

The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*)

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Summary

Arboreal animals often move in habitats with dense vegetation, narrow perches and variable inclines, but effects of arboreal habitat structure on locomotor function are poorly understood for most animals. Several species of *Anolis* lizards, which have served as a model group for relating locomotor performance to morphology, have decreased maximal sprinting speeds when perch diameter decreases. However, the effects of perch diameter on the limb movements of *Anolis* have not been previously studied. Hence, we quantified the hindlimb movements of *Anolis sagrei*, which naturally occurs on a wide variety of perch diameters and inclines. We analyzed similar speeds of steady locomotion for combinations of flat surfaces and round perches with diameters of 1, 3, 6 and 10 cm and inclines of 0° and uphill 45° and 90°. Diameter significantly affected more kinematic variables than incline, but many kinematic variables changed little with increases in diameter beyond 6 cm. As surface diameter increased, the limb posture of *A. sagrei* became progressively more sprawled. Significantly greater knee

flexion during stance was important for locating the foot more medially during movement on narrow perches. Stride length increased and femur depression, femur retraction and long-axis femur rotation decreased significantly as the surface diameter increased. The low hip heights on the vertical incline and the narrowest perches suggest that bringing the center of mass closer to the locomotor surface is important in these circumstances for reducing the tendency to topple backwards or sideways. Most of the kinematic changes of *A. sagrei* with decreased perch diameter were opposite those correlated with increased speeds of locomotion for terrestrial lizards. The foot was most lateral to the hip during the swing phase and maximal lateral displacements decreased with decreased perch diameter. Consequently, the width required to accommodate limb movement also decreased as perch diameter decreased.

Key words: arboreal, locomotion, kinematics, lizard, *Anolis sagrei*, incline, perch diameter, limb posture.

Introduction

The structure of arboreal habitats imposes several functional demands for the locomotion of animals including steep inclines, narrow round perches and cluttered, obstacle-filled pathways. Increased inclines commonly increase energetic cost of locomotion (Full and Tullis, 1990; Farley and Emshwiller, 1996), decrease maximal speeds and acceleration (Huey and Hertz, 1982; Irschick and Jayne, 1998; Zaaf et al., 2001a) and affect kinematics (Buczek and Cavanagh, 1990; Jayne and Irschick, 1999), but many of these incline effects are size dependent (Taylor et al., 1972). The discrete footholds of perches may also constrain locomotion by limiting the lateral extent of foot placement, and the increased curvature of perches with decreased diameter could also change the orientation of the foot and decrease the vertical clearance between the body and the perch (Cartmill, 1974; Moermond, 1986; Fig. 1). Decreased perch diameter significantly decreases maximal speed of several species of *Anolis* lizards

(Losos and Sinervo, 1989). Moreover, decreases in diameter are usually accompanied by increased density of branches and decreased distance between nodes that may interfere with movement of appendages (Crome and Richards, 1988) and influence habitat selection (Pianka, 1969; Williams, 1983).

Although the limb function of primates is well studied (reviewed in Jenkins, 1974; Strasser et al., 1998), limb function and movement is poorly understood for most other lineages of vertebrates with well-documented arboreal specializations. For example, the adaptive radiation of nearly 400 species within the lizard genus *Anolis* forms a diverse clade of arboreal vertebrates that has been a model system for correlating morphology to habitat partitioning and locomotor speed. Anoles have morphologically and behaviorally distinct forms, or ecomorphs, which have evolved convergently (Williams, 1983). The morphology of anoles is correlated to both habitat selection and locomotor performance. For example, species of

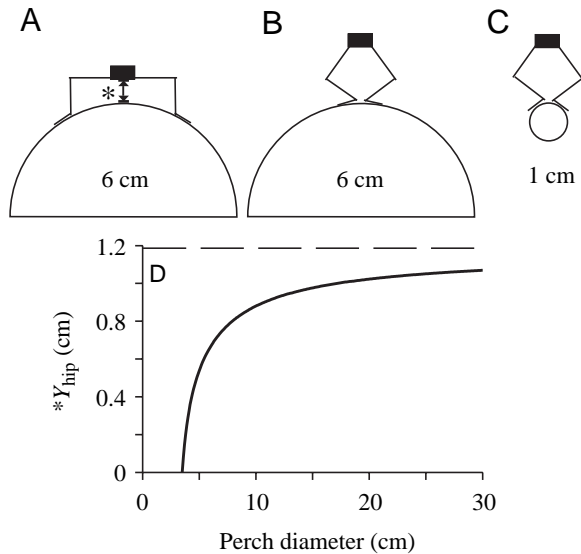


Fig. 1. An anterior, schematic view of potential effects of perch diameter on limb posture showing a sprawling limb (A) and a more upright limb posture on a wide (B) and narrow perch (C). The pelvic width, and lengths of the femur and tibia, are anatomically correct for *A. sagrei*. The transverse axis of the pelvis, femur and tibia, are all in the plane of the illustration. (D) The expected effects of perch diameter on hip height (*), and the clearance between the top of the perch and the ventral surface of the lizard when the limbs have the posture shown in A. The horizontal broken line indicates the length of the tibia.

Anolis with short limbs, such as the twig ecomorphs, generally use narrow perches and have slow maximal running speeds (Moermond, 1979; Williams, 1983; Losos, 1990). Consequently, limb length, combined with locomotor behavior, may directly influence the ability to traverse a given habitat (Losos, 1990; Higham et al., 2001). However, little is known of how the limbs move and are used by any species of *Anolis*, much less how diameter or incline affect limb function. Hence, we quantified the limb movements during arboreal locomotion with varying perch conditions using *Anolis sagrei*, which naturally occurs on perches with a wide range in diameter and inclines (Mattingly and Jayne, 2004).

Phylogenetically diverse animals moving on inclines often stay nearer to the surface by reducing hip height and vertical oscillation of the hip (Vilensky et al., 1994; Carlson-Kuhta et al., 1998; Jayne and Irschick, 1999). By having a more crouched limb posture with greater flexion at the hip (= femur elevation in sprawling limb vertebrates), knee and ankle joints can contribute to decreasing hip height of animals with either upright or sprawling limbs. Furthermore, a terrestrial species of lizard has greater long-axis femur rotation associated with decreased hip height on inclined surfaces (Jayne and Irschick, 1999). Thus, for locomotion of *Anolis* lizards on inclined surfaces, we expected decreased hip height as a result of increased femur rotation and increased flexion of the joints within the limb. Decreased hip height should reflect a decreased distance between the center of mass and the

locomotor surface, which would decrease the tendency to topple backwards when climbing a steep surface.

Variation in perch diameter may also affect limb posture in several ways. On perches with large diameters, a lizard could have either an overall sprawling limb posture, with the knees lateral to the hip (Fig. 1A), or a more upright posture with both the knees and ankles located more medially (Fig. 1B). On narrow perches, if the limbs were sprawled and the ankles were directly below the knees, the foot would be too lateral to touch a perch with a diameter less than the inter-knee distance (Fig. 1A,D). When the feet must be placed more medially to fit onto a narrow perch, hip height might decrease to lower the center of mass and reduce the torques that tend to topple the animal sideways (Cartmill, 1985). Thus, we expected anoles moving on narrow perches to use some combination of femur depression and knee flexion to facilitate placing the feet more medially, as well as reducing hip height with the same mechanisms expected for locomotion on inclined surfaces.

Many aspects of the geometry of placing the limbs on a round perch do not have simple linear increases with increased perch diameter. For example, for a constant lateral distance between the two feet within a girdle, the slope of clearance between the ventral surface of the body and the top of the perch *versus* perch diameter decreases with increased perch diameter (Fig. 1D). Similarly, for a given distance between contralateral feet, the steepness of the perch surface making contact with the feet declines with increased perch diameter as the values for large diameter perches asymptotically approach those of a horizontal flat surface. Thus, for those kinematic variables changing significantly with perch diameter, a non-linear pattern of change similar to that in Fig. 1D would seem likely. Non-linear changes in kinematics with increased perch diameter may also be likely because variation in perch diameters less than the inter-knee distance may pose a greater need to modify kinematics than variation in perch diameters that exceed the inter-knee distance of lizards with an overall sprawling limb posture.

We focused on the hind limb function of anoles for the following reasons. First, previous studies of anoles correlating morphology, locomotor speed and perch diameter have dealt primarily with the dimensions of the hind limb (Losos and Sinervo, 1989; Losos and Irschick, 1996). Second, more comparative data are available for the hind limbs of lizards because kinematic studies of terrestrial species have concentrated on the hind limb since it is used during all speeds of locomotion (Irschick and Jayne, 1999; Jayne and Irschick, 1999; Reilly and Delancey, 1997). Finally, the shoulders of lizards have some translational movements that complicate kinematic analyses (Goslow and Jenkins, 1983; Peterson, 1984).

This study had the following four main objectives. First, we manipulated perch diameter and incline to determine their effects on hind limb posture and kinematics during steady-speed locomotion. Second, we used a large range of perch diameters to determine whether kinematics changed more for a change in diameter among narrower perches than for a

change in diameter among wider perches. Third, we tested whether the effects of perch diameter depended on incline (had interactive effects). Finally, we compared the effects of surface and incline on hind limb kinematics between *A. sagrei* and other tetrapod vertebrates including the specialized arboreal lizard *Chamaeleo calytratus* (Higham and Jayne, 2004) and the more generalized terrestrial lizard, *Dipsosaurus dorsalis* (Jayne and Irschick, 1999).

Materials and methods

Experimental subjects

Anolis sagrei Dumeril and Bibron 1837 has many of the morphological specializations for arboreality found throughout the clade of *Anolis* lizards. For example, this species has toes with specialized adhesive structures (Williams and Peterson, 1982; Irschick et al., 1996). However, *A. sagrei* lacks the extreme reduction of limb length found in narrow perch specialists (Irschick and Losos, 1996). *A. sagrei* is categorized as a trunk-ground ecomorph because it commonly occurs on the lower portions of tree trunks, but adult males of this species move on perches with diameters ranging from a few mm to several cm (Schoener, 1968; Mattingly and Jayne, 2004). Morphological correlates of habitat use and locomotor performance within *Anolis* lizards are based primarily on adult males (Williams, 1983; Losos, 1990). For this reason and to avoid the confounding effects of size, we used only adult males with very similar size (ranges of snout–vent length and mass of 5.2–5.5 cm and 4.0–5.0 g, respectively).

All lizards used in the study were obtained from a commercial supplier in Florida and shipped to the University of Cincinnati for experiments. Lizards were caged individually and maintained on a diet of crickets with a vitamin supplement and given water *ad libitum*. Incandescent bulbs provided light and heat for 14 h per day and adequate conditions for the lizards to thermoregulate to their active field temperature range (29–31°C).

