

Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist

Timothy E. Higham* and Bruce C. Jayne

Department of Biological Sciences, University of Cincinnati, PO Box 210006, Cincinnati, OH 45221-0006, USA

*Author for correspondence at present address: Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA (e-mail: tehigham@ucdavis.edu)

Accepted 24 October 2003

Summary

Arboreal animals, especially lizards, often traverse three-dimensional networks of narrow perches with variable and steep inclines, but the effects of both incline and narrow surfaces on the locomotor movement and function of limbs are poorly understood. Thus, we quantified the three-dimensional hindlimb kinematics of a specialized arboreal lizard, *Chamaeleo calyptrotus*, moving horizontally, and up and down a 30° incline on a narrow (2.4 cm) perch and a flat surface. We compared the flat-surface data of *C. calyptrotus* with those of an anatomically generalized terrestrial lizard, *Dipsosaurus dorsalis*. Incline had significant main effects for relatively few kinematic variables of *C. calyptrotus* (11%) compared to *D. dorsalis* (73%). For *C. calyptrotus*, the main effects of locomotor surface were nearly three times more widespread than those of incline. The foot of *C. calyptrotus* was markedly anterior to the hip at footfall, primarily as a

result of an unusually extended knee for a lizard. A large amount of knee flexion during early stance may be used by *C. calyptrotus* to actively pull the body forward in a manner not found in *D. dorsalis*. Unexpectedly, the pelvic rotation of *C. calyptrotus* greatly exceeded that of *D. dorsalis* and, unlike *D. dorsalis*, was not affected by incline. The more medial location of the foot of *C. calyptrotus* on the narrow perch during stance was primarily a result of knee flexion rather than femur depression. Unlike previous qualitative descriptions of chameleons, our data for the hindlimb posture of *C. calyptrotus* during stance indicate that the limb was not particularly erect.

Key words: locomotion, lizard, *Chamaeleo calyptrotus*, *Dipsosaurus dorsalis*, arboreal, terrestrial, kinematics, incline, slope, hindlimb, posture.

Introduction

Most studies of animal locomotion examine movement on level (horizontal) surfaces. However, to traverse many habitats, animals often must move up and down inclines. For diverse lineages of animals, inclines often affect maximal speed and acceleration (Huey and Hertz, 1982), kinematics of the limbs (Schmitt, 1998; Jayne and Irschick, 1999; Zaaf et al., 2001), muscular activity (Roberts et al., 1997; Carlson-Kuhta et al., 1998) and energetics (Farley and Emshwiller, 1996). To date, the diverse taxa and methods used in previous studies of the effects of incline on locomotion complicate making generalizations.

Steep inclines are common in arboreal habitats, which also impose other interesting demands on function. For example, arboreal habitats require that animals grasp or adhere to the locomotor surface to avoid falling to the ground, or tipping over when on a narrow branch. Thus, many animals living in these habitats have morphological, behavioral and/or ecological specializations that allow them to move effectively under these conditions. For example, primates have prehensile feet (Cartmill, 1974; Schmitt, 1998) and geckoes and anoles have toe pads (Irschick et al., 1996; Russell, 2002). Some

morphological specializations for arboreal locomotion on narrow perches may compromise other aspects of locomotion, such as maximal speed (Losos et al., 1993). Thus, studying arboreal locomotion is important to fully understand the morphological variation found in animals. However, with the exception of primates, arboreal locomotion is poorly studied compared to terrestrial locomotion (reviewed in Jenkins, 1974; Strasser et al., 1998).

Another functional difference between moving on inclines and level surfaces is that gravity will assist downhill and hinder uphill movement of animals. To resist the added influence of gravity when moving downhill, animals can modify the kinematics of their body or increase the activity of certain muscles to perform 'negative' work that actively resists movement. When moving uphill, animals increase propulsive forces to perform work against the added force of gravity (Roberts et al., 1997). Some terrestrial lizards also modify the kinematics of the limbs when moving on inclines. For example, hip height is lower on inclines than on level surfaces (Jayne and Irschick, 1999). The demands of inclined locomotion may also vary with the properties of the substrate, such as diameter

or texture. Claws, adhesive systems and prehensile feet are all examples of morphological specializations that could increase gripping ability and thus reduce the chances of slipping (Cartmill, 1985).

Many species of lizards are particularly adept at moving on steep inclines (Huey and Hertz, 1982) and the discrete networks of perches in arboreal habitats often force them to do so (Mattingly and Jayne, in press). Thus inclines are ecologically relevant to the study of lizard locomotion. Lizard taxa also vary considerably in their morphology, ecology and behavior, and include both terrestrial and arboreal forms. Many attributes of habitat are known to affect the locomotion of lizards, such as firmness of the substratum (Carothers, 1986), turning angles of perches (Higham et al., 2001) and perch diameter (Losos and Sinervo, 1989; Losos and Irschick, 1996). Inclines affect the speeds (performance) and limb movements (kinematics) of lizards in both laboratory experiments (Huey and Hertz, 1982, 1984; Irschick and Jayne, 1998; Jayne and Ellis, 1998; Jayne and Irschick, 1999; Zaaf et al., 2001) and field experiments (Irschick and Jayne, 1999a; Jayne and Irschick, 2000). Thus, we examined the effects of incline on the three-dimensional hindlimb kinematics of the arboreal specialist, *Chamaeleo calytratus* (veiled chameleon) and compared this to the terrestrial generalist, *Dipsosaurus dorsalis* (desert iguana).

We studied the hindlimb only of *C. calytratus*, for several reasons. First, the only previous three-dimensional kinematic study of lizard locomotion on inclines is for the hindlimb of *D. dorsalis* (Jayne and Irschick, 1999). Second, previous kinematic studies of terrestrial species of lizards have focused on the hindlimb because it is used for all speeds of locomotion, whereas the forelimbs of many species do not contact the ground during high-speed bipedal locomotion (Irschick and Jayne, 1999b). Furthermore, the shoulders of lizards have some translational movements that complicate kinematic analyses (Goslow and Jenkins, 1983; Peterson, 1984).

Chameleons are a specialized group of arboreal lizards with several derived traits including prehensile feet with opposable digits, a prehensile tail, a laterally compressed body, and a relatively upright limb posture (Peterson, 1984; Abu-Ghalyun et al., 1988; Fig. 1). Several of these features make chameleons particularly adept at climbing on narrow branches, but whether chameleons move differently on narrow branches and flat surfaces is unknown. The morphological and behavioral specializations of chameleons for an arboreal habitat may be so divergent from the ancestral condition that limb movement and function during locomotion may also differ considerably from more generalized terrestrial species of lizards (Russell and Bels, 2001).

The purpose of this study was to address the following questions regarding the effects of incline on the three-dimensional hindlimb kinematics of an arboreal specialist (veiled chameleon) and a terrestrial generalist (desert iguana). (1) Are the hindlimb movements in chameleons affected by the inclination of the substrate? We hypothesized that chameleons would be affected by incline, as was the case for the desert

iguana (Jayne and Irschick, 1999). (2) Are chameleons affected by inclines in the same way as a non-arboreal lizard (desert iguana)? We hypothesized that chameleons and desert iguanas would respond similarly to inclines, despite substantial differences in morphology. (3) Do chameleons alter their limb movements when moving on a flat surface compared to a narrow circular perch? We hypothesized that chameleons would modify the movement patterns of their hindlimbs in response to different surfaces.

Materials and methods

Experimental subjects

We studied the veiled chameleon *Chamaeleo calytratus* Dumeril and Bibron because it is relatively large, is easily kept in captivity, and is arboreal and morphologically specialized compared to a generalized terrestrial lizard (Peterson, 1984). We obtained all chameleons from a commercial dealer, and they were transported to the University of Cincinnati for experiments. Lizards were caged alone and were fed crickets, which were 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. After videotaping several chameleons, we chose four individuals that moved on each combination of incline and surface required for a balanced experimental design. For each individual and combination of incline and surface, we chose strides that had similar speeds (approximately 50 cm s⁻¹). The four chameleons were of similar size, as indicated by the following mean values (\pm S.E.M.) (ranges in parentheses): mass 80.8 \pm 4.3 g (57–98 g), snout–vent length (SVL) 18.1 \pm 1.1 cm (16.9–19.5 cm).

For each of the lizards used for the kinematic analysis, we measured several anatomical lengths. We measured snout–vent length, tail length and pelvic width to the nearest mm from the specimens after preservation. We used life-size lateral view radiographs of preserved specimens and digital calipers (\pm 0.05 mm) to measure a total of four limb distances from the right side of each lizard. The lengths of the femur and tibia were measured from their most proximal to their most distal portion. The length of the hindfoot was measured from the heel to the base of the fourth metatarsal. The length of the fourth toe of the hindfoot was measured from the base of the claw on the fourth digit to the base of the fourth metatarsal. We also determined the location of the paint mark on the pelvis relative to the hip joint so that the coordinates of the pelvic landmark could be transformed to estimate the location of the hip.

The mean lengths from the hip to the tip of the toe of *C. calytratus* (8.2 \pm 0.2 cm) and *Dipsosaurus dorsalis* Baird and Girard (8.1 \pm 0.3 cm) were almost identical, but the lengths of the elements that make up the limb differ substantially between these two species. The lengths of both the femur and tibia of chameleons (3.6 \pm 0.1 cm and 2.7 \pm 0.1 cm, respectively) were much longer than those of the desert iguanas (2.4 \pm 0.02 cm and

Table 1. F values from three-way ANOVAs performed separately on each variable

Dependent variable	<i>C. calypttratus</i> + <i>D. dorsalis</i>			<i>C. calypttratus</i> only		
	Species d.f.=1,6	Incline d.f.=2,12	Species×Incline d.f.=2,12	Incline d.f.=2,6	Surface d.f.=1,3	Incline×Surface d.f.=2,6
Duty factor	0.1	0.2	3.4	3.1	1.9	0.2
Stride length ¹	1.1	4.5*	2.8	1.0	1.9	0.4
Step length ¹	1.9	3.6	5.9*	2.3	0	0.3
Y _{min} hip ¹	2.2	18.4***	7.6**	0.5	19.2*	2.0
Y _{max} hip ¹	0.2	9.5**	4.0	0.9	17.7*	2.0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
Main effects and interaction terms are listed above each column.
d.f., degrees of freedom.
¹Units are cm for *C. calypttratus* only and proportions for *C. calypttratus* + *D. dorsalis*.

