 cm s⁻¹ ($N=26$) and 76±7 cm s⁻¹ ($N=25$), respectively. Dividing by the mean net durations of these strides yields estimates of average acceleration of 11.4, 8.7 and 8.4 m s⁻², respectively. Other species of lizard also accelerate rapidly and can attain nearly maximal speeds within two strides of accelerating from a standstill (Huey and Hertz, 1984; Irschick and Jayne, 1998).

Most previous studies of the escape locomotion of lizards have used racetracks with photocells and, hence, are unable to detect pausing (Garland and Losos, 1994). The escape distances of two species of terrestrial lizard studied in their natural habitat range from approximately 1.5 to 35 m, and no pauses occur for this locomotion in relatively open areas on the surface of a sand dune (Irschick and Jayne, 1999; Jayne and Ellis, 1998). Whether terrestrial and arboreal species of lizard have different average tendencies to perform intermittent locomotion remains unclear, and conclusions may differ for observations of escape *versus* voluntary locomotion.

Rather than locomotion on arboreal perches being the primary cause of intermittent locomotion, pausing in the three *Anolis* species was correlated with the severity of the turn imposed by the perches. The occurrence of pausing in *Anolis* species is likely to be affected by factors in addition to biomechanical considerations. For example, the greater

occurrence of pausing in *A. valencienni* compared with the other two species of *Anolis* on a similar perch may reflect a greater reliance on crypsis rather than speed for evading predators. Furthermore, the pauses may be related to processing the sensory information that is related to changing the path of the animal. This leads to the prediction that increasing the number of branches at the node in a network of perches would increase the number or duration of pauses.

Jumping

All three species of *Anolis* in our study commonly traversed the 90° turn by jumping. The rank order of the three species in our study, based on the percentage of individuals that used a jump to traverse the 90° turn, was *A. valencienni* (75%), *A. grahami* (64%) and *A. lineatopus* (53%), whereas the field observations of Losos (1990a) found the rank order based on the percentage of movement bouts that were jumps was *A. lineatopus* (27%), *A. grahami* (19%) and *A. valencienni* (11%). Thus, the incidence of jumping that we observed in our laboratory experiments differed substantially from our expectation that it would reflect the incidence of jumping observed in the field. However, these field observations did not differentiate between straight and maneuvering locomotion or between high-speed and low-speed locomotion. Consequently, the different probabilities of *Anolis* species. Jumping in our laboratory experiments compared with the field observations of Losos (1990a) could reflect a species-dependent use of jumping either for maneuvering *versus* straight-ahead locomotion or for escape *versus* voluntary locomotion. Furthermore, the striking difference in the probability of jumping by *A. valencienni* in the field *versus* the laboratory tests may result from an inhibitory effect on jumping from the high density of twigs that create obstructions for the locomotion of this species in its natural habitat.

Potential benefits of jumping include increasing locomotor speed, decreasing the distance traveled and allowing different turning angles compared with those defined by perches. Jumping may also allow animals to reach destinations that it may not be possible to reach *via* a discrete network of perches. Potential costs of jumping include difficulty in the transition from using the limbs alternately and then bilaterally, falling if the landing site is missed and grasping the perch during landing.

The high values of net velocity of jumps compared with striding locomotion for *A. grahami* and *A. lineatopus* were caused by the long lengths of jumps, for which net duration differed little from that of striding locomotion. However, during jumping for *A. grahami* and *A. lineatopus*, pausing commonly occurred as the lizard prepared to jump or recovered after landing. Consequently, the benefits of jumping for enhancing speed are less obvious if the measure of performance is gross velocity rather than net velocity. For evading predators, the most relevant measure of performance is presumably gross velocity since this determines the total time taken to traverse a particular distance.

To estimate potential decreases in the distance traveled

between the footfalls immediately before and after the turn, we calculated the distance of a path along the top of the two perches comprising a turn and then subtracted the straight-line distance of the cycle of locomotion that straddled the turn (Table 6, path length minus jump length, path length minus stride length). Because of only minor differences in the jump angles among the three species of *Anolis*, the distances saved by jumping compared with moving along the perches is largely explained by the interspecific differences in jump length (Table 6). The paths defined by traveling strictly along the tops of perches can also be circumvented by taking a stride that straddles the turn. Thus, to isolate the benefits of jumping *versus* striding locomotion, one should compare the distances saved by these two methods for decreasing distance traveled. Compared with striding locomotion, jumps saved average distances of 2.5 cm for *A. grahami*, 2.0 cm for *A. lineatopus* and 0.8 cm for *A. valencienni*, and these values correspond to rather modest savings of time of 29, 29 and 11 ms, respectively, on the basis of the average net velocities for stride 0. For equal jumping distances, a species with a slower speed of striding locomotion would have a greater reduction in the elapsed time taken to travel between two points compared with striding locomotion. However, because the jump distances of *A. valencienni* were relatively short, this species had the smallest benefit to travel time as a result of jumping. Despite the theoretical benefits of time and distance being saved from jumping across a corner, the actual benefits are so small that they may be of limited biological significance.