To obtain dorso-ventral view radiographs, we anesthetized the lizards with Halothane following a protocol approved by the Institutional Animal Care and Use Committee of the University of Cincinnati. We measured skeletal dimensions from radiographs for all four *A. sagrei* and the measurements and mean values (\pm S.E.M.) were as follows: tail length (97 \pm 0.9 mm), longitudinal distance between the shoulder and hip joints (32.3 \pm 0.2 mm), width between the two hip joints (6.4 \pm 0.1 mm), and the lengths of the femur (13.3 \pm 0.3 mm), tibia (11.6 \pm 0.5 mm), hind foot (8.1 \pm 0.2 mm) and fourth toe (12.2 \pm 0.2 mm) of the right hind limb. Hence, the average distances from the hip to the tip of the fourth toe and between outstretched knees were 45.0 \pm 1.2 and 33.0 \pm 0.7 mm, respectively.

Experimental protocol

We obtained simultaneous dorsal and lateral views of steady speed locomotion using a two-camera NAC (Tokyo, Japan) HSV-500 high-speed video system operating at 250 images s⁻¹.

Lizards were placed in a thermally insulated container at a temperature similar to the active field body temperature of this species (29–31°C) for at least 30 min prior to eliciting locomotion. We determined body temperature immediately before trials using a thermocouple and a Tegam model 871A digital thermometer (Geneva, Ohio, USA). We covered all perch and treadmill surfaces with 1.5 mm mesh fiberglass screen to enhance the traction of the lizards, as in Irschick and Losos (1998) and Higham et al. (2001). All of the round perches were 122 cm long with diameters of 1 cm (wooden dowel), 3, 6 or 10 cm (polyvinylchloride pipe). For each round perch, we obtained locomotion on a level, 45° and 90° uphill incline. The flat surface trials, which used a rubberized belt of a stationary treadmill, as in Fieler and Jayne (1998) and Higham and Jayne (2004), were either level or uphill at 45°. We could not obtain data for the flat, vertical surface because the lizards would not move reliably under this condition. Thus, a total of 14 combinations of surface and incline were used for each of the four individuals in our experimental design.

To facilitate frame-by-frame motion analysis, we painted landmarks on a prominent protuberance of the pelvis and several joints of the right hind limb (Fig. 2). The pelvic landmark coordinates were transformed to approximate the coordinates of the hip as in Fieler and Jayne (1998) and Jayne and Irschick (1999). All lizards ran no more than four times in rapid succession within each testing session, and were allowed to recover for more than 2 h between sessions. Over the course of several weeks, we randomized the order of perch conditions and we always provided at least one day of rest between successive days of testing.

Each stride analyzed was from a different trial. As a result of using a stationary surface and because *A. sagrei* often moves in short bursts rather than steadily, we had to conduct a large number of trials to obtain adequate samples of reasonably steady locomotion with similar speeds. The strides selected for analysis were in the middle of a bout of locomotion with three or more strides that subjectively appeared to be of similar speed. Hence, we selected strides with little if any acceleration.

Rather than selecting a random sample of all strides videotaped on the different perches, we selected a subset of data to avoid speed confounding the potential effects of diameter and incline. Although our experimental protocol was not designed to elicit maximal locomotor speed, we did observe some regular patterns of variation in the speeds of locomotion. Speeds greater than 60 cm s⁻¹ were rare on the 1 cm perch regardless of incline. Speeds greater than 100 cm s⁻¹ were fairly common for horizontal and 45° perches with diameter >3 cm, and some individuals obtained speeds between 120 and 130 cm s⁻¹ under these conditions. For a given perch diameter, speeds were usually slowest on the vertical surface compared to the other inclines.

For our frame-by-frame motion analysis, we selected 2–4 strides of similar-speed, steady locomotion for each individual on each combination of surface and incline. An analysis of variance (ANOVA) of speed for the strides on round perches confirmed the lack of significant main effects of diameter

($F_{3,9}=1.12$, $P=0.39$) and incline ($F_{2,6}=2.87$, $P=0.13$) effects on speed, and none of the two-way interaction terms involving individual, diameter and incline was significant. The ANOVA of strides including the flat surface but excluding data from vertical inclines also confirmed a lack of diameter ($F_{4,12}=1.91$, $P=0.30$) and incline ($F_{1,3}=0.66$, $P=0.48$) effects on speed. This lack of significant variation in speed with variation in locomotor surface is important since speed often has significant effects on kinematics (Jayne and Irschick, 1999). The grand

means ($N=185$) for speed and duty factor (\pm S.E.M.) were 54 ± 0.5 cm s^{-1} and $54\pm 0.6\%$, respectively.

Kinematics

We used custom-designed video-analysis software (Stereo Measurement TV, written by Garr Updegraff, San Clemente, CA, USA; garr@uci.edu) to digitize all of the two- and three-dimensional coordinates. We calculated all of the kinematic quantities from these coordinates using macros for Microsoft

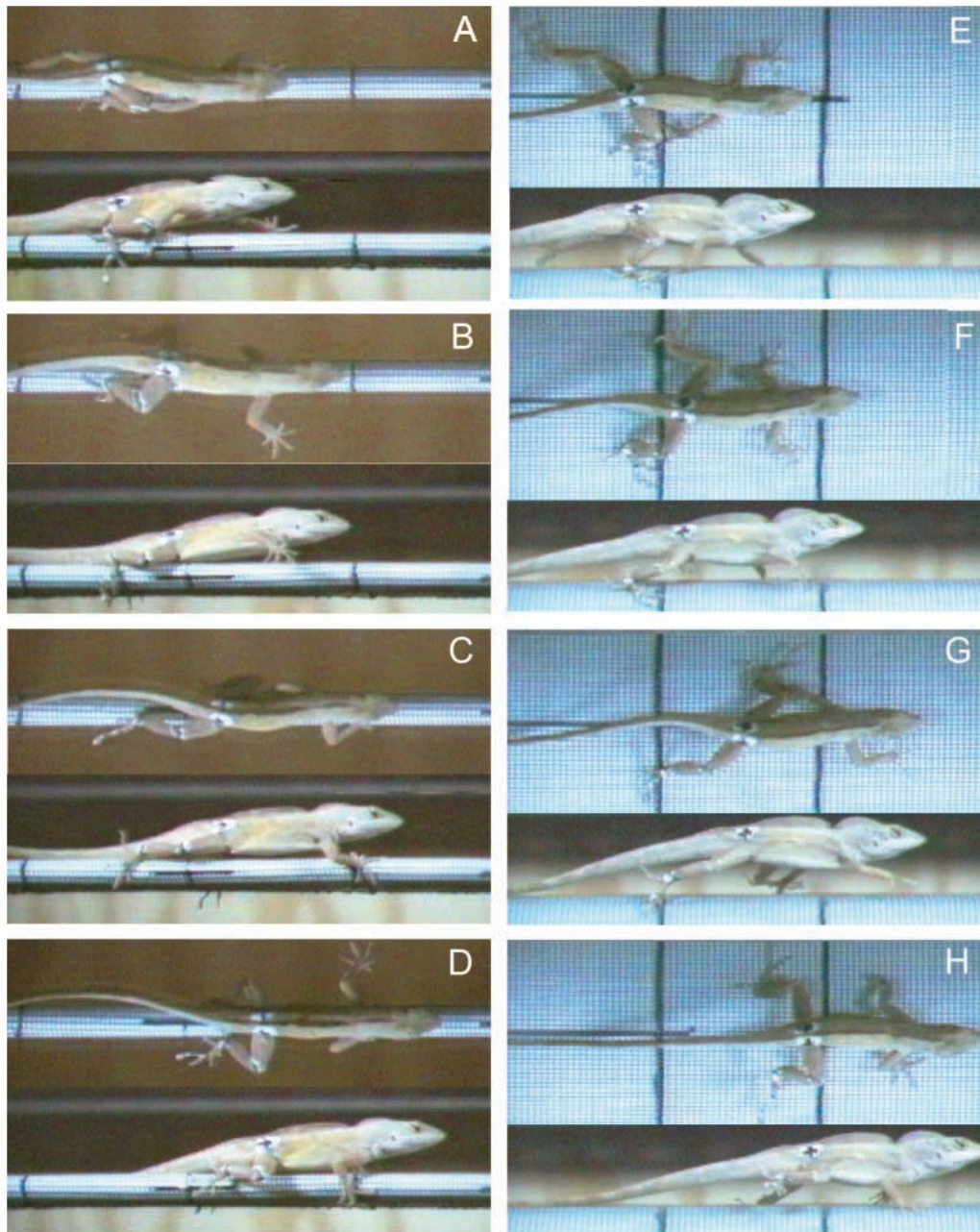


Fig. 2. Right lateral and dorsal views of *A. sagrei* (snout-vent length 5.5 cm, mass 5.0 g) moving on level 1 cm (A-D) and 10 cm (E-H) diameter perches at footfall (A,E), midstance (B,F), endstance (C,G) and midswing (D,H). The elapsed times after footfall of successive images for the 1 cm and 10 cm are 32, 60 and 88 ms and 36, 72 and 108 ms, respectively. The vertical lines on the perches are 5 cm apart. The forward speeds of the strides on the 1 cm and 10 cm perches were 52 and 55 cm s^{-1} , respectively. See <http://www.biology.uc.edu/faculty/jayne/videos.htm> for digital videos of *Anolis* locomotion.

Excel version 7.0 (written by G. Updegraff and B. Jayne). We sampled images every 4 ms, which provided 20 or more images per stride. Two two-dimensional coordinates digitized from a dorsal perspective were the right and left pelvic landmarks. Three-dimensional coordinates digitized from both a dorsal and lateral view included the right pelvic landmark, knee, ankle, distal end of the fourth metatarsal and both the middle (joint) and tip of the fourth toe. For our fixed frame of reference, the x -axis was parallel to the overall direction of travel, which was parallel to the long axis of the locomotor surface. The y -axis was within a vertical plane containing the x -axis. The z -axis was perpendicular to the x - y plane.

The following seven variables described attributes of the entire locomotor cycle or orientation of the pelvis. Stride length was the difference between x -axis positions of successive right hind footfalls, and step length was the x -distance traveled by the body during stance of one limb. Stride duration was the elapsed time between successive right hind limb footfalls, and stride frequency was the inverse of stride duration (Hz). Duty factor was the percentage of the total stride cycle when the right hind foot contacted the perch, and mean forward velocity was stride length (cm) divided by stride duration (s). A two-dimensional (x, z) angle indicated the angle between the line passing through both hips and the x -axis, and the difference of the maximum and minimum values of these angles was pelvic rotation.