2.1±0.02 cm, respectively). Additionally, the lengths from the heel to the base of the fourth toe and of the fourth toe were larger in desert iguanas (1.4±0.02 cm and 2.3±0.03 cm, respectively) than in chameleons (1.1±0.04 cm and 0.7±0.04 cm, respectively).

Experimental protocol

We obtained simultaneous dorsal and lateral views of the chameleons moving on both the perch and (non-moving) treadmill using a two-camera NAC HSV-500 high-speed video system (Tokyo, Japan) operating at 250 images s⁻¹. All of the locomotor surfaces were approximately 1 m long and included a 2.4 cm diameter wooden dowel and the same treadmill that was used for *D. dorsalis* by Jayne and Irschick (1999). All of the surfaces were inclined at 30° (uphill), -30° (downhill) and 0° (level) relative to the horizontal plane, and the midpoint of each surface was approximately 1 m above the ground. To provide fixed points of reference we drew lines at 10 cm intervals along the length of the surfaces. To facilitate digitizing the location of points on the lizards, we painted landmarks on the pelvis, knee, ankle, metatarsal and toe tip (Fig. 1). Prior to each trial, we measured the body temperature of the chameleon using a thermocouple and a Tegam (Geneva, OH, USA) model 871A digital thermometer. We allowed the chameleon to bask under a light until its temperature approximated 30°C (range: 29–31°C).

The data for the desert iguana (*D. dorsalis*) were a subset of those analyzed by Jayne and Irschick (1999). We only analyzed the slowest speed trials (50 cm s⁻¹) from desert iguanas moving steadily on a motorized treadmill. Although they differ considerably in shape, these two species have grossly similar size, as indicated by the combined length of the limb elements in *C. calypttratus* (8.2±0.2 cm) and *D. dorsalis* (8.1±0.3 cm). The grand means ± 95% confidence limits (CL) for the speeds of 48 strides of *D. dorsalis* and 90 of *C. calypttratus* were 52±1.7 cm s⁻¹ and 17±1.0 cm s⁻¹, respectively. Similar duty factors commonly indicate equivalent speeds and gaits, and we selected strides of *D. dorsalis* and *C. calypttratus* such that no statistically significant variation was present in duty factor among any of the main

experimental treatments (Table 1) and for which the grand means ± 95% CL were 62±1.9% and 63±1.2%, respectively. Thus, the locomotion that was analyzed was a relatively slow walk for both species.

For the chameleons, we analyzed non-consecutive strides from different trials, and the stationary surfaces used to obtain locomotion required a large number of trials to obtain reasonably steady-speed locomotion of 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.

Kinematics

We used customized video analysis software (Measurement TV, written by Garr Undergraff, San Clemente, CA, USA; garru@uci.edu, garru@fea.net) to reconstruct the three-dimensional coordinates of each landmark. The *x*-axis of each video image was parallel to the overall direction of travel along the long axis of the locomotor surface. The *y*-axis was perpendicular to the surface and within a vertical plane passing through the long axis of each walkway, and *y*=0 for the top of the walkway along its entire length. The *z*-axis was perpendicular to the *x*-*y* plane.

For each chameleon on each incline and surface, we selected 3–4 strides of steady-speed locomotion for frame-by-frame motion analysis. We digitized 25–35 images per stride, which provided images between 30–60 ms apart. Three-dimensional coordinates were digitized for the hip, knee, ankle, base and tip of the fourth toe (excluding claw). From a dorsal perspective, two-dimensional coordinates (*x*, *z*) were digitized for the right and left hips.

To facilitate visualizing the limb elements, we transformed all of the three-dimensional coordinates of limb elements distal to the hip so that the hip was located at (0, 0, 0). Positive values of the relative *x*, *y* and *z* coordinates indicate anterior, dorsal, and lateral movements, respectively. For each stride we determined minimum (*X*_{min}, *Y*_{min}, *Z*_{min}) and maximum (*X*_{max}, *Y*_{max}, *Z*_{max}) values of the relative three-dimensional coordinates, as well as the difference (Δ) between the

minimum and maximum values. To facilitate the inter-specific comparisons, each linear variable was scaled to the cumulative lengths of all limb elements proximal to that location. For example, the positions of the ankle were divided by the combined lengths of the femur and tibia.

Three-dimensional angles described angles of joints within the hindlimb at footfall and at the end of stance. A detailed explanation of the angular measurements can be found in Jayne and Irschick (1999). Smaller values of knee angle between 0° and 180° indicate greater flexion of the joint. For the ankle angle, decreasing values between 0° and 180° indicate greater dorsiflexion of the foot. The orientation of the pelvis was determined by a two-dimensional angle obtained from a dorsal perspective, and from the differences between maximum and minimum values we were able to determine the amount of pelvic rotation. For locomotion on the treadmill, the angle of toe orientation was the angle of the fourth toe relative to the x -axis and larger angles between 0° and 90° indicated that the toe was more laterally oriented. Toe orientation could not be reliably measured for locomotion on a perch since the toe was often not visible in dorsal view. Thus we did not include toe orientation in analyses involving the round perch.

For three angles that describe the orientation of the femur, we determined the maximum and minimum values for each complete stride cycle. Femur retraction was the two-dimensional angle between a line connecting the left and right hips and the long axis of the femur projected onto the x - z (horizontal) plane. Femur retraction values of 0° indicate when the femur is perpendicular to the longitudinal axis of the pelvis, and positive and negative values indicate measures of femur retraction and protraction, respectively. Long-axis rotation of the femur was a three-dimensional angle between a vertical reference plane passing through the femur and the plane containing the femur and tibia. 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. Femur depression was the three-dimensional angle between the long axis of the femur and a horizontal reference plane. Positive and negative values of femur depression indicate that the distal femur was either ventral or dorsal to the hip, respectively.

Statistical analyses

We used SAS version 8.0 for all statistical analyses, and $P < 0.05$ was the criterion for statistical significance. In the tabular summaries of the statistics, we provide degrees of freedom and F -values to clarify the potential effects of making multiple comparisons. The following two analyses were conducted for each linear and angular variable: (1) A comparison within *C. calytratus* examining the effects of surface (perch and treadmill). For this analysis, individual was a random factor while surface and incline were fixed factors. (2) We compared *C. calytratus* to *D. dorsalis* for locomotion on a treadmill. For this analysis, individual was a random

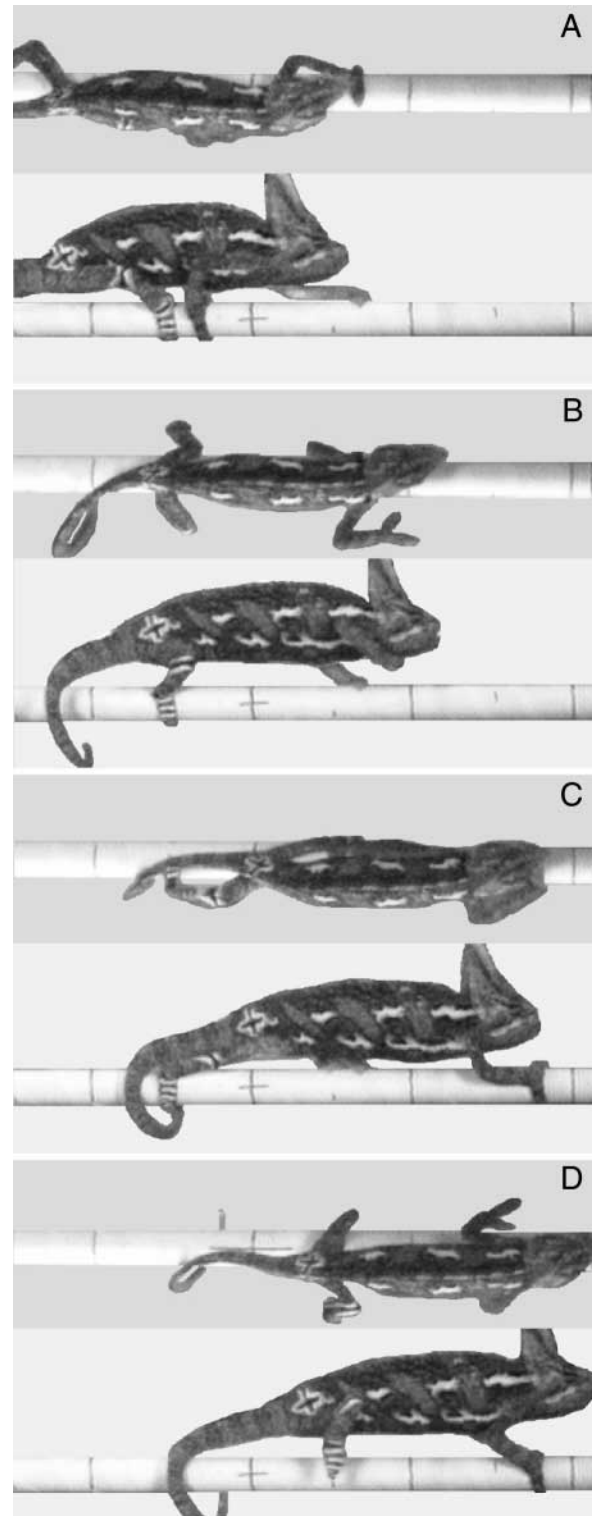


Fig. 1. Lateral and dorsal views of *Chamaeleo calytratus* moving on a level perch including (A) footfall (0 ms), (B) midstance (488 ms), (C) endstance (972 ms) and (D) midswing (1240 ms). The lizard is moving at approximately 17 cm s^{-1} .

factor nested within species while species and incline were fixed factors. Consequently, the denominators for the F -tests on the main effects of incline and surface were the mean