During jumps, while the lizards in our study were airborne, the tail often flexed towards the side of the turn and, hence, may have contributed to changing the orientation of the body. Two mechanisms besides tail movements are likely to contribute to mid-air rotation. The left and right hindlimbs could exert different forces during take-off, and the forelimbs could initially push and rotate the anterior body away from the inner side of the take-off perch before the hindlimbs leave the perch. The species of *Anolis* used in our study reflect the trend that ecomorphs with greater jumping capacity and that show an increased occurrence of jumping in the field generally having longer tails (Losos, 1990a). Naturally occurring interspecific variation in tail length thus implies that the tail has an important role in jumping. Tail loss and tail autotomy in lizards are common (Arnold, 1988) and could be used experimentally to clarify the importance of the tail for contributing to mid-air turning or checking rotation near the end of the jump.

After jumps, we observed long pauses and landing on the inner surface of perches, both of which suggest that stopping and recovering balance are important functional considerations for how morphology affects jumping performance. For the lacertid lizard *Podarcis muralis*, arboreal locomotor performance decreases with tail loss, which may decrease balancing ability (Brown et al., 1995). When landing after a jump, the lizards in our study commonly draped their tails over the inner surface of the perch after the turn, which may facilitate stopping (Fig. 6A, 272 ms; Fig. 6C, 100 ms).

Jumping can decrease the angle of a turn made by an animal compared with the angle defined by a network of perches and, if all other factors remain constant, an animal should be able to move more quickly while turning more gradually. However, for the species that we studied, and for most species of animal, much remains to be learned regarding the extent to which speed *versus* maneuverability determine whether a predator is evaded. Jumping could allow an animal to make more abrupt turns than those between perches. Sharp turns could theoretically be an especially effective escape tactic if a predator were larger than the lizard that was executing sharp turns.

Arboreal habitats are advantageous for testing differences in escape tactics because one can quantify and compare the frequencies of turning angles defined by networks of perches *versus* the turning angles actually taken by the animals. Turning angles less than or greater than those in the habitat would imply that the escapes of animals are relying predominantly on speed or turning ability, respectively. The tendency of *Anolis* species to jump in their natural habitat increases with decreased perch diameter, which also decreases the speed of running along a perch (Losos and Irschick, 1996). Our laboratory study suggests that the angles between perches are another important factor determining whether or not arboreal species jump in a natural setting.

The obstructions present in natural arboreal habitats may negate some of the advantages of jumping that were observed in our laboratory tests. To accommodate a jump, an unobstructed space must be present that is equal to the frontal area of the laterally rotating lizard (Fig. 6) times the length of the jump. Consequently, although long limbs and tails may facilitate jumping and mid-air turning of the more proficient jumping species (*A. grahami* and *A. lineaptous*) in our study, the short tail and limbs of *A. valencienni* may decrease the likelihood of collision with obstructions in dense arboreal habitats. Jumping behavior had considerable importance for understanding interspecific variation in turning performance. However, pausing was another behavioral trait with profound consequences for the speed with which turns were negotiated. Unlike the plausible correlations between morphology and jumping, pausing seems unlikely to have any morphological correlates. Consequently, the central role of pausing in explaining variation in turning performance complicates correlating morphology and performance among these three ecomorphs of *Anolis*.

Our tests forced the animals to turn rather than giving them a choice of running straight or turning. Experimental designs that provide a choice of varying turning angles and perch diameters hold much promise for clarifying the choice of paths and the trade-offs that occur for animals in the wild. For example, if the continuation of a straight path has a decrease in perch diameter, would the animal be more likely to run straight with a decreased speed or would it decrease its speed to turn or jump onto a larger-diameter perch, which would then enhance the speed of running after the turn?

NSF grants IBN 9983003 and IBN 9514585 to D. J. Irschick and B.C.J. provided support for research, and a Research Experience for Undergraduates Supplement provided support for M.D. The acquisition of a high-speed video system was supported by NSF grant BIR 9217409 to B.C.J. We would like to thank D. Irschick, W. Mattingly and J. Rodenburg for their help in the field and the staff at the Discovery Bay Marine Laboratory for facilitating our research.

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