Five linear variables described positions and displacements relative to the locomotor surface or the hip. Hip height relative to the top of the path surface (location of the greatest value of Y in a y - z section through the perch) was described with three linear variables, standardized so that the top of the path surface was $y=0$: hip height at the moment of footfall ($Y_{\text{hipfootfall}}$), hip height at footfall minus minimum hip height or the change in hip height during stance ($\Delta Y_{\text{hipstance}}$), and the maximum hip height minus the minimum hip height (total vertical oscillation of the hip) for the entire stride cycle ($\Delta Y_{\text{hiptotal}}$). Effective limb lengths were also measured as the straight-line distance between the hip and the ankle in both two (x, y) and three dimensions.

Thirty-six linear variables used relative coordinates so that the hip was located at (0, 0, 0) and positive x, y and z values indicated anterior, dorsal and lateral, respectively. For the relative coordinates of each dimension, we determined minimum ($X_{\text{min}}, Y_{\text{min}}, Z_{\text{min}}$) and maximum ($X_{\text{max}}, Y_{\text{max}}, Z_{\text{max}}$) positions and the difference (excursion) between the two ($\Delta X, \Delta Y, \Delta Z$) for the knee, ankle, distal end of the fourth metatarsal and the tip of the fourth toe during each entire stride cycle.

Six variables described three-dimensional angles of knee, ankle and the joint between the metatarsal and fourth toe within the right hind limb at footfall and the end of stance. Smaller values of the knee angle (between 0° and 180°) indicated greater flexion of the joint. The ankle angle was measured between the tibia and the metatarsal on the dorsal surface of the foot so that decreasing values (between 0° and 180°) indicated greater dorsiflexion of the foot. Toe angle, measured at both footfall and end of stance, was the angle between the

fourth metatarsal and a straight line extending from the base to the tip of the fourth toe, such that values greater than 180° indicated plantar flexion.

For each of three angles describing the orientation of the right femur, we determined the maximum, minimum and excursion (maximum – minimum), during an entire stride cycle. Femur retraction was the two-dimensional (x, z) angle, between the femur and a line connecting the hips such that a value of 0° indicated the femur was perpendicular to the long axis of the pelvis, and greater magnitude positive and negative values indicated greater retraction and protraction, respectively. Long-axis femur rotation was determined from a three-dimensional angle between the plane containing the femur and the tibia and a vertical reference plane passing through the femur. Greater clockwise long-axis rotation of the right femur, as seen in right lateral view, is indicated by greater positive values, and a value of zero indicates that the plane containing the femur and tibia is within the vertical reference plane passing through the femur. Lastly, femur depression was a three-dimensional angle between the femur and a horizontal plane passing through the right hip where greater positive and negative values equalled greater amounts of depression (knee below the hip) and elevation (knee above the hip), respectively.

Statistical analyses

We used SAS version 8.0 for all of the statistical analyses, and a 3-way mixed model ANOVA, for which incline and diameter were fixed factors and individual was a random factor. Thus, according to Scheffe (1959) the denominators for the F -tests of the main effects were the mean squares of the two-way interaction terms involving the fixed effect and individual, and the denominator for the F -test of the diameter \times incline interaction term was the incline \times diameter \times individual interaction mean square. Although we used $P < 0.05$ as the primary criterion for statistical significance, we provide tables with degrees of freedom (d.f.) and F -values to clarify potential effects of making multiple comparisons. Unless stated otherwise, all mean values are presented \pm S.E.M., where N equals the total number of strides observed for each combination of surface and incline.

We performed principle component analyses, primarily to clarify the relative importance of kinematic variables when considered simultaneously for explaining the total variance associated with different locomotor surfaces rather than for testing for the effects of different inclines and perches. Thus, we were most interested in the factor loadings for providing insights that were not evident in the univariate analyses. We used 15 kinematic variables used previously to analyze terrestrial lizard locomotion in *Dipsosaurus dorsalis* (Jayne and Irschick, 1999). For our multivariate analysis of *A. sagrei*, each stride ($N=185$) was a data point.

Results

General description of *A. sagrei* limb movements

Fig. 2 shows lateral and dorsal views of *A. sagrei* during the

stride cycle for locomotion on level surfaces. At footfall, the femur was protracted and slightly depressed resulting in a knee position anterior and slightly ventral to the hip (Figs 2A,E, 3, 4A,B). At footfall, long-axis femur rotation commonly exceeded 40° (Fig. 5). Consequently, the ankle was usually

substantially posterior to the knee and occasionally even slightly posterior to the hip (Figs 2–4). The knee angle at footfall was usually less than 90°, but the ankle angle at footfall could be either acute or obtuse depending on the locomotor surface (Fig. 5). The fourth metatarsal and toe were usually

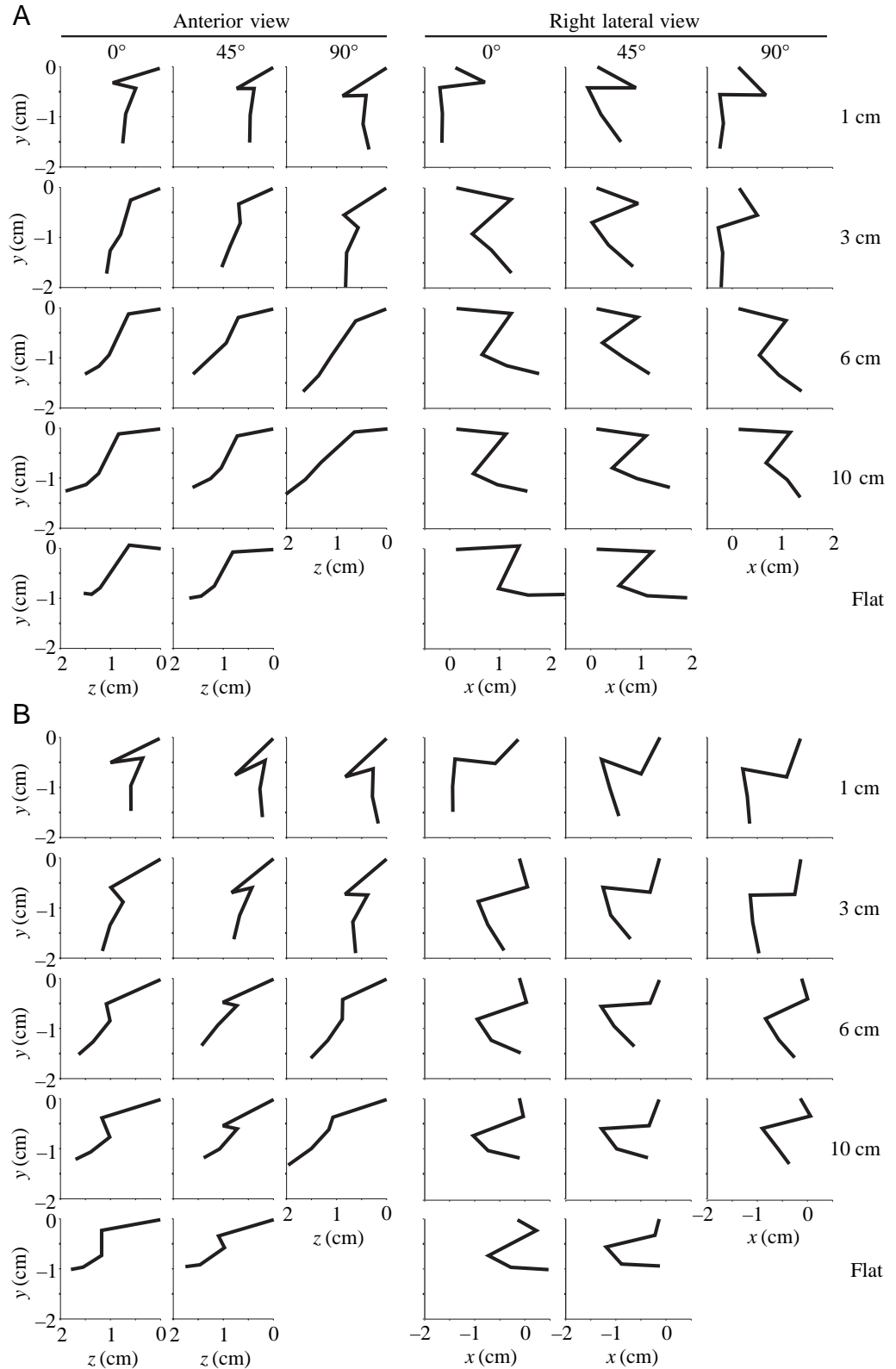


Fig. 3. Mean values for the positions of the right hindlimb relative to the right hip ($x=0$, $y=0$, $z=0$, where x , y and z indicate anterior, dorsal and lateral, respectively) for each combination of incline (0°, 45° and 90°; columns) and locomotor surface (rows) at footfall (A) and midstance (B) on different diameter perches (1 cm, 3 cm, 6 cm, 10 cm and flat). From proximal to distal the endpoints of the line segments represent the hip, knee, ankle, distal end of the metatarsals and tip of the fourth toe. Sample sizes range from 10 to 16 strides (from four individuals per species) for each combination of the two factors. The projections onto the $y-z$ and $y-x$ planes correspond to anterior view and right lateral views, respectively.

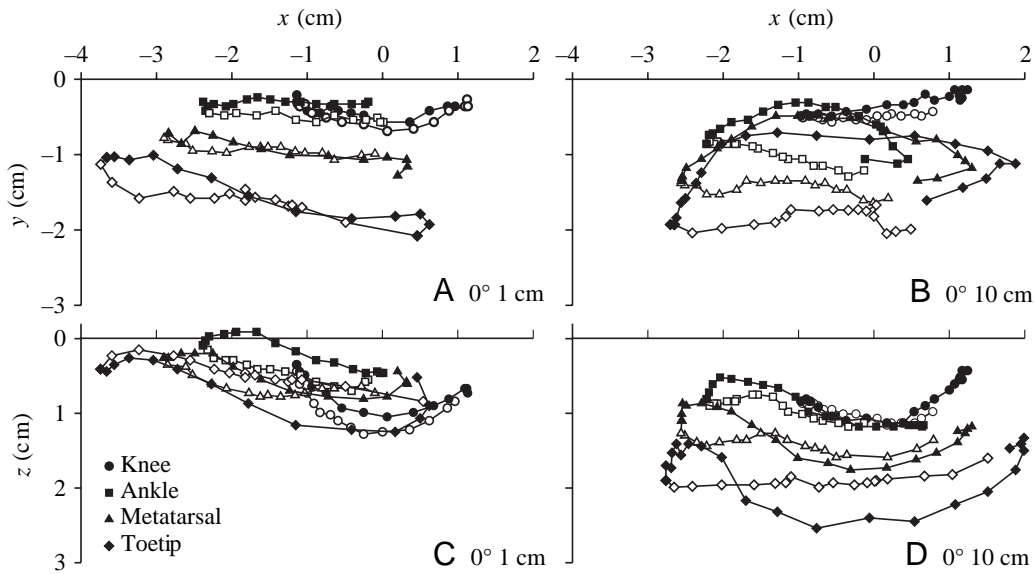


Fig. 4. Lateral (A,B) and dorsal (C,D) views of the positions for the right knee, ankle, metatarsal and toe tip relative to the hip (0, 0, 0) during one stride on a level 1 cm (A,C) and 10 cm (B,D) diameter perch. Positive values of x , y and z indicate anterior, dorsal and lateral movement, respectively. Open symbols, stance; filled symbols, swing portions of the stride; the overall direction of movement is clockwise. The time between successive points is 4 ms, and the strides are from the same individual.

anterior and lateral to the ankle rather than being pointed directly forward at footfall (Figs 2A,E, 3).