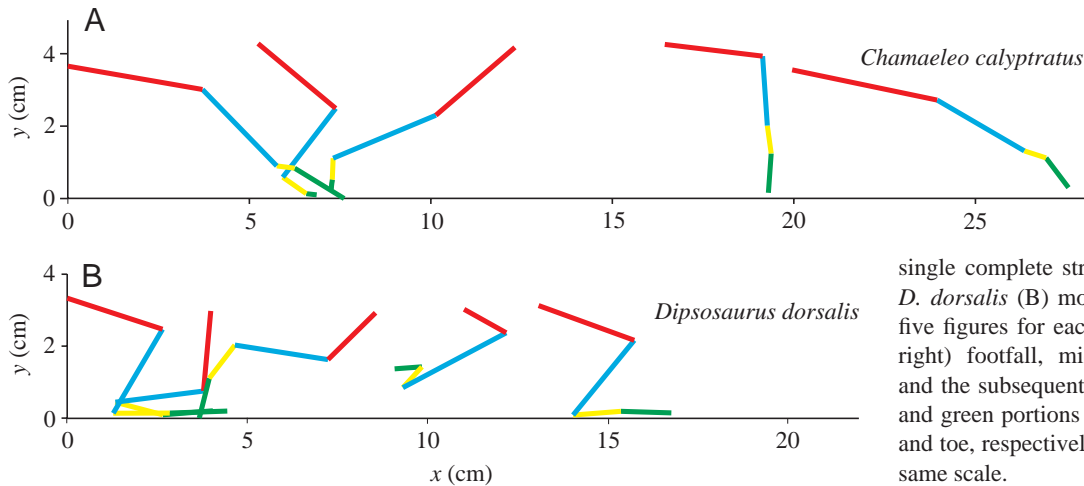


Fig. 2. Schematic figures of the right hindlimb for a single complete stride for *C. calytratus* (A) and *D. dorsalis* (B) moving on a level treadmill. The five figures for each animal indicate (from left to right) footfall, midstance, endstance, midswing and the subsequent footfall. The red, blue, yellow and green portions are the femur, tibia, metatarsal and toe, respectively. Both of the strides are to the same scale.

squares of two-way interaction terms of the fixed effect and the individual factor, and the denominator for the *F*-test for the main species effect was the mean squares of the individual factor (Zar, 1996).

Multivariate statistics were performed to evaluate whether locomotion was unique for a particular species and for a particular surface within *C. calytratus*. We used 17 kinematic variables in two discriminant function analyses. The first analysis of *C. calytratus* data included each stride ($N=89$) as an individual point and each combination of surface ($N=2$) and incline ($N=3$) as a categorical variable. The second analysis of treadmill data for both species included each stride ($N=90$) as an individual data point and each combination of incline ($N=3$) and species ($N=2$) as a categorical variable.

Results are presented as means \pm S.E.M., unless stated otherwise.

Results

General description of limb movements for *C. calytratus*

At the time of footfall the foot of *C. calytratus* was substantially anterior to the hip as a result of femur protraction and knee extension (Figs 1A, 2A). Femur protraction was so extreme at footfall that the medial surface of the thigh often touched the body (Figs 1A, 3). The angles of both the knee and ankle at footfall usually exceeded 120° and 130° , respectively. The foot of *C. calytratus* was oriented such that the x position of the toes closely approximated that of the ankle at footfall (Fig. 1A). Maximal pelvic rotation was approximately coincident with footfall.

Femur retraction of *C. calytratus* began at footfall and continued to a maximum slightly before the end of stance (Fig. 4A). After footfall, the knee flexed to an acute angle near mid-stance, whereupon the knee extended to a maximum at the end of stance (Figs 1, 4A). At midstance, the height of the knee was often similar to that of the hip (Fig. 3). The vertical distance between the foot and hip was nearly constant for the first two-thirds of stance (Fig. 5D,E). The anterior (positive x) and posterior (negative x) excursions of the limb relative to the

hip were nearly symmetrical (Fig. 5A,B,D,E). Clockwise long-axis femur rotation (as seen in right lateral view) began at footfall and continued throughout stance (Fig. 4A).

Counter-clockwise long-axis femur rotation of *C. calytratus* began near the beginning of swing and continued until footfall (Fig. 4A). Most femur protraction occurred in early swing, and in the second half of swing this angle was nearly constant (Fig. 4A). The knee began to flex just prior to swing and continued to flex until mid-swing, whereupon the knee extended until footfall (Figs 1, 2, 4A). Values of femur depression decreased sufficiently during early swing such that the knee was often higher than the hip (Figs 1D, 5D,E). The maximum lateral positions of all portions of the limb usually occurred near mid-swing (Figs 1, 5A,B), and shortly thereafter the distal portions of the limb were anterior to the knee (Figs 1, 2A). As seen from a dorsal view, the path traveled by the knee during swing almost exactly retraces the path traveled during stance (Fig. 5A,B).

Effects of incline and surface on *C. calytratus*

For *C. calytratus*, 17 out of 30 variables (excluding duty factor) had no significant variation with either the main or interactive effects of incline and surface (Tables 1, 2). For example, neither stride nor step length varied significantly among any of the experimental treatments (Table 1; Fig. 6A). In contrast, the minimum and maximum heights of the hip relative to the locomotor surface varied significantly between the perch and treadmill such that values on the treadmill were greater than those on the perch (Table 1; Fig. 6B).

For the linear positions and excursions of the hindlimb of *C. calytratus*, surface and incline affected 10 and 5 of the 27 variables, respectively (Table 2). The most anterior (X_{\max}) positions of the knee, ankle and metatarsal were all significantly greater on the perch than on the treadmill (Table 2; Fig. 6C). Furthermore, incline significantly affected five of the six variables describing the most posterior (X_{\min}) and anterior (X_{\max}) locations of the knee, ankle and metatarsal such that the lowest values were on the uphill incline (Table 2; Fig. 6C).

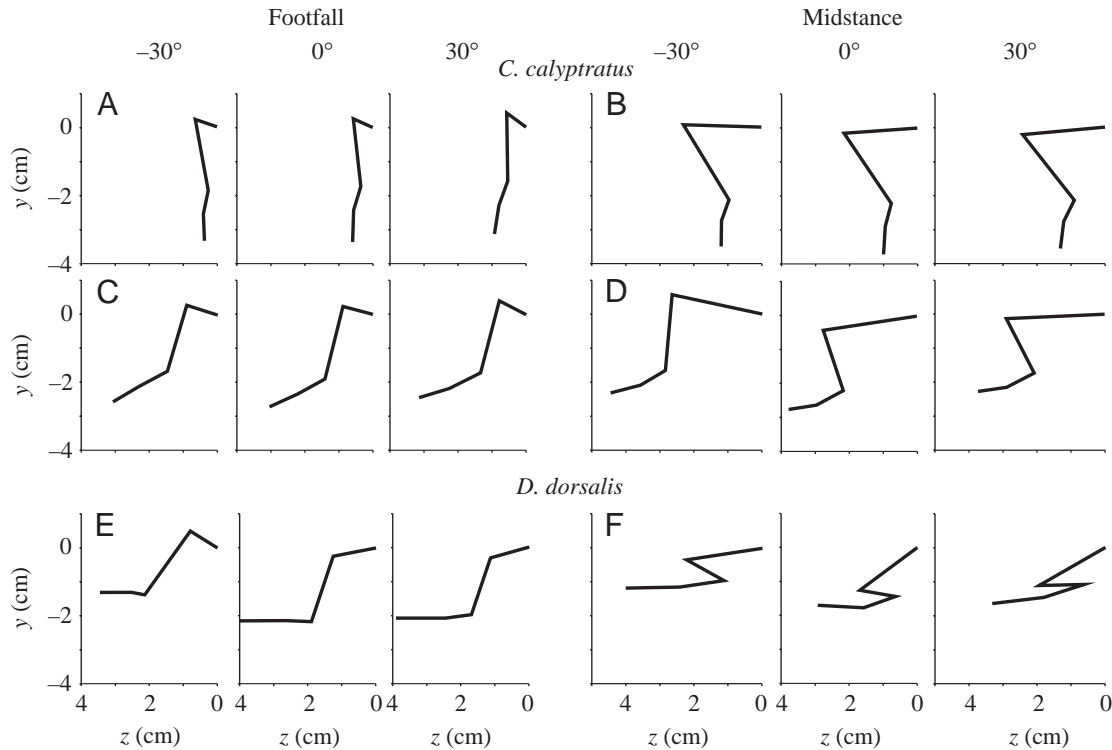


Fig. 3. Mean values of y and z of the right hindlimb relative to the hip ($y=0$, $z=0$) for each combination of species (rows; A–D, *C. calyptratus*; E, F, *D. dorsalis*), surface (rows; A, B, 2.4 cm perch; C–F, treadmill), and incline (columns; -30° , 0° , 30°). From proximal to distal the endpoints of the line segments represent the hip, knee, ankle, distal end of the metatarsala and tip of the toe. Sample sizes range from 14 to 16 strides (from four individuals per species) for each combination of the three factors. The projection onto the y – z plane corresponds to an anterior view. With the exception of downhill locomotion on the treadmill at footfall, the femur of *D. dorsalis* is more erect than that of *C. calyptratus*.

For *C. calyptratus*, the most dorsal positions (Y_{max}) of the ankle and the metatarsal relative to the hip were significantly greater on the treadmill than on the perch (Table 2). Incline

and surface also had significant interactive effects on the maximum dorsal positions of the ankle and metatarsal such that values were nearly invariant with incline on perches, whereas

Table 2. F values from three-way ANOVAs performed separately on each kinematic variable that indicates maximum and minimum linear positions and displacements in the x , y and z dimensions relative to the hip during the stride cycle for *C. calyptratus* moving on a perch and treadmill

Anatomical location	X_{min}	X_{max}	ΔX	Y_{min}	Y_{max}	ΔY	Z_{min}	Z_{max}	ΔZ
Incline (2,6)									
Knee	7.1*	20.5**	1.0	2.3	1.2	1.1	1.3	1.7	3.9
Ankle	5.6*	6.7*	0.4	2.7	2.1	0.5	2.3	1.9	2.5
Metatarsal	4.2	8.7**	0.2	2.7	1.2	0.2	1.1	2.5	2.3
Surface (1,3)									
Knee	4.3	66.4**	12.1	3.9	9.1	0	5.4	0.1	13.8*
Ankle	0.1	32.0*	7.7	2.2	55.6**	1.0	76.5**	6.3	1.5
Metatarsal	1.3	50.4**	0.9	11.2*	21.5**	0.9	98.8**	15.8*	5.5
Incline×Surface (2,6)									
Knee	3.9	0.2	3.7	1.5	1.6	0.6	0	2.1	0.3
Ankle	3.9	0.2	4.0	0.3	14.6**	1.7	1.0	0.3	0.3
Metatarsal	2.6	0.3	2.5	0.1	8.9**	2.5	3.9	0.5	1.0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ANOVA effects and degrees of freedom (in parentheses) are given above each group of rows indicating different locations within the hindlimb.

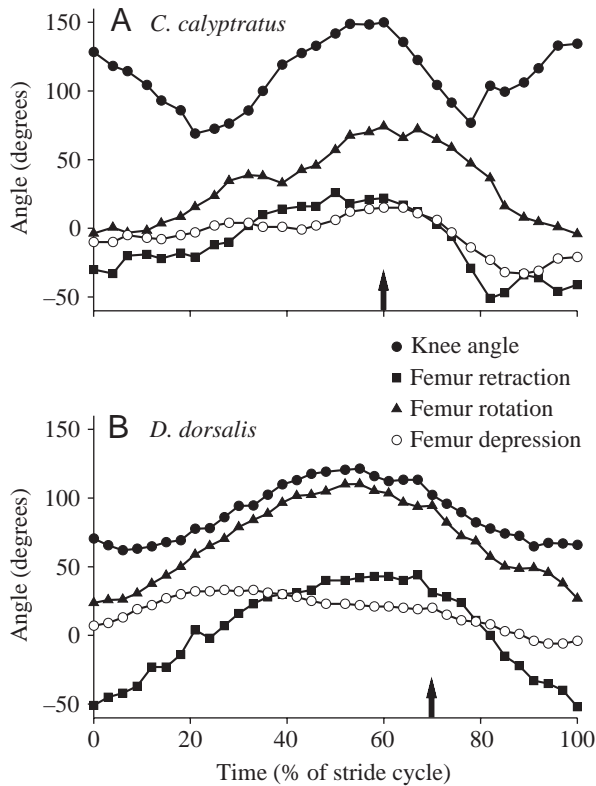


Fig. 4. Angles of the knee joint, femur retraction, femur rotation and femur depression *versus* time (as a percentage of stride cycle) for a single stride for *C. calypttratus* (A) and *D. dorsalis* (B) moving on a level treadmill. The arrows indicate the end of stance, and footfall occurs at time 0%. The speeds for *C. calypttratus* and *D. dorsalis* were approximately 17 cm s⁻¹ and 50 cm s⁻¹, respectively.

the level values on the treadmill were substantially less than the values for both inclines (Table 2).

The most medial positions (Z_{\min}) of the ankle and metatarsal were also significantly affected by surface (Table 2). The ankle and foot of *C. calypttratus* were positioned much more medially when moving on the perch rather than the treadmill (Figs 3, 6D). The negative mean values of Z_{\min} for the perch indicate that the ankle and foot were momentarily medial to the hip on the perch (during stance), whereas these structures were always lateral to the hip for locomotion on the treadmill (Figs 5, 6D). The maximum lateral values (Z_{\max}) of the metatarsal and the lateral excursion (ΔZ) of the knee were both significantly greater for treadmill locomotion than for perch locomotion (Table 2; Fig. 5A,B).

Incline and surface each significantly affected three of the 15 angular variables for *C. calypttratus*, and only two variables had significant interactive effects of incline and surface (Table 3). Maximum femur depression of *C. calypttratus* changed significantly with incline, and the mean values for downhill locomotion on the treadmill ($13 \pm 3^\circ$) were less than half those for uphill treadmill locomotion ($28 \pm 2^\circ$) (Fig. 7B). Surface significantly affected minimum femur rotation (Table 3). Minimum femur rotation on the perch approximated zero, indicating that the femur and tibia were in a vertical plane, whereas the negative values for the treadmill indicate that the ankle was anterior and medial to the vertical plane passing through the femur (Fig. 7A). For *C. calypttratus*, the femur was protracted significantly more on the level surface compared to the inclined surfaces (Fig. 7C), and the excursions of femur retraction were significantly greater for perch locomotion compared to that on the treadmill (Table 3). The

Table 3. F values from three-way ANOVAs performed separately on each angular kinematic variable

Dependent variable	<i>C. calypttratus</i> + <i>D. dorsalis</i>			<i>C. calypttratus</i> only		
	Species d.f.=1,6	Incline d.f.=2,12	Species×Incline d.f.=2,12	Incline d.f.=2,6	Surface d.f.=1,3	Incline×Surface d.f.=2,6
Knee (ff)	90.2***	3.7	3.4	1.4	0.9	3.2
Knee (es)	41.2***	7.5**	3.2	4.0	7.5	6.2*
Ankle (ff)	218.2***	1.1	1.2	0.9	12.6*	0.2
Ankle (es)	9.1*	0.3	0.1	0.1	5.9	1.8
Toe orientation (ff)	17.4**	2.3	0.2			
Pelvic rotation	21.0**	1.8	0.6	0.5	0.5	1.0
Max. femur retraction	0	6.4*	3.7	3.5	9.9	4.5
Min. femur retraction	3.2	3.1	2.3	6.2*	8.6	0.7
Retraction excursion	2.9	2.9	5.4*	2.1	11.7*	9.0*
Max. femur depression	2.9	17.5***	2.1	11.7**	6.1	2.2
Min. femur depression	316.1***	7.2**	8.1**	0.8	0.1	0.5
Depression excursion	16.9**	2.8	3.4	4.8	3.5	1.9
Max. femur rotation	10.4*	12.1**	3.0	2.0	0.3	1.0
Min. femur rotation	78.3***	7.3**	2.1	5.7*	76.5**	0.9
Rotation excursion	8.1*	21.1***	6.7*	1.1	9.8	2.3

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Main effects and interaction terms are listed above each column.

d.f., degrees of freedom; ff, footfall; es, end stance; Max, maximum; Min, minimum.

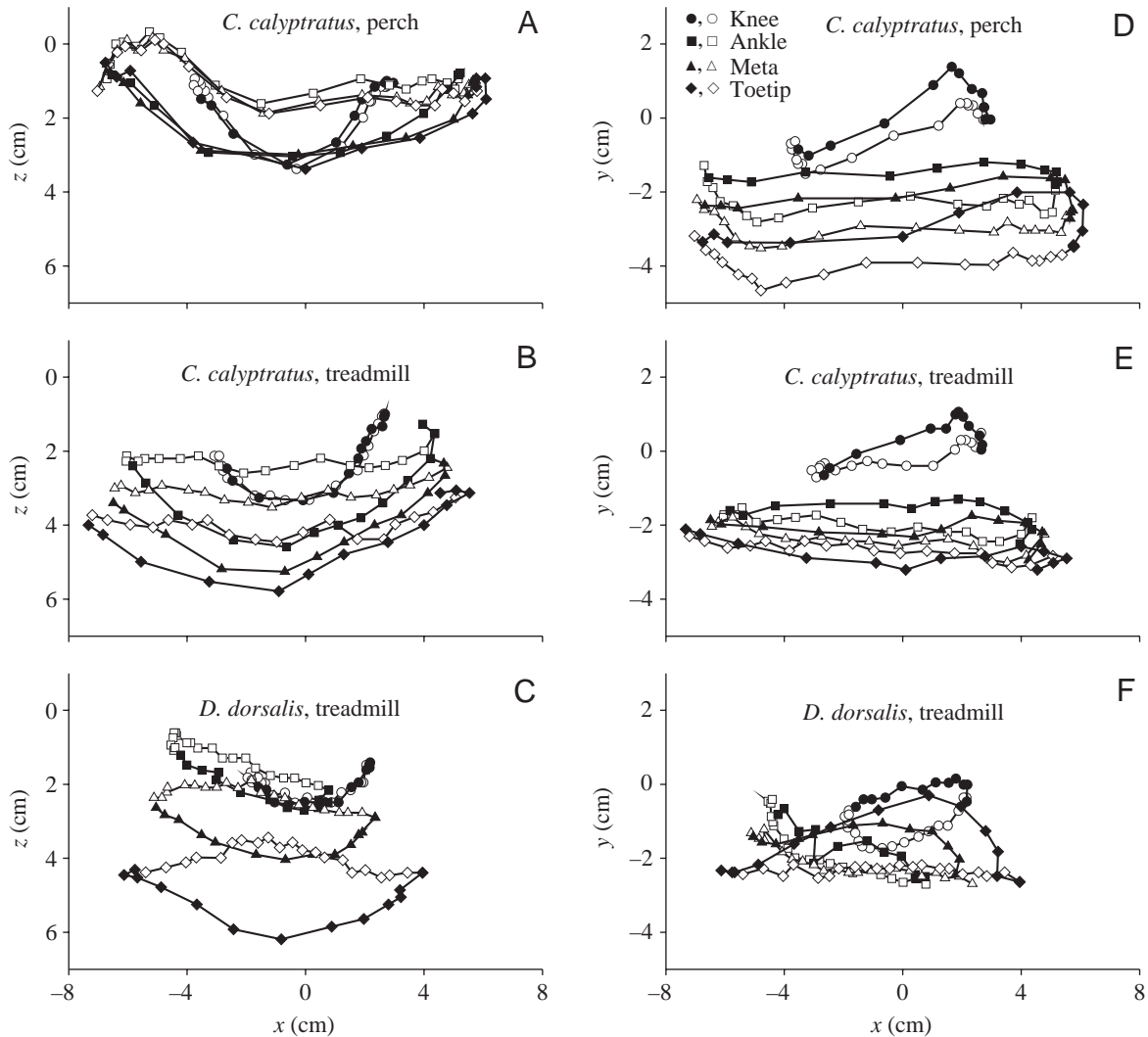


Fig. 5. Dorsal (A–C) and lateral (D–F) views of paths moved by different parts of the hindlimb relative to the hip (0, 0, 0) for *C. calypttratus* moving on a level perch (A,D) and a level treadmill (B,E) and *D. dorsalis* (C,F) moving on a level treadmill. Anterior is towards to the right of each plot. The closed and open symbols indicate the swing and stance phases, respectively. The overall direction of movement in the loops is clockwise.

ankle angles of *C. calypttratus* at footfall were significantly greater for locomotion on the perch compared to that on the treadmill (Table 3; Fig. 8C) such that the foot was dorsiflexed approximately 20° more on the treadmill compared to the perch.