During most of stance, the knee extended, and the femur retracted and rotated in a clockwise direction, and all of these angles usually attained maximum values near the end of stance

(Figs 2, 5). At midstance the tibia was often nearly horizontal (Fig. 3) as values of long-axis femur rotation often approximated 90° (Fig. 5). During the first half of stance femur depression often increased slightly to a maximum value and then femur depression usually decreased gradually during the

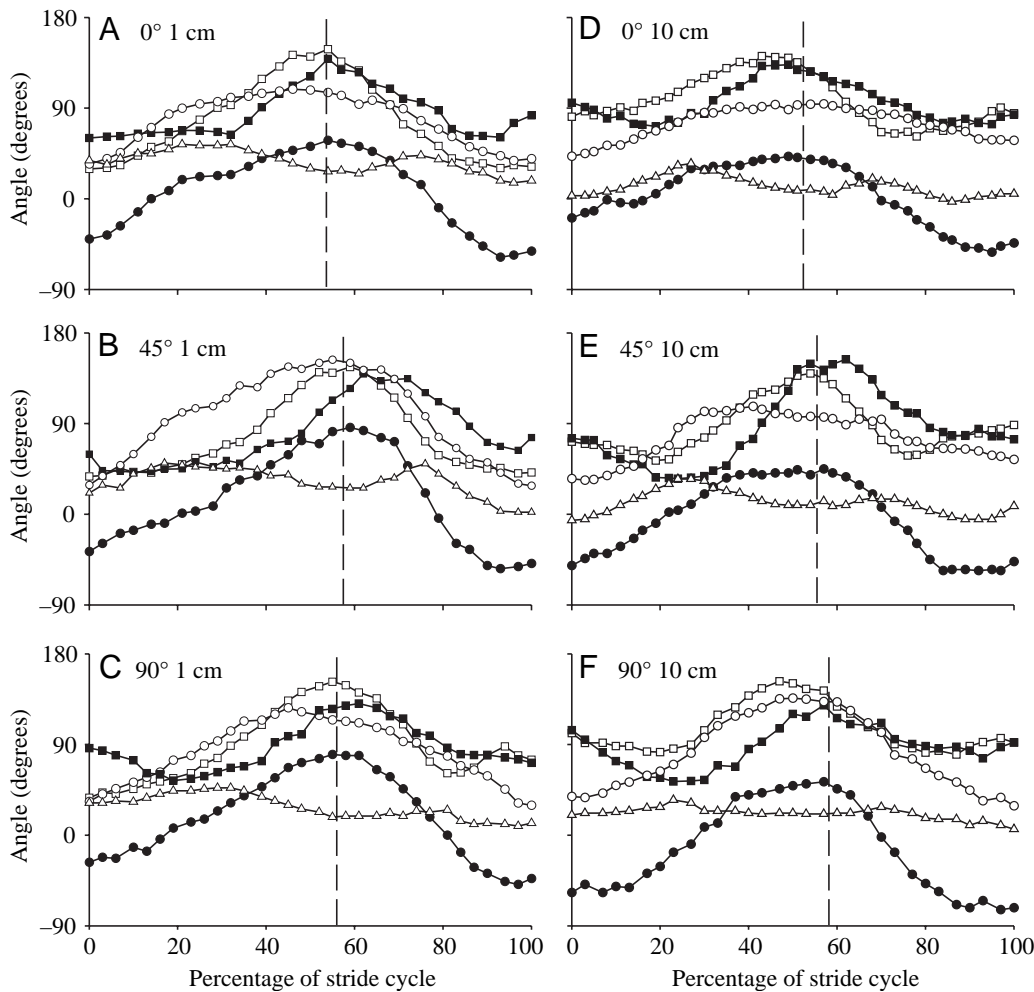


Fig. 5. Angles of the knee, ankle, femur rotation, femur retraction and femur depression, *versus* time for one stride of a single individual on a 1 cm (A-C) and 10 cm (D-F) diameter perch inclined at 0° (A,D), 45° (B,E) and 90° (C,F). Footfall occurred at 0%, and the vertical broken line represents the end of stance.

later half of stance (Figs 3, 4). Despite considerable variation in femur depression associated with variation in the locomotor surfaces, values of femur depression during stance were rarely less than zero (Fig. 5), indicating that the knee usually remained ventral to the hip throughout stance (Figs 3, 4). The ankle usually flexed during the first half of stance and extended during the latter half of stance (Fig. 5). All portions of the limb were usually most posterior relative to the hip at the end of stance (Fig. 4).

Femur protraction usually started and continued for the first two-thirds of the swing phase of the stride (Fig. 5). Consequently, the arc traveled by the knee relative to the hip during swing had its most lateral position near mid swing (Figs 2D,H, 4). In contrast to the early lateral movements of the knee relative to the hip, the more distal portions of the limb often moved medially relative to the hip during early stance (Fig. 4). Counter-clockwise long-axis rotation of the femur usually started and continued throughout the swing phase, and the femur was usually elevated slightly during the first half of swing and depressed slightly during the latter half of swing (Fig. 5). The knee and ankle usually began to flex near the beginning of swing and continued to flex until mid-swing (Fig. 5). During the latter one-half to one-third of swing, the angles of the knee, ankle and femur retraction often changed little or increased slightly (Fig. 5).

Effects of diameter and incline

Variation in the locomotor surfaces had profound effects on the hindlimb kinematics of *A. sagrei* (Tables 1–4). For example, of 45 linear and timing variables, 38 variables for the round perch data (Tables 1, 2) and 36 variables for the data including the flat surface (Tables 1, 3) had significant effects of either diameter, incline or the diameter \times incline interaction term. Of 14 angular variables (Table 4) for the round and flat

surface data, 8 and 12 variables had either a significant main or interaction effect of diameter and incline, respectively.

Diameter had more widespread effects on kinematics than incline. For example, the main effect of diameter was significant for 26 variables, whereas the main effect of incline was significant for only 17 of the 45 linear and timing variables for the round perch data (Tables 1, 2). For the ANOVA results summarized in Tables 2 and 3, only seven diameter \times incline interactions were significant, and five of these seven interaction terms were only marginally significant ($0.01 < P < 0.05$).

Stride length and step length increased significantly with increased diameter, whereas stride frequency decreased significantly with increased diameter (Table 1, Fig. 6A,B). Of the four whole-stride characteristics, incline only had significant main effects on stride length (Table 1). For a particular perch diameter, mean values of stride length were consistently the smallest on vertical inclines (Fig. 6A), and the smallest mean value of stride length was for the 1 cm perch inclined at 90°.

Hip height at footfall and effective limb length indicate the extent to which the limb is directly beneath the hip and straight. Diameter and incline had significant interactive effects on hip height at footfall (Table 1) such that values were nearly constant on the 90° incline, but usually increased with increased perch diameter on the other inclines (Fig. 6C). Values of hip height at footfall on the flat surface were nearly twice as large as those for the 1 cm perch (Fig. 6C). The three-dimensional effective limb length had highly significant increases with increased diameter (Table 1), but it increased less with increased diameters beyond an intermediate diameter (Fig. 6D). The three-dimensional effective limb length also differed significantly among inclines, and the 45° incline consistently had the lowest values for each diameter (Fig. 6D).

As diameter increased the most anterior positions of the

Table 1. F-values from three-way ANOVAs performed separately on each kinematic variable describing pelvic rotation, whole-stride characteristics and select linear measurements

Dependent variable	ANOVA effects (d.f.)					
	Round perches only			All surfaces except 90°		
	Incline (2,6)	Diameter (3,9)	Incline \times Diameter (6,18)	Incline (1,3)	Diameter (4,12)	Incline \times Diameter (4,12)
Stride length [†]	10.3*	8.8*	2.4	0.5	8.8*	0.6
Step length [†]	0.8	9.1*	0.9	0.3	4.5*	0.9
Stride frequency	1.8	14.3**	0.2	0.2	14.5**	0.8
Duty factor	5.5*	1.5	0.1	0.1	1.4	1.7
Y_{hip} footfall [†]	5.2*	1.4	3.3*	2.6	10.9**	1.4
ΔY_{hip} stance	0.1	3.5	0.3	0.0	0.9	0.9
ΔY_{hip} total	1.5	0.6	1.2	1.6	1.8	1.3
2-D effective length (ff)	3.1	8.3*	0.5	5.3	4.4*	0.7
3-D effective length (ff)	8.9*	27.8**	0.2	170.1**	16.5**	0.2

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

[†]Used in the principle component analysis (Table 5).

Y_{hip} footfall, the hip height at time of footfall; ΔY_{hip} stance, the change in hip height during stance; ΔY_{hip} total, the total vertical oscillation of the hip for entire stride cycle; ff, footfall; 2-D, two-dimensional; 3-D, three-dimensional.

Table 2. F-values from three-way ANOVAs of round perch data performed separately on each kinematic variable indicating maximum and minimum linear positions and displacements in the x, y and z dimensions relative to the hip during the stride cycle

Limb location	Kinematic variable								
	X_{\min}	X_{\max}	ΔX	Y_{\min}	Y_{\max}	ΔY	Z_{\min}	Z_{\max}	ΔZ
Incline (2,6)									
Knee	5.0	0.7	5.3*	5.5*	0.6	5.5*	2.8	6.2*	2.7
Ankle	6.0*	2.4	0.6	4.4	9.9*	2.8	3.6	2.9	12.2*
Metatarsal	10.9*	1.2	4.4	3.7	4.0	6.1*	4.2	3.1	10.0*
Toe tip	17.9*	0.0	4.3	1.9	2.7	8.1*	3.5	2.2	9.2*
Diameter (3,9)									
Knee	6.2*	3.1	1.5	5.5*	5.0*	0.7	4.7*	2.3	3.7
Ankle	2.9	29.6**	12.9*	2.9	2.3	5.1*	16.3**	30.8**	0.8
Metatarsal	4.7*	43.3**	21.2**	4.6*	2.3	0.8	14.1**	26.9**	0.8
Toe tip	3.0*	39.6**	9.7*	26.9**	2.9	0.2	17.0**	32.5**	3.7
Diameter \times Incline (6,18)									
Knee	1.8	2.0	1.9	1.0	0.6	1.9	1.4	0.6	0.2
Ankle	1.6	1.3	1.1	1.9	0.3	3.0*	1.1	1.0	1.5
Metatarsal	1.1	1.3	1.4	1.2	0.6	2.2	0.6	1.8	0.8
Toe tip	1.0	1.7	2.3	0.3	0.6	1.3	0.6	1.2	0.8

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

ANOVA effects (d.f.) are above each group of hind limb locations.
x, anterior; y, dorsal; z, lateral dimensions.

ankle, metatarsal and toe tip relative to the hip (X_{\max}) increased significantly, whereas the most posterior positions (X_{\min}) of these distal limb locations had less regular or significant change with increased diameter (Tables 2, 3; Fig. 7A). Consequently, the longitudinal excursions (ΔX) of the ankle,

metatarsal and toe tip increased significantly with increased diameter, and the distal limb was positioned progressively more anterior to the hip as diameter increased. Average values of the ankle at footfall were posterior to the hip for the 1 cm diameter perches on all inclines and some of the 3 cm diameter

Table 3. F-values from three-way ANOVAs of all surfaces except vertical inclines performed separately on each kinematic variable indicating maximum and minimum linear positions and displacements in the x, y and z dimensions relative to the hip during the entire stride

Limb location	Kinematic variable								
	X_{\min}	X_{\max}	ΔX	Y_{\min}	Y_{\max}	ΔY	Z_{\min}	Z_{\max}	ΔZ
Incline (1,3)									
Knee	5.0	0.2	4.9	5.9	0.5	12.9*	2.6	7.6	0.3
Ankle	7.8	3.9	14.5*	8.1	18.6*	3.1	4.8	0.4	15.8*
Metatarsal	8.7*	2.8	9.7	3.8	17.9*	15.7*	4.4	0.2	10.9*
Toe tip	15.6*	2.8	9.4	1.3	12.5*	8.8	3.8	0.1	10.7*
Diameter (4,12)									
Knee	3.7*	5.7*	0.5	18.6**	16.0**	1.1	3.4	21.5**	0.9
Ankle	1.2	21.6**	6.8*	7.3*	18.5**	28.9**	57.4**	62.0**	1.9
Metatarsal	1.9	28.2**	11.4**	4.2*	30.7**	17.2**	79.7**	66.5**	0.9
Toe tip	1.6	33.0**	9.0*	41.4**	30.9**	1.3	79.7**	43.3**	2.1
Diameter \times Incline (4,12)									
Knee	3.4	2.3	1.2	1.4	1.0	1.2	2.2	1.4	0.2
Ankle	3.8*	1.3	0.6	0.3	1.0	0.8	1.0	0.6	0.5
Metatarsal	4.0*	1.3	1.1	0.5	3.2	3.8*	1.4	1.7	0.4
Toe tip	5.1*	1.7	2.7	0.2	4.3*	4.7*	0.9	1.5	0.3

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

ANOVA effects (d.f.) are above each group of hind limb locations.
x, anterior; y, dorsal; z, lateral dimensions.

Table 4. F-values from three-way ANOVAs performed separately on each angular kinematic variable

Dependent variable	ANOVA effects (d.f.)					
	Round perches only			All surfaces except 90°		
	Incline (2,6)	Diameter (3,9)	Incline × Diameter (6,18)	Incline (1,3)	Diameter (4,12)	Incline × Diameter (4,12)
Knee angle (ff) [†]	8.0*	47.8**	0.5	16.3*	18.2**	0.1
Knee angle (es) [†]	3.3	1.2	1.7	5.2	0.7	3.7*
Ankle angle (ff) [†]	5.5*	3.7	1.5	70.0**	1.4	0.6
Ankle angle (es) [†]	1.5	2.8	0.7	0.9	5.7*	1.4
Pelvic rotation [†]	3.1	1.9	1.8	3.5	1.8	1.0
Max. femur retraction [†]	11.8*	7.6*	1.0	12.9*	7.0*	2.0
Min. femur retraction [†]	0.3	1.1	0.6	1.9	0.9	0.4
Retraction excursion	3.4	5.4*	2.2	9.9	6.2*	3.6
Max femur depression [†]	5.5*	4.3*	0.8	8.5	24.0**	1.9
Min. femur depression [†]	2.3	5.1*	0.6	1.7	12.8**	1.0
Depression excursion	5.0	2.5	1.8	15.3*	0.6	1.9
Max. femur rotation [†]	7.3*	1.6	1.1	35.2*	4.6*	1.5
Min. femur rotation [†]	0.5	4.5*	0.8	0.8	6.5*	15.4*
Rotation excursion	3.5	2.5	1.1	10.2	20.3**	5.4*

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

ff, footfall; es, end of stance

[†]Used in the principle component analysis (Table 5).

perches, whereas for broader surfaces the ankle was well anterior to the hip at the beginning of stance (Fig. 3). Incline significantly affected X_{\min} of both the metatarsal and the toe tip such that the greatest magnitude of the values was uniformly observed for the 45° incline for each perch diameter (Fig. 7A). For all combinations of diameter and incline, the magnitude of X_{\min} exceeded that of X_{\max} for the ankle and more distal locations of the limb (Fig. 7A). Thus, the extreme longitudinal positions of the limb relative to the hip are not symmetric, and positions posterior to the hip dominate the stride cycle (Fig. 4).

For most portions of the limb, the most ventral position relative to the hip (Y_{\min}) changed significantly, whereas the most dorsal position (Y_{\max}) changed little with the diameter of round perches (Table 2). For the knee, Y_{\min} had decreased magnitude with increased diameter, whereas Y_{\min} of the toe tip often had the greatest magnitude on the narrowest perch as a result of the foot and the toe pointing downward and wrapping around the narrow perches (Fig. 2). The height of the ankle at footfall often approximated that of the knee on the 1 cm diameter perches, but with increasing surface diameter the height of the knee relative to the ankle at footfall generally increased (Fig. 3).

Both the most medial (Z_{\min}) and the most lateral (Z_{\max}) positions of the ankle, metatarsal and toe tip increased significantly with increased diameter (Tables 2, 3), and the most conspicuous increases were from the smallest to intermediate diameter (Fig. 7C). On the 1 cm diameter perches, the ankle was consistently located medial to the knee at footfall, but for larger perch diameters the ankle was commonly slightly lateral to the knee at footfall (Fig. 3). In contrast to Z_{\min} and Z_{\max} , the

lateral excursion (ΔZ) was unaffected by diameter (Tables 2, 3). Thus, although the amounts of lateral limb movement were similar for different diameters, the overall location of the limb throughout the entire stride cycle shifted laterally as diameter increased (Figs 4A,B, 8).

Knee angle at footfall increased significantly with diameter and the largest increases were from the smallest to intermediate diameter (Table 4; Fig. 9A). For each perch diameter, the values of both knee and ankle angle at footfall were uniformly the smallest for the 45° incline (Fig. 9A,B). Pelvic rotation was not affected significantly by either diameter or incline alone (Table 4). However, the mean values of pelvic rotation on the level surfaces were usually the lowest for each perch diameter (Fig. 9C).

Maximum (most posterior) femur retraction decreased significantly with increased diameter, and the most conspicuous decrease was from the 1 cm to the 3 cm diameter (Table 4; Fig. 10A). However, minimum femur retraction was nearly equal for all surfaces (Fig. 10A). Consequently, the mean values of protraction–retraction excursion decreased significantly with increased perch diameter in a manner similar to that of maximum femur retraction (Table 4; Fig. 11A). Both minimum and maximum femur depression had highly significant decreases with increased diameter (Table 4; Fig. 10B), but the excursion of femur depression was nearly constant for increases in perch diameter greater than 3 cm (Fig. 11B). For each perch diameter, the maximum (most clockwise) long-axis rotation of the femur was less for the level surface compared to the other two inclines, and this variable generally decreased with increased surface diameter (Fig. 10C). The amount of femur rotation decreased

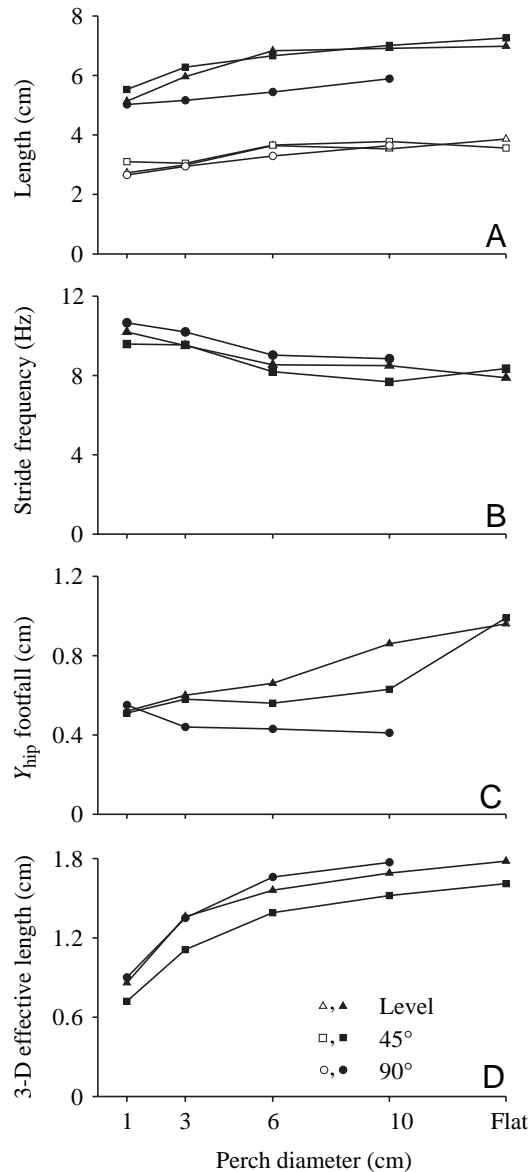


Fig. 6. Mean values of stride (black symbols) and step (white symbols) length (A), stride frequency (B), hip height at footfall (C) and three-dimensional effective limb lengths at footfall (D) for each perch diameter and incline. Table 1 summarizes statistical comparisons of these variables among all surfaces.

considerably from the 1 cm to the 3 cm diameter surface, but changed little with further increases in diameter (Fig. 11C).