Overall, the discriminant function (DF) analysis using each combination of surface and incline as the independent variable was highly significant (Wilks' $\lambda=0.03$, $F_{75,339}=4.7$, $P<0.001$). The first DF (DF1) cleanly separated locomotion on the perch from the treadmill in *C. calypttratus* (Fig. 9). All strides were correctly classified as being either on the perch or on the treadmill. At least 65% of strides for each combination of surface and incline were correctly classified, which indicates that the experimental combinations produced fairly distinct kinematics. The second DF (DF2) separated most of the uphill from downhill strides on the treadmill, but not on the perch (Fig. 9A). Y_{hip} at footfall, ankle angle at footfall, and maximum

femur rotation loaded the highest for DF1 (Table 4). Knee angle at footfall and at the end of stance, maximum femur retraction, and maximum femur depression loaded highest for DF2, and stride length, knee angle at the end of stance and maximum femur depression loaded highest for the third DF (DF3; Table 4).

C. calypttratus versus *D. dorsalis*

The main effects of species (*C. calypttratus* versus *D. dorsalis*) were not significant for the relative values of stride and step lengths and hip heights (Table 1). However, the species by incline interaction term was highly significant for minimum hip height as a result of the extremely low value of hip height for *D. dorsalis* on the downhill compared to the level and uphill values (Table 1; Fig. 6B).

Of the 36 relative values of maximal positions and excursions of x , y and z , 17 had significant main effects

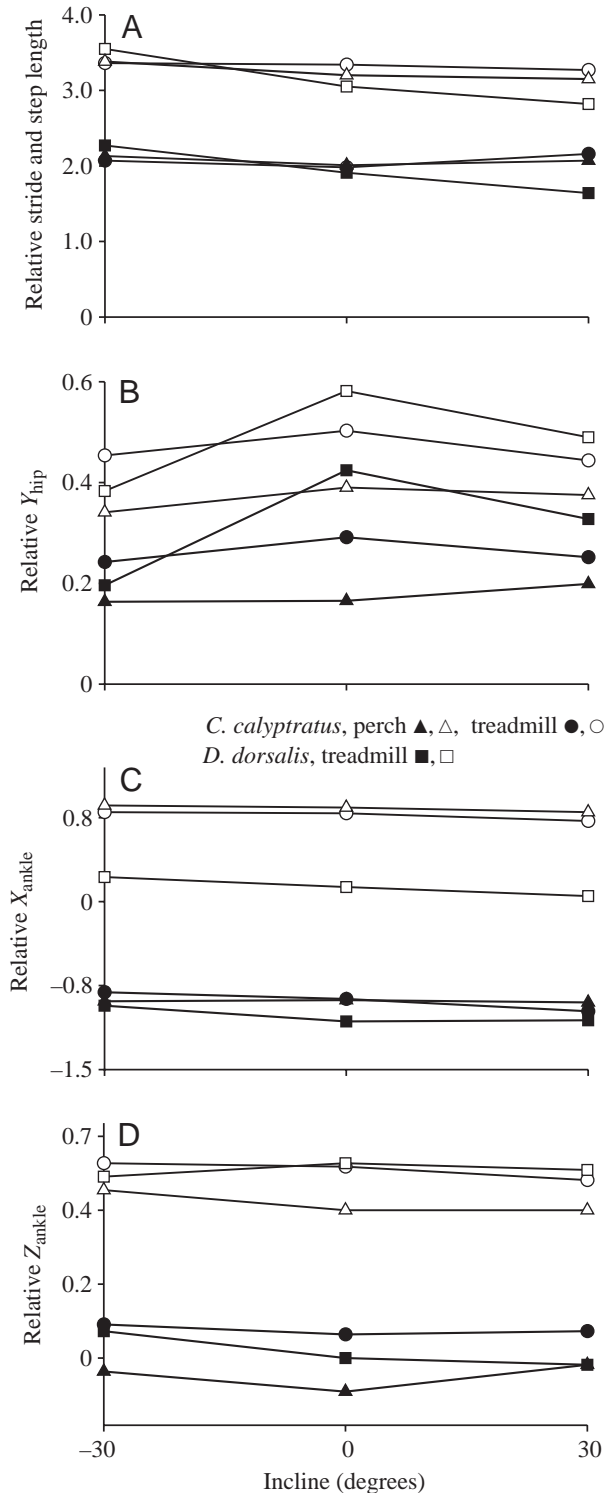


Fig. 6. Mean values of (A) relative stride length (open symbols) and step length (filled symbols), (B) relative minimum (filled symbols) and maximum (open symbols) hip height (Y_{hip}), (C) relative longitudinal position of the ankle (X_{ankle}) and (D) relative lateral position of the ankle (Z_{ankle}). Circles and triangles represent *C. calyptratus* on the treadmill and perch, respectively. Squares represent *D. dorsalis* on the treadmill. Tables 1, 2 and 4 summarize the results of the statistical comparisons among species, inclines and surfaces.

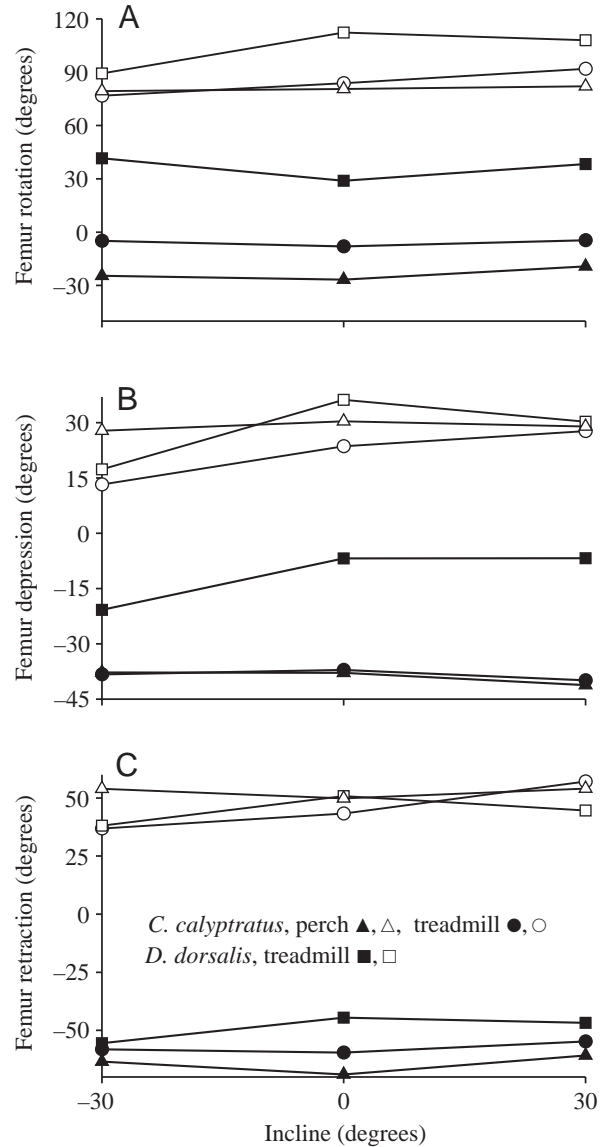


Fig. 7. Mean values of the femur angles of *C. calyptratus* on the perch (triangles) and treadmill (circle) and *D. dorsalis* on the treadmill (squares). Values include minimum (filled symbols) and maximum (open symbols) long-axis femur rotation (A), femur depression (B), and femur retraction (C). Table 3 summarizes the statistical comparisons among species, inclines and surfaces.

between the two species (Table 5). One of the most conspicuous differences between species was the very large value of the most anterior position of the distal limb of *C. calyptratus* compared to *D. dorsalis* (Table 5, X_{max}). The significantly greater longitudinal excursion of the distal limb of *C. calyptratus* compared to *D. dorsalis* was primarily a result of the large values of X_{max} of *C. calyptratus* rather than substantial variation in the most posterior position (Table 5). For all inclines the most ventral (Y_{min}) and dorsal (Y_{max}) relative positions of the knee for *C. calyptratus* were both significantly more dorsal than those of *D. dorsalis* (Table 5; Figs 5E,F, 10). The most ventral relative positions (Y_{min}) of all

Table 4. Loadings from a discriminant function (DF) analysis on 89 strides of uphill, downhill and level locomotion for *C. calypttratus* on the perch and treadmill

Variable	DF1	DF2	DF3
Stride length	-0.05	-0.14	0.54
Step length	-0.01	0.16	0.19
$Y_{\text{hip}}\text{footfall}$	-0.30	-0.16	-0.08
$\Delta Y_{\text{hip}}\text{total}$	-0.03	-0.22	-0.17
Knee angle (footfall)	0.07	-0.34	0.13
Knee angle (end stance)	-0.26	0.36	-0.38
Ankle angle (footfall)	0.32	0.12	0.27
Ankle angle (end stance)	-0.12	0.02	-0.11
Pelvic rotation	-0.01	-0.03	0.09
Min. femur retraction	-0.16	0.17	0.20
Max. femur retraction	0.08	0.45	-0.17
Min. femur depression	0	-0.18	-0.14
Max. femur depression	0.14	0.35	-0.46
Min. femur rotation	0.07	-0.25	0.23
Max. femur rotation	0.42	-0.02	-0.20

Loadings with a magnitude ≥ 0.3 are marked in bold type.

Canonical correlations for DF1, DF2 and DF3 were 0.93, 0.72 and 0.57, respectively.

$Y_{\text{hip}}\text{footfall}$, hip height at footfall; $\Delta Y_{\text{hip}}\text{total}$, total vertical oscillation of the hip for the entire stride cycle.

points along the limb had significant interactive effects of incline and species such that their magnitude was very small for *D. dorsalis* on the downhill compared to all the other combinations of species and incline (Table 5). For all inclines the most medial (Z_{min}) and lateral (Z_{max}) relative positions of the knee for *C. calypttratus* were both significantly more medial than those of *D. dorsalis* (Table 5).

For a total of 15 angular variables in Table 3, 11 had significant main effects between the two species. For all inclines, the knee of *C. calypttratus* was more extended at footfall and the end of stance than that of *D. dorsalis* (Fig. 8B), and the values of the ankle angle at footfall and pelvic rotation were also significantly greater for *C. calypttratus* (Table 3; Fig. 8A,C). Maximum femur elevation (as indicated by minimum femur depression) of *C. calypttratus* greatly exceeded that of *D. dorsalis* on all inclines and the significant species \times incline interaction indicated that values changed little with incline for *C. calypttratus*, whereas the downhill value for *D. dorsalis* differed substantially from the level and uphill values (Table 3; Fig. 7B). For all inclines, *C. calypttratus* had a significantly greater counterclockwise long-axis rotation of the femur (Table 3, minimum femur rotation) than that of *D. dorsalis* (Fig. 7A).

The second discriminant function analysis using each combination of species and incline as the independent variable was overall highly significant (Wilks' $\lambda=0.001$, $F_{80,336}=13.3$, $P<0.001$). All observations were correctly classified by the discriminant function analysis as belonging to each of the two species, which were cleanly separated by the first DF (Fig. 11). The four variables that loaded highest

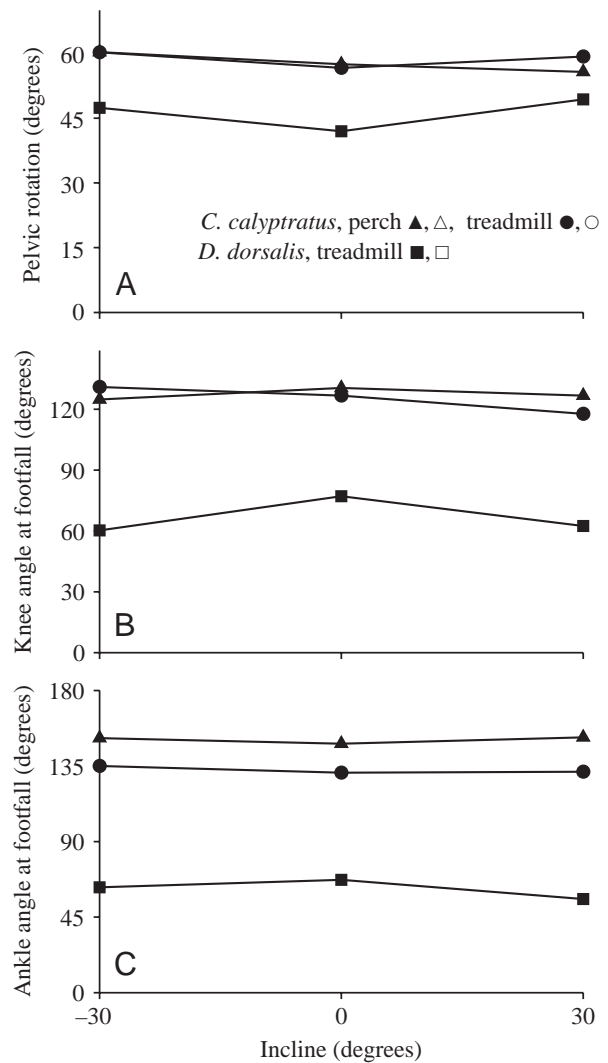


Fig. 8. Mean values of the two-dimensional angle of pelvic rotation (A), and the three-dimensional angles of knee angle at footfall (B) and ankle angle at footfall (C). Circles and triangles represent *C. calypttratus* on the treadmill and perch, respectively. Squares represent *D. dorsalis* on the treadmill. Table 3 summarizes the statistical comparisons among species, inclines and surfaces.

for DF1 were ankle and knee angles at footfall, minimum femur depression, and maximum femur rotation (Table 6). The second DF clearly separated the downhill strides from the other strides of *D. dorsalis* (Fig. 11A). The four variables that loaded highest for DF2 were relative Y_{hip} at footfall, minimum and maximum femur depression, and minimum femur rotation (Table 6). The third DF separated the downhill from uphill strides for *C. calypttratus* (Fig. 11B). The four variables that loaded highest for DF3 were relative step length, knee angle at end of stance, maximum femur retraction, and maximum femur depression (Table 6). Within *C. calypttratus* more strides (7 of 42) were misclassified according to incline than for *D. dorsalis* (1 of 48), hence the multivariate effects of incline on the kinematics of *C. calypttratus* were not as conspicuous as for *D. dorsalis*.

Table 5. F values from three-way ANOVAs performed separately on each kinematic variable that indicates maximum and minimum relative linear positions and displacements in the x, y and z dimensions relative to the hip during the stride cycle for *C. calypttratus* and *D. dorsalis* moving on a treadmill

Anatomical location	X_{\min}	X_{\max}	ΔX	Y_{\min}	Y_{\max}	ΔY	Z_{\min}	Z_{\max}	ΔZ
Incline (2,12)									
Knee	16.3***	1.4	17.4***	29.5***	22.5***	3.0	3.5	3.2	1.1
Ankle	17.5***	7.4**	1.0	38.8***	7.1**	23.0***	3.5	0.4	1.9
Metatarsal	13.9***	6.5*	0.7	26.9***	16.0***	3.7	13.4***	1.9	4.7*
Toetip	7.1**	4.7	0.5	22.7***	13.1***	3.4	3.7	1.6	0.3
Species (1,6)									
Knee	0.4	0.6	1.8	26.2**	49.8***	0.4	182.1***	16.9**	6.2*
Ankle	7.2*	456.4***	117.0***	5.6	1.7	3.8	6.3*	0	1.3
Metatarsal	7.9*	223.3***	49.6***	0.2	0.4	0	11.3*	1.2	1.1
Toetip	0	205.8***	27.7**	8.0*	17.3**	0.8	12.1*	1.5	1.7
Incline×Species (2,12)									
Knee	3.0	6.0*	1.9	6.5*	7.3**	3.1	6.5*	0.6	3.2
Ankle	2.8	1.1	3.0	13.9***	1.2	28.7***	1.4	0.5	2.7
Metatarsal	0.1	0.4	0.3	12.1**	1.7	2.0	5.4*	3.6	6.3*
Toetip	0.1	0.6	0.8	9.6**	1.2	0.8	1.9	3.9*	2.3

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ANOVA effects and degrees of freedom (in parentheses) are given above each group of rows indicating different locations within the hindlimb.

Discussion

Limb posture

The limb postures of different groups of vertebrates vary considerably. Traditionally, the limb postures for mammals and birds are considered erect, whereas those of salamanders and lizards are sprawling (Rewcastle, 1983; Russell and Bels, 2001). Diagrams illustrating sprawling limb posture typically show a horizontal femur, the knee directly lateral to the hip, a 90°-knee angle, and the ankle directly below the knee. The somewhat intermediate limb posture of crocodylians is considered 'semi-erect' as a result of the femur position (Reilly and Elias, 1998). In light of the continuum of variation in limb postures within vertebrates, such discrete categories may be of limited utility, as discussed at length in Gatesy (1991). However, determining where a particular species occurs along the continuum of variation may be useful.

Abu-Ghalyun et al. (1988) and Peterson (1984) previously suggested that the limb posture of chameleons is more erect than that of a generalized iguanian lizard. When chameleons are stationary the elbows and knees are sometimes close to the body and hence, in an anterior view, the limbs appear to be nearly in a parasagittal plane. Unlike most birds and mammals, during the locomotion of lizards retraction of the femur (in a horizontal plane) changes the position of the limb in a manner that effects the perception of limb erectness, based on an anterior view (Fig. 3). Presumably the position of the limb some time during the stance phase is of most interest for indicating erectness, but the time during stance for determining limb posture has never been standardized. As indicated by maximal femur depression (during stance) in our study, the anatomically generalized *D. dorsalis* had a more

erect limb than *C. calypttratus* on the level surface. Furthermore, two-dimensional anterior views of the limb at footfall and midstance illustrate that the femur of *D. dorsalis* usually has a steeper downward orientation than that of *C.*

Table 6. Loadings from a discriminant function analysis on 90 strides of uphill, downhill and level locomotion for both *C. calypttratus* and *D. dorsalis* on a treadmill

Variable	DF1	DF2	DF3
Relative stride length	0.29	-0.19	-0.04
Relative step length	0.25	-0.20	-0.34
Relative $Y_{\text{hipfootfall}}$	-0.06	0.39	0.15
Relative $\Delta Y_{\text{hiptotal}}$	0.05	0.02	0.19
Knee angle (footfall)	0.34	0.16	0.26
Knee angle (end stance)	0.22	0.16	-0.46
Ankle angle (footfall)	0.43	0.06	0
Ankle angle (end stance)	0.07	0.01	-0.11
Toe orientation (footfall)	0.13	0.13	-0.07
Pelvic rotation	0.12	-0.05	0.10
Min. femur retraction	-0.08	0.18	-0.09
Max. femur retraction	0.01	0.19	-0.48
Min. femur depression	-0.42	0.38	0.26
Max. femur depression	-0.06	0.38	-0.38
Min. femur rotation	0.13	-0.31	0.28
Max. femur rotation	0.39	0.23	0.08

Loadings with a magnitude ≥ 0.3 are marked in bold type.