Non-linear changes in kinematics with increased diameter were very common. The most common pattern of non-linear change was that the magnitude of change in the kinematic variable decreased with increased diameter for a similar incremental increase in perch diameter (Figs 6D, 7C, 9A, 11C). For example, 22 of the 32 kinematic variables with a significant main effect of diameter (round perch data in Tables 1, 2, 4) had a greater difference between the mean values (pooled across all inclines) of 3 cm and 1 cm than those of the 10 cm and 6 cm diameter.

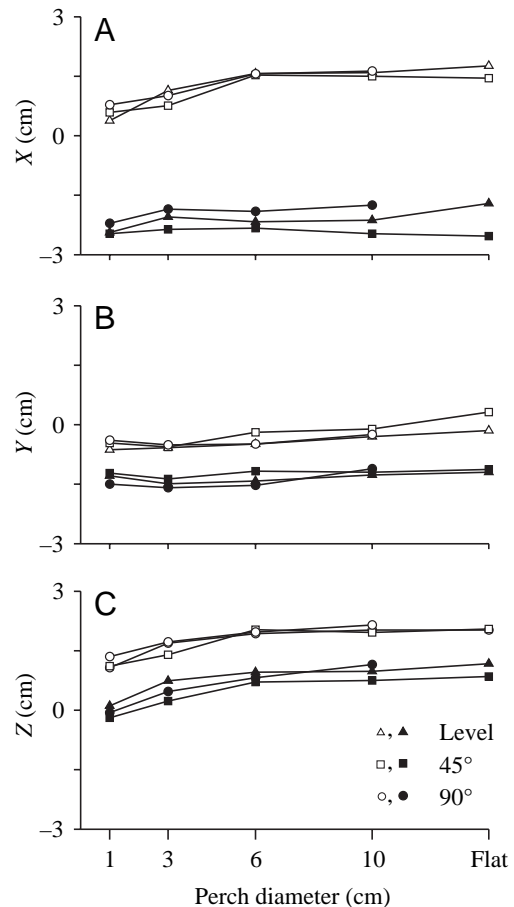


Fig. 7. Mean values of the minimum (black symbols) and maximum (white symbols) during the entire stride cycle for the longitudinal (A), vertical (B) and lateral (C) position of the tip of the fourth metatarsal relative to the hip for each perch diameter and incline. Tables 2 and 3 summarize the statistical comparisons of these variables.

In the principle components (PC) analysis (performed without rotation of the axes), values of the first PC generally increased with increased surface diameter (Fig. 12). In multivariate space, locomotion on different inclines was not kinematically very distinct (Fig. 12). A more extended knee at footfall, smaller values of maximum femur retraction and smaller values of femur depression all contributed to the high scores of PC1 (Table 5). The first three principle components accounted for 28%, 21% and 9.6% of the total variance in kinematics, respectively.

Discussion

Limb posture

Limb posture of tetrapodal vertebrates is a continuum of variation (Gatesy, 1991) ranging from sprawling (salamanders and lizards) to erect (birds and mammals). The distinctions between sprawling and erect limbs often emphasize the appearance of the limbs in two-dimensional anterior views in which the femur is oriented horizontally and projected laterally

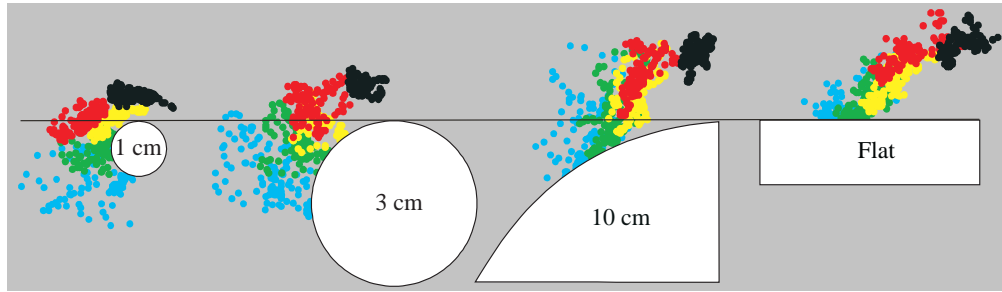


Fig. 8. Anterior view of the cumulative *y* and *z* (dorsal and lateral, respectively) positions of the right hip (black), knee (red), ankle (yellow), tip of the fourth metatarsal (green) and tip of the fourth toe (blue) of all the strides of one individual for each diameter on the level incline. For overlapping data, the more proximal points are layered on top of the more distal points. The horizontal line represents the top of the perch.

from the hip, and the ankle is directly below the knee (e.g. Fig. 1A; Russell and Bels, 2001). Two-dimensional definitions of limb posture can be misleading because, when the femur is slightly depressed, increased amounts of femur protraction appear to increase erectness in an anterior view even though the height of the distal femur is unchanged relative to the hip. Additional aspects of an erect limb posture include whether limb bones move in a parasagittal plane, whether the foot is

below the hip and the extent to which joints are flexed (crouched) or extended (erect). Thus, many species of mammals (Biewener, 1989) and birds (Gatesy and Biewener, 1991) have limb bones and movements that are mostly coplanar, but the limbs are often crouched rather than straight. Consistent with most previous definitions, our operational definition of ‘typical’ sprawling posture is: femur depression=0°, femur rotation=0°, femur retraction=0° and knee angle=90°.

The nearly horizontal femur (femur depression=0°) of *A. sagrei* at footfall on the flat level surface conforms to one key attribute of sprawling limb posture. For femur rotation, femur retraction and knee angle, the minimum values approximate the values at footfall and the mean values of these variables were 36°, -60° and 82°, respectively (Figs 9A, 10A,C). Near midstance, femur retraction of *A. sagrei* approximated zero as is the case for nearly all vertebrates with sprawled limbs, and values of femur depression, femur rotation and knee angle approximated 16°, 62° and 90°, respectively. Thus, on the flat level surface, at both footfall and midstance, femur depression and knee angles conformed closely to typical sprawling posture. However, the rotated femur results in the foot being considerably posterior to the knee rather than below it (Fig. 3).

Of the previously studied species of lizards, the limb posture of *A. sagrei* most closely resembles that of *Sceloporus clarkii*, which commonly traverses steep rock faces. For locomotion of *S. clarkii* on a flat surface and with duty factors similar to those of *A. sagrei*, *S. clarkii* has a nearly horizontal femur and the foot is markedly posterior to the knee (Reilly and Delancy, 1997) as a result of long-axis femur rotation. Thus, the hind limbs of both *A. sagrei* and *S. clarkii* have an overall dorsal-ventrally flattened appearance as a result of this limb posture. In contrast, for a more generalized terrestrial lizard, *Dipsosaurus dorsalis*, on a flat level surface with slightly higher duty factors (63%) and similar speeds (50 cm s⁻¹), compared to *A. sagrei* and *S. clarkii* at footfall the ankle is more nearly beneath the knee and the tibia is more nearly perpendicular to the ground as a result of less femur rotation (Jayne and Irschick, 1999). Similar to *A. sagrei* on the flat surface, the knee angle at midstance of *S. clarkii* (Reilly and Delancy, 1997), *D. dorsalis* (Jayne and Irschick, 1999), several

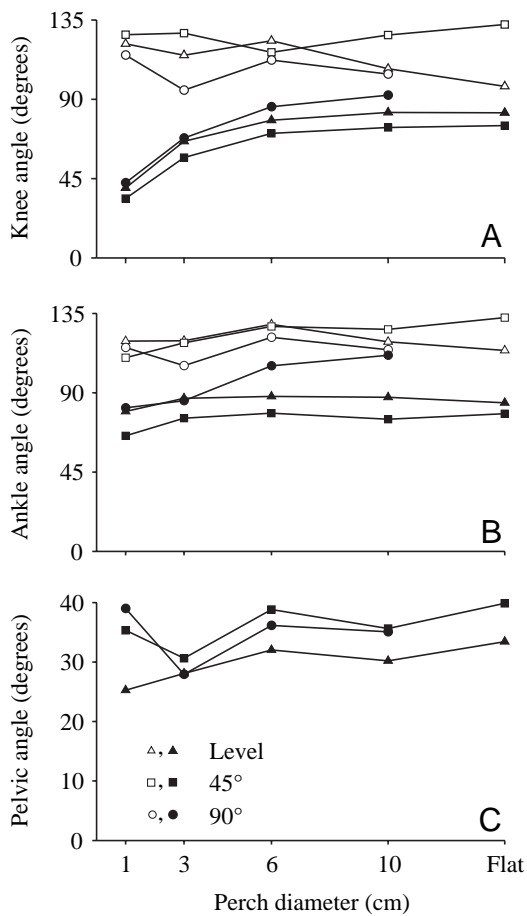


Fig. 9. Mean values of knee (A) and ankle (B) angles at footfall (black symbols) and end of stance (white symbols) and pelvic rotation (C) for each perch diameter and incline. Table 4 summarizes the statistical comparisons of these variables.

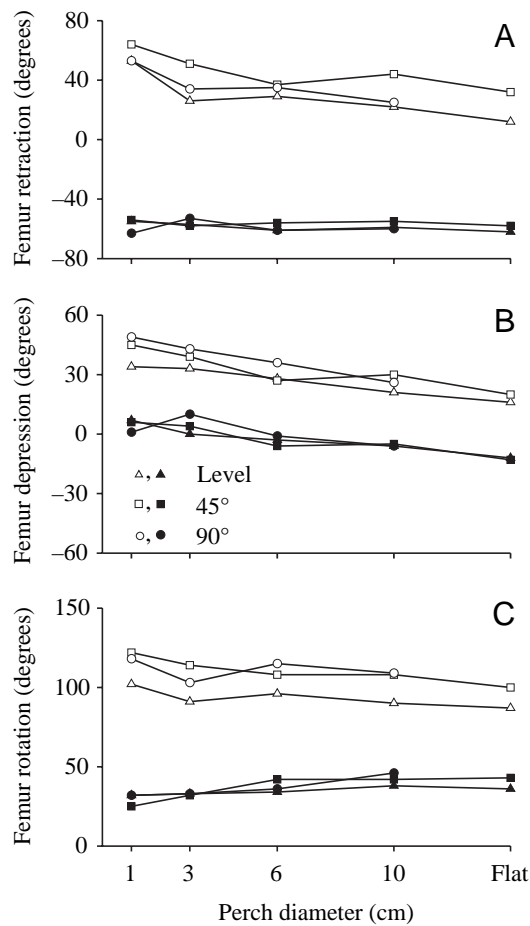


Fig. 10. Mean values of the minimum (black symbols) and maximum (white symbols) angles of femur retraction (A), depression (B) and long-axis rotation (C) for each perch diameter and incline during the entire stride cycle. Table 4 summarizes the statistical comparisons of these variables.

terrestrial lizard species (Irschick and Jayne, 1999) and an arboreal specialist, *Chamaeleo calytratus* (Higham and Jayne, 2004) all approximate 90°. However, unlike *A. sagrei* and terrestrial species of lizards at low speeds, the knee of *C. calytratus* is much more extended at footfall (125°). Hence, *A. sagrei*, *S. clarkii* and *C. calytratus* all have morphological and behavioral specializations for climbing, but only the former two species have similar limb posture.