Canonical correlations for DF1, DF2 and DF3 were 0.99, 0.91 and 0.70, respectively.

$Y_{\text{hipfootfall}}$, hip height at footfall; $\Delta Y_{\text{hiptotal}}$, total vertical oscillation of the hip for the entire stride cycle.

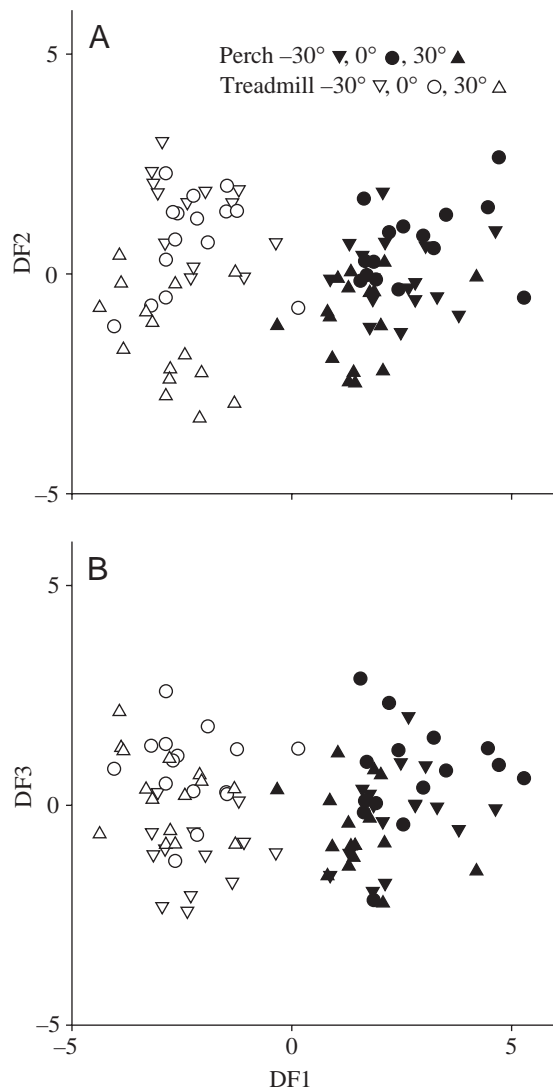


Fig. 9. (A) Discriminant function 1 (DF1) versus discriminant function 2 (DF2) and (B) DF1 versus discriminant function 3 (DF3), from an analysis of 15 kinematic variables for *C. calyptratus* moving on a perch (filled symbols) and a treadmill (open symbols). Each point is for an individual stride. Table 5 provides the canonical loadings for the discriminant functions.

calyptratus (Fig. 3). During swing *C. calyptratus* also elevated the femur substantially more than *D. dorsalis*. Thus, both our three- and two-dimensional data do not support previous assertions that chameleons have a relatively upright limb posture for a lizard.

The kinematic variables used to quantify limb erectness are not standardized. One approach is to determine the two-dimensional angle between the proximal limb segment and a vertical reference line as seen in a two-dimensional anterior view. Limbs that appear to be vertical in an anterior view are usually considered erect, but an 'erect' limb may not be straight. Thus, the 'erect' limbs of many birds and mammals are 'crouched' to varying degrees, depending on both the extent to which the femur is not vertical and the amounts of

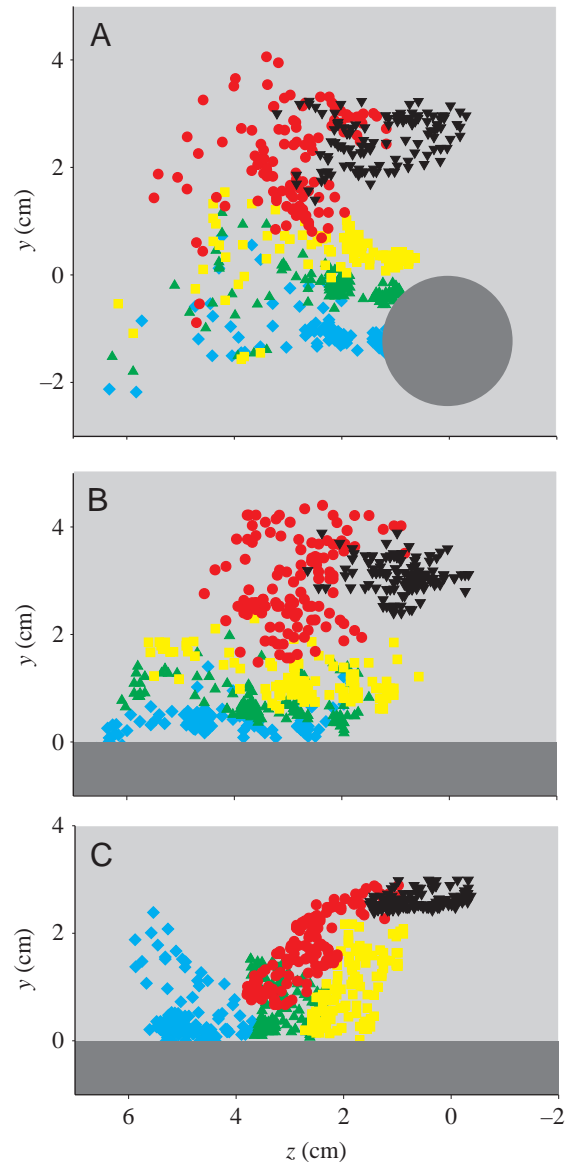


Fig. 10. Anterior views of the position of the hip (black inverted triangles), knee (red circles), ankle (yellow squares), metatarsal (green triangles), and toe tip (blue diamonds) for a single *C. calyptratus* moving on a level perch (A) and a level treadmill (B), and a single *D. dorsalis* moving on a level treadmill (C). Each panel is a composite of four strides, with approximately 25 points per stride. The mean position traveled by the mid-dorsal line was standardized to $z=0$.

flexion of the joints within the limb (Biewener, 1989; Gatesy and Biewener, 1991).

If the femur of a lizard is protracted 90° and the femur is only slightly depressed, then one would conclude from a two-dimensional anterior-view data that the limb is erect (Fieler and Jayne, 1998). The amounts of femur protraction did not differ significantly between *C. calyptratus* and *D. dorsalis*. However, the large amount of pelvic rotation in *C. calyptratus* combined with femur protraction resulted in the femur being nearly parallel to the x -axis (Fig. 1A), creating the impression, from

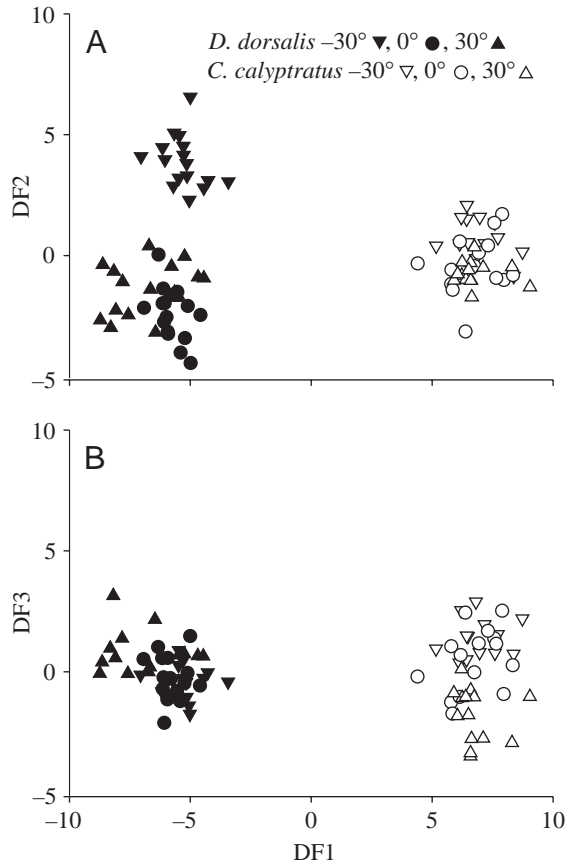


Fig. 11. (A) Discriminant function 1 (DF1) versus discriminant function 2 (DF2) and (B) DF1 versus discriminant function 3 (DF3), from an analysis of 16 kinematic variables for *D. dorsalis* (filled symbols) and *C. calypttratus* (open symbols) moving on a treadmill. Each point is for an individual stride. Table 6 provides the canonical loadings for the discriminant functions.

an anterior view, that the limb is relatively erect at footfall, although it is highly crouched rather than straight (Fig. 3). However, the femur of *C. calypttratus* is not usually depressed (i.e. knee is not lower than the hip) at footfall, and at mid-stance the knee is nearly lateral to the hip (Figs 1B, 3), similar to most descriptions of sprawling posture. Unlike typical sprawling posture, the knee of *C. calypttratus* at mid-stance on the perch is flexed at an acute angle, resulting in the foot being substantially medial to the knee rather than directly beneath it (Fig. 3).

Sceloporus clarkii is a lizard that frequently climbs on steep flat surfaces and has a very sprawling limb posture (Reilly and Delancey, 1997). For much of stance the femur and tibia of *S. clarkii* are nearly parallel to the horizontal plane and the foot is often lateral to the knee (Reilly and Delancey, 1997). When moving on inclines, *D. dorsalis* has a greater amount of femur rotation at footfall, which orients the tibia more nearly parallel to a horizontal plane (Jayne and Irschick, 1999). Many arboreal geckoes and anoline lizards have specialized toe morphologies that facilitate their adherence to steep surfaces (Irschick et al., 1996), and the plane formed by their femur and tibia is often

at a shallow angle relative to the locomotor surface (although quantitative data are lacking). Thus, within lizards, the more nearly vertical orientation of the femur–tibia plane (femur rotation near zero) in early stance of *C. calypttratus* in this study is strikingly different from other arboreal specialists and some generalists on steep surfaces.