As expected, with decreased perch diameter the femur of *A. sagrei* became more depressed throughout stance (Fig. 10B), and femur depression is one mechanism for locating the foot more medially. Although increased femur protraction is another potential mechanism for locating the foot more medially, this angle at footfall did not change significantly with decreased perch diameter (Fig. 10A). Increasing the amount of knee flexion is perhaps the most important mechanism used by *A. sagrei* for locating the foot more medially when moving on narrow perches, and the most conspicuous difference in knee flexion of *A. sagrei* was between the 3 cm and 1 cm diameter perches.

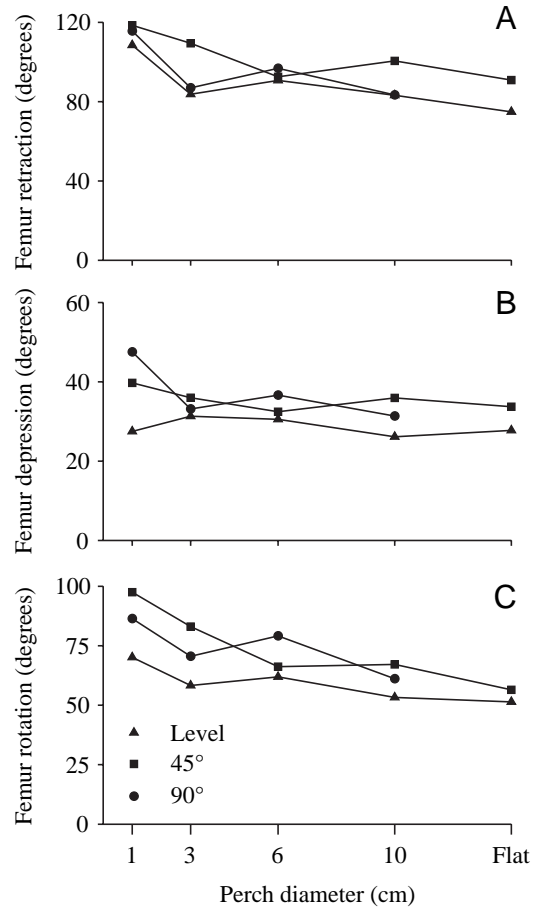


Fig. 11. Mean values of angular excursions for the femur during retraction (A), depression (B) and long-axis rotation (C) for each perch diameter and incline during the entire stride cycle. Table 4 summarizes the statistical comparisons of these variables.

If *A. sagrei* had a typical sprawling posture (Fig. 1A), then the ankles could not contact the 1 cm diameter perch because it is considerably narrower than the distance between outstretched knees of the lizard (33 mm). The midline of the pelvis of *A. sagrei* is approximately centered over the perch at footfall, which facilitates the following calculations for the level 1 cm diameter perch. If the knee angle were 90° and femur depression and femur rotation were 0°, then for the observed mean values of pelvic rotation (25°) and femur protraction (−55°) the ankle would be more than 4 mm lateral to the perch. Accounting for the observed value of femur depression (34°) only decreases this distance by approximately 1 mm. For the observed value of knee angle (40°) while holding other angles constant, the lateral distance from the middle of the pelvis to the ankle is only 2.6 mm and hence fits well within a 1 cm diameter perch.

For perches with diameters larger than 1 cm, all of the above mechanisms are used to varying degrees to locate the feet more medially. After meeting the requirements to make contact with the perch, further medial locations of the foot on a round perch will change the orientation of the locomotor surface that contacts the foot. On a perch of a given diameter, a foot located

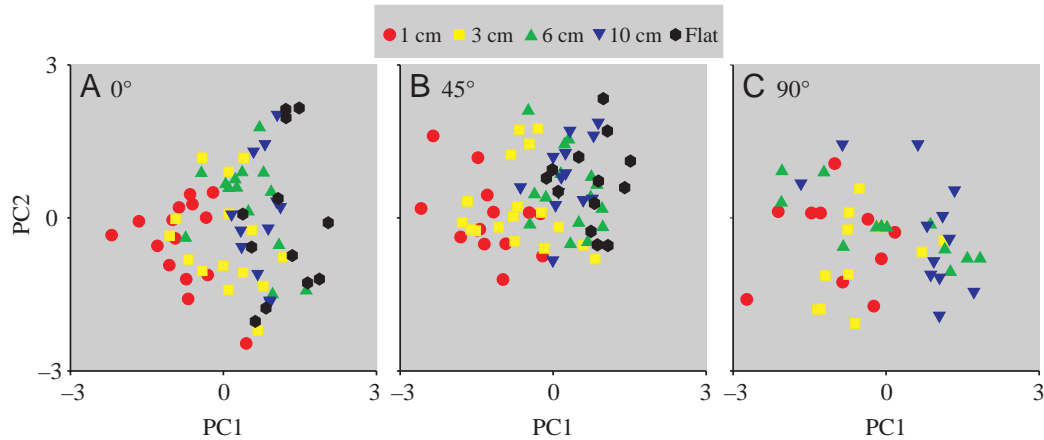


Fig. 12. Principle component 2 (PC2) versus principle component 1 (PC1) from a single analysis of 15 kinematic variables of *A. sagrei* for all strides observed on each perch diameter and incline. Each point is an individual stride ($N=185$), and the points are separated by incline: level (A), uphill 45° (B) and 90° (C). Red circles, yellow squares, green triangles, blue inverted-triangles and black hexagons represent strides on 1, 3, 6, 10 cm and flat surfaces, respectively. Table 5 provides the loadings for the principle components.

more medially will be on a surface that is more nearly horizontal, similar to the manner in which the feet on larger diameter perches are located on more nearly horizontal surfaces (Fig. 8). Unlike *A. sagrei*, the values of knee angle and femur depression for *C. calypttratus* did not change significantly for locomotion on a narrow round perch compared to a flat surface (Higham and Jayne, 2004).

Although many kinematic variables of *A. sagrei* changed significantly with increased incline, fewer variables changed than with perch diameter. With increased incline, hip height decreases in many diverse groups of vertebrates to minimize the risk of falling backwards (Cartmill, 1985; Vilensky et al.,

1994; Carlson-Kuhta et al., 1998; Jayne and Irschick, 1999). For *A. sagrei*, incline and perch diameter had significant interactive effects such that hip height was lowest on the steepest incline for most perch diameters and hip height did not change conspicuously with perch diameters for the steepest incline (Fig. 6C). Reducing the height of the hip and the center of mass reduces some of the adverse effects of torques that tend to make the animal fall off of the locomotor surface (Cartmill, 1985). For a vertical uphill perch, falling by tipping from side to side is not a problem, but the tendency to fall backwards is greatest and constant regardless of perch diameter. The tendency to tip from side to side increases with decreased perch diameter, but for both the level and 45° inclines the tendency to fall backwards is absent or constant. Thus, the interactive effects of incline and diameter on hip height correspond well with the different functional problems associated with the three inclines in our study of *A. sagrei*.

A more crouched limb posture will decrease hip height, and diverse groups of vertebrates commonly use increased amounts of flexion at the knee and ankle as mechanisms for increasing the extent to which the limb is crouched on uphill surfaces compared to level surfaces (Vilensky et al., 1994; Carlson-Kuhta et al., 1998; Jayne and Irschick, 1999). Unexpectedly, the angles of the knee and ankle at footfall of *A. sagrei* on 45° uphill were lower than those of both the level and 90° uphill (Fig. 9). Additional mechanisms of decreasing hip height include orienting the femur more nearly parallel to the locomotor surface and increasing long-axis femur rotation in animals with sprawling limbs. Femur depression of *A. sagrei* did not change significantly with incline. In contrast, the values of femur rotation of *A. sagrei* were significantly less on the level surface compared to the uphill inclines (Fig. 10), which is similar to the manner in which a generalized terrestrial lizard decreases hip height with increased femur rotation on downhill inclines (Jayne and Irschick, 1999).

Table 5. Loadings from a principle component (PC) analysis on 185 strides of level, 45° and 90° uphill locomotion for *A. sagrei* on surfaces that were 1, 3, 6 and 10 cm diameter and flat

Variable	PC1	PC2	PC3
Stride length	0.418	0.801	0.059
Step length	0.517	0.620	0.176
Stride duration	0.384	0.754	-0.037
Y_{hip} footfall	0.294	0.022	-0.221
Knee angle (ff)	0.661	0.091	0.233
Knee angle (es)	-0.359	0.758	0.041
Ankle angle (ff)	0.464	-0.307	0.386
Ankle angle (es)	0.221	0.526	0.039
Pelvic rotation	0.175	0.366	0.320
Min. femur retraction	0.001	0.237	-0.747
Max. femur retraction	-0.777	0.480	-0.023
Min. femur depression	-0.800	0.106	-0.126
Max. femur depression	-0.852	0.112	0.216
Min. femur rotation	0.277	0.187	-0.598
Max. femur rotation	-0.741	0.373	0.252

Substantial loadings (magnitude ≥ 0.5) are marked in bold type. ff, footfall; es, end of stance; Y_{hip} footfall, hip height at footfall.

Responses to incline and diameter of specialized and generalized lizards

The three lizard taxa for which the most detailed comparisons are possible regarding the effects of incline are *Anolis*, *Chamaleo calypttratus* and *Dipsosaurus dorsalis*. Both *Anolis* lizards (Losos, 1990; Irschick and Losos, 1996) and chameleons (Peterson, 1984; Russell and Bels, 2001) have several divergent morphological and behavioral specializations for moving in arboreal habitats. For example, chameleons have prehensile feet and tails, move very slowly and have unusually high proportions of slow muscle fibers in their limbs (Abu-Ghalyun et al., 1988). *Anolis* lizards have toe pads that adhere to surfaces (Williams and Peterson, 1982; Irschick et al., 1996). The low endurance and rapid running speeds of many *Anolis* species suggest they have a preponderance of fast glycolytic fibers, as seen in most other lizards (Bonine et al., 2001). Anoles commonly jump to bridge gaps between perches. Chameleons do not jump, but do have several features of forelimb and hindlimb movement that appear to facilitate reaching forward (Peterson, 1984; Higham and Jayne, 2004). In contrast to *A. sagrei* and *C. calypttratus*, the desert iguana *D. dorsalis* lacks feet with specializations for either adhesion or prehension, and most of its locomotion is on the ground rather than on perches. Consequently, *D. dorsalis* is a good model for a morphologically and behaviorally generalized lizard (Fieler and Jayne, 1998).

In *A. sagrei*, the percentage of kinematic variables that had significant main effects of incline (incline factor significant regardless of interaction term significance) was 40%. This value is intermediate between the low percentage (11%) of variables affected in *C. calypttratus* (Higham and Jayne, 2004) and the high percentage (73%) of kinematic differences reported by Jayne and Irschick (1999) for *D. dorsalis*. Unlike our study of *A. sagrei*, the data for *D. dorsalis* and *C. calypttratus* included both uphill and downhill inclines. The downhill locomotion of *D. dorsalis* is kinematically most distinct and hence, was likely responsible for many of the significant main effects of incline (Jayne and Irschick, 1999). The only other study to quantify diameter effects on hind limb kinematics of lizards was for *C. calypttratus* on 2.4 cm diameter round perches versus flat surfaces (Higham and Jayne, 2004). Diameter had significant main effects for approximately twice the percentage of variables for *A. sagrei* (67%) compared to *C. calypttratus* (32%) (Higham and Jayne, 2004). *C. calypttratus* is striking for its uniformly small changes in limb kinematics with changes in incline and perch diameter compared to the former two species of lizards, and the tokay gecko *Gekko gecko* is another arboreal specialist that may have only minimal changes in limb kinematics with variable incline (Zaaf et al., 2001b). Perhaps, the greater modulation of limb kinematics in *A. sagrei* and *D. dorsalis* facilitates their ability to move with a wider range of speeds on different locomotor surfaces than some climbing specialists.

A very general feature of the hind limb kinematics of lizards and other vertebrates is that the knee flexes briefly during early stance (Higham and Jayne, 2004), as would be expected if the

limb was functioning according to the 'mass-spring' model (Blickhan, 1989). However, for *A. sagrei* on narrow perches, early stance flexion of the knee was absent as the knee extended throughout stance (Fig. 5). Perhaps, the extremely posterior location of the foot relative to the knee and the nearly horizontal orientation of the tibia at footfall (Fig. 2A) make using the limb as a spring unlikely.

Implications of variable perch diameter for performance

Previous studies of anoles have described linear increases in maximal speed (V_{\max}) with increased perch diameter (Losos and Sinervo, 1989; Losos and Irschick, 1996), but closer examination suggests this relationship for may be nonlinear for some species. For *A. sagrei*, running up a 38° incline in the laboratory, mean values of V_{\max} are 0.97, 1.44, 1.73 and 1.77 m s⁻¹ for perch diameters (D) of 0.6, 1.6, 2.5 and 5.1 cm, respectively (from fig. 1 in Losos and Irschick, 1996). We calculated least-squares regressions for these values of V_{\max} of *A. sagrei* and found that a simple linear regression predicting V_{\max} from D was not statistically significant ($F_{1,2}=4.2$, $P=0.18$). However, a quadratic polynomial of D (not calculated in the previous study) predicting V_{\max} was significant overall ($F_{2,1}=7000$, $P<0.01$, $r^2=0.99$), and the coefficients of both the linear and quadratic terms of D were both significant ($P<0.01$) in the regression model $V_{\max}=0.60+0.66D-0.085D^2$. The negative quadratic effect of diameter on V_{\max} corresponds well with the non-linear effects of increased diameter that we found for several kinematic variables. However, we note that our kinematic data for *A. sagrei* were for a constant speed (54 cm s⁻¹) that was substantially less than V_{\max} , and the data for narrower perches were greater fractions of V_{\max} than the data for wider perches.

The hindlimb kinematics of several species of terrestrial lizards have several general trends with increased speed (Jayne and Irschick, 1999; Irschick and Jayne, 1999) that are nearly opposite the changes in kinematics that we observed for *A. sagrei* as perch diameter decreased. For example, stride length and hip height have the greatest values at maximal speeds of terrestrial lizards, and in some species stride width increases with speed on level surfaces (Jayne and Irschick, 1999). Pelvic rotation during high-speed locomotion of terrestrial locomotion usually exceeds 45°. At footfall during high speed running, the knee of most lizards is extended slightly more than 90°. Furthermore, the minimum values of femur rotation often approximate 0° for high-speed quadrupedal running, and negative values of femur rotation often occur during bipedal locomotion (Irschick and Jayne, 1999). As a combined consequence of knee extension and femur rotation, the foot is generally anterior to the knee at footfall and the greatest forward reach of the distal limb usually occurs at highest speeds during terrestrial locomotion. In addition, the long-axis of the foot is nearly oriented parallel to the overall direction of travel at high speeds, whereas at low speeds the long-axis of the foot is often oriented laterally with an angle greater than 30°. At very high speeds, the effective limb length of terrestrial lizards is often enhanced as a result of increased plantar flexion

resulting in digitigrade foot posture throughout the stance phase (Jayne and Irschick, 1999). For terrestrial lizards running rapidly, the large amounts of plantar flexion during late stance and hyperextension of the toe during early swing imply these movements have an important role for increasing force (Irschick and Jayne, 1999) or increasing the period of time during which force can be applied to the substrate.

The following examples illustrate some of the changes in hind limb kinematics of *A. sagrei* with decreased perch diameter that are contrary to those changes observed with increased speeds in terrestrial lizards. With decreased perch diameter on the level surface, stride length decreased, hip height decreased, effective limb length at footfall decreased, pelvic rotation decreased, femur rotation at footfall was considerable (greater than 30°), knee flexion increased and the foot was located more posterior relative to the knee at footfall. The angle between the long-axis of the metatarsals and the perch also increased dramatically from a mean value of 19° on the flat surface to 79° on the 1 cm diameter perch. As perch diameter decreases, the orientation of the surface from which the foot pushes off becomes less horizontal (Fig. 8). Thus, the combination of the lateral orientation of the foot and the surface that it contacts on narrow perches is likely to reduce the ability to use plantar flexion to produce a large forward directed component of the ground reaction force as appears likely for rapidly running terrestrial species.

Although our observations of *A. sagrei* are for speeds substantially less than maximal speeds, the kinematics that we observed on narrow perches are so contrary to those observed for the high speed locomotion of other lizards, they strongly suggest some of the functional difficulties for obtaining high speeds on narrow perches. Future studies determining ground reaction forces on perches of different diameter would be very useful for further resolving why locomotor performance decreases with decreased perch diameter. Perhaps the orientation of the foot and limb on narrow perches will result in disproportionate increases in the laterally oriented reaction force and decreases in the reaction forces in the *y* direction relative to the forward-directed forces.

Clearance in arboreal environments

For the arboreal locomotion of lizards, the effects of habitat structure on locomotor performance have been discussed widely (Losos and Sinervo, 1989; Losos, 1990; Irschick and Losos, 1998). However, a neglected but important functional consideration for movement in arboreal habitats is the clearance between the body of the lizard and the perch upon which it moves and adjacent perches that obstruct the path traveled by the animal.

The clearance between the ventral surface of the body of a lizard and the locomotor surface depends on both the curvature of the locomotor surface and the lateral distance between the contralateral points of contact with the locomotor surface. Decreasing the height of the hip relative to the point of foot contact with the perch is beneficial for decreasing the tendency of the body to tip away from the locomotor surface. On a flat

surface, theoretically, the height of the hip and ankle could be equal if the femur were either rotated or elevated considerably. However, on a round perch the upward bulge of the surface between the points of foot contact precludes the possibility of having the foot and hip at the same height. For example, for typical sprawling limb posture and the anatomical dimensions of *A. sagrei* (Fig. 1A), the upward bulge of a 3.5 cm diameter perch is as great as the length of the tibia and hence, the ventral surface of the lizard would contact the top of this perch (Fig. 1D). For perch diameters of 4.0, 4.8 and 9.7 cm the clearances between the ventral surface and the top of the perch are 25%, 50% and 75% of the length of the tibia, respectively (Fig. 1D). Thus, for *A. sagrei*, potentially large differences in the clearance between the body and the top of the perch occur for perches with diameters less than 10 cm. Locating the feet more medially reduces the magnitude of the effects of perch curvature on the clearance between the top of the perch and the ventral surface of the lizard, and we previously discussed several mechanisms that the lizards use to locate the foot more medially.

In natural arboreal habitats, as perch diameter decreases the distances between nearest neighbor perches usually decrease, resulting in a relatively cluttered environment. Thus, the diameter of a cylinder that could penetrate vegetation without touching it would be expected to decrease as the average diameter of perches in an area decrease. Consequently, the limbs of a moving animal are more likely to bump into an obstacle when it travels through environments that are increasingly cluttered with smaller perch diameters. The limbs of *A. sagrei* used less lateral space for locomotion on perches with decreased diameters (Figs 7C, 8). Thus, altering the kinematics of the limbs can facilitate moving through a cluttered environment, and the kinematics during the swing phase of the stride are likely to be most important for affecting the clearance of the limbs relative to the obstacles in the environment.

Shorter limbs have evolved convergently in several species of *Anolis* lizards that are found mostly on narrow perches and known as twig ecomorphs (Moermond, 1979; Williams, 1983; Losos, 1990). Twig ecomorphs uniformly have slow maximal speeds of running, which change little with perch diameter, whereas species with longer limbs can attain quite rapid maximal speeds, which decrease substantially with decreased perch diameter (Losos and Sinervo, 1989; Irschick and Losos, 1996). Some studies suggest the short limbs of twig ecomorphs may increase their stability when moving on narrow perches (Losos and Sinervo, 1989; Irschick and Losos, 1996). However, a frequently neglected fact is that long-limbed species manage to run faster on narrower perches than short-limbed species in laboratory tests. We suggest that the short limbs of twig ecomorphs have additional benefits that have rarely been considered. If the kinematics of species with different limb dimensions are similar, then the shorter-limbed species will have more medial foot placement, which may benefit the orientation of the foot on the substrate as well as increasing the clearance between the top of the perch and the ventral surface of the body. Furthermore, shorter-limbed

species will have greater lateral clearance in cluttered natural environments. Most studies of locomotion emphasize morphology and movements that are involved in enhancing propulsive forces and hence are relevant to variation in maximal locomotor speed. However, a relatively neglected factor for locomotion in arboreal and cluttered environments is the simple ability to fit the body within confined spaces.

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