Specializations of chameleons

Arboreal habitats pose many functional challenges, including (1) bridging gaps between branches, (2) traveling on perches with small diameter and (3) avoiding obstructions created by the clutter of branches. Two key morphological specializations of chameleons that probably facilitate accomplishment of some of these tasks are the prehensile feet and tail. Behavioral specializations of chameleons that facilitate arboreal locomotion include a slow, but stable, walking gait (Peterson, 1984). Many species of arboreal animals bridge gaps by jumping (Cartmill, 1985), but chameleons do not. Thus, the reaching ability of chameleons is likely to be important.

Peterson (1984) found that chameleons have an increased longitudinal translation of the shoulder joint compared to other lizards, which enables chameleons to reach farther to bridge gaps. We also found that chameleons have an unusually large forward reach of the hindlimb, which is a result of large amounts of femur protraction and knee extension rather than mobility of the hip joint. Besides bridging gaps, increased forward reach can contribute to increased step length. Unlike the running gaits of many species of lizards, which have a prolonged suspended phase (Jayne and Irschick, 1999; Irschick and Jayne, 1999b), we have never observed a suspended phase for *C. calypttratus*. Thus, longitudinal displacement during stance is the primary determinant of stride length of *C. calypttratus*.

The different orientation of the hindlimb of *C. calypttratus* compared to other lizards during stance may indicate a different reliance on pulling versus pushing to move the body forward from the limb contacting the ground. The extreme forward reach of the hindlimb of *C. calypttratus*, combined with considerable flexion of the knee (Fig. 4A) during early stance, may indicate a reliance on actively pulling the body forward rather than simply vaulting over a relatively straight limb. In contrast, only a modest amount of knee flexion occurs during early stance of many terrestrial lizards (Fig. 4B), and the tibia is often nearly perpendicular to the ground during early stance (Jayne and Irschick, 1999; Irschick and Jayne, 1999b). The extreme forward reach of *C. calypttratus* at the beginning of stance may also result in a ground reaction force with a large posterior-directed component that could impede forward progression. In contrast, dorsoventrally flattened arboreal lizards, such as anoles and geckos, may be more reliant on pushing with the hindlimbs, since the tibia at footfall forms an acute angle with the locomotor surface and the ankle is markedly posterior to the knee. Thus, future comparative data on passive versus active mechanisms of knee flexion and the orientation of the ground reactive force in early stance of lizards would be very informative.

The prehensile feet of chameleons allow them to cling tenaciously to small diameter perches (Losos et al., 1993), which may have some advantages for locomotion not previously considered. For example, if active knee flexion of *C. calypttratus* pulls the body forward when on level and uphill surfaces, then knee flexion would tend to lift the foot up from the locomotor surface. However, *C. calypttratus* grasps the locomotor surface immediately after footfall, which could facilitate use of a pulling mechanism for generating propulsive forces. In contrast, extending the limbs to push the body forward should add to the normal force with the locomotor surface and hence enhance traction and reduce the need to grasp the surface.

For measurements of the pectoral girdle and mid trunk, Peterson (1984) previously characterized *C. calypttratus* as having less axial undulation than the more generalized iguanian lizard, *Agama agama*. Peterson (1984) estimated that the increased amount of undulation of *A. agama* nearly doubled its importance to contributing to step length in this species compared to *C. calypttratus*. Unexpectedly, we found that the pelvic rotation of *C. calypttratus* was approximately twice that of *D. dorsalis* moving at an equivalent speed. These different conclusions regarding the relative amounts of axial undulation in *C. calypttratus* could be the result of longitudinal differences in bending, but no previous study has quantified axial bending of *C. calypttratus* along its entire length. Among mammals, the subfamily of lorises, within the primates, are exceptional for using unusually large ($\pm 30^\circ$) amounts of pelvic rotation in the horizontal plane during locomotion (Demes et al., 1990). Lorises have additional convergent similarities with *C. calypttratus*, including prehensile feet and behavioral specializations for moving slowly on slender branches (Demes et al., 1990).

The laterally compressed bodies of chameleons compared to most generalized iguanian lizards may allow the limbs to be more medial during certain portions of the stride. The thigh of *C. calypttratus* was often protracted so much that its medial surface touched the side of the body (Fig. 1A,C). Thus, *C. calypttratus* might be able to protract the femur more than if its body had considerable lateral bulges. For a particular incline at footfall, the femur of *C. calypttratus* was commonly protracted 10° more than that of *D. dorsalis*, but these differences between species were not statistically significant (Fig. 7C; Table 3). Pelvic rotation is an additional mechanism for moving the knee medially, and the combination of pelvic rotation and femur protraction of *C. calypttratus* was such that its thigh was nearly parallel to the *x*-axis when moving on the round perch (Fig. 1A,C).

Minimizing the width of the swath created by a lizard as it moves through the environment should facilitate avoiding obstructions in cluttered arboreal habitats. Unexpectedly, the lateral space required for *C. calypttratus* on the level perch and *D. dorsalis* on the level treadmill were approximately the same (Fig. 10). The *C. calypttratus* and *D. dorsalis* used in our experiments had very similar hip-to-toe lengths. The tip of the toe occurred in the most lateral portion of the swath created by

D. dorsalis, whereas the knee of *C. calypttratus* often occurred in the most lateral portion of the swath (Fig. 10A,C). Some of these differences between the swaths created by *D. dorsalis* and *C. calypttratus* are the result of a much greater heel-to-toe distance and lateral orientation of the foot of *D. dorsalis* (Fig. 5C).

Effects of incline and surface

Inclines affected the hindlimb movements of *C. calypttratus* minimally compared to the terrestrial species, *D. dorsalis*. For a total of 64 variables quantified by Jayne and Irschick (1999) for *D. dorsalis* on a flat treadmill, 47 had significant main effects of incline. Our study is the first to determine the effects of incline on the three-dimensional hindlimb kinematics of an arboreal lizard. For a total of 47 kinematic variables quantified for *C. calypttratus*, incline had less widespread main effects than surface (5 versus 15).

D. dorsalis increases the amount of pelvic rotation when moving uphill which may indicate an increased reliance on axial structures to provide propulsive forces (Jayne and Irschick, 1999). In contrast, chameleons did not increase pelvic rotation when moving uphill, and may rely primarily on modifications of appendicular muscle activity for increased force. Perhaps, the large amount of pelvic rotation in *C. calypttratus* on all surfaces indicates that no further pelvic rotation is possible on uphill inclines.

The detrimental effects of decreased surface diameter on the sprinting speeds of *Anolis* lizards are well documented (Losos and Sinervo, 1989; Losos and Irschick, 1996;), but previous kinematic data of lizards moving on perches of varying diameter are lacking. However, Schmitt (1994, 1998) quantified the effects of diameter on the three-dimensional kinematics of the forelimb for the locomotion of some species of primates.

A common response of diverse vertebrate taxa to narrow perches and inclines is to reduce the heights of the hip and shoulder relative to the locomotor surface and hence lower the center of mass relative to the locomotor surface. Lowering the center of mass should decrease the torques that tend to topple an animal over when on a round perch, or make it fall away from a steeply inclined surface (Cartmill, 1985). The hip heights of *C. calypttratus* decreased significantly on round perches compared to flat surfaces but were unaffected by incline (Table 1; Fig. 6B). In contrast to *C. calypttratus*, the hip heights of *D. dorsalis* decreased significantly on inclined surfaces compared to the level surface (Jayne and Irschick, 1999). The mechanisms for changing hip height in these two species of lizards differ. Reduced hip height was largely a result of greater knee flexion during mid-stance for *C. calypttratus* on perches, and increased clockwise long-axis (right lateral view) femur rotation for *D. dorsalis* on inclines (Jayne and Irschick, 1999).

Hip or shoulder heights also decrease for monkeys on narrow round perches compared to flat surfaces (Schmitt, 1998), and for monkeys (Vilensky et al., 1994) and cats (Carlson-Kuhta et al., 1998; Smith et al., 1998) on inclines

compared to level surfaces. Hip and shoulder heights are lowered in monkeys (Vilensky et al., 1994; Schmitt, 1998) and cats by increased flexion of the elbow or knee joints, and cats also increase hip flexion to lower hip height (Carlson-Kuhta et al., 1998; Smith et al., 1998). When the knee is anterior to the hip, retracting the femur in a parasagittal plane will increase hip height unless flexion at other joints compensates for this movement. Thus, for many mammals a key mechanism of propulsion also affects hip height and oscillations in hip height. In contrast, when amphibians and reptiles retract the femur in a horizontal plane, this mechanism of propulsion has little effect on hip height.

The initial position of a limb bone during stance also has important consequences for the extent to which a particular rotational movement will cause displacements perpendicular to the locomotor surface. For example, the component of movement perpendicular to the locomotor surface resulting from femur retraction in mammals will be maximized when the initial position of the femur is parallel to the locomotor surface. Similarly, for long-axis femur rotation in sprawling limbed animals, the component of movement perpendicular to the locomotor surface will be maximized when the plane containing the femur and the tibia is parallel to the horizontal surface. Thus, two species could have identical angular excursions but profound differences in height and oscillation in height above the locomotor surface, as well as differences in longitudinal excursions.

The angular excursions of humeral and femoral retraction in primates are usually larger than those of other mammalian groups (Larson et al., 2000, 2001), and chameleons have a significantly greater excursion of femoral retraction than a terrestrial lizard (desert iguana). Furthermore, the combination of the initial limb position and the angular excursions of the chameleon hindlimb are such that chameleons have a greater relative longitudinal excursion of the distal limb (ΔX_{ankle} in Table 5; Fig. 6C) than that of desert iguanas. Thus, relative to terrestrial species, arboreal species may be notable for having kinematics that maximize the longitudinal displacement that occurs during stance.

Some additional variation in knee angles associated with inclines differs between chameleons and terrestrial lizards and mammals. For example, as cats (Carlson-Kuhta et al., 1998) and desert iguanas (Jayne and Irschick, 1999) move on steeper inclines, the values of knee angle at footfall are smaller (more flexed) than those for the level surface. In contrast, the angles of the knee and ankle (at footfall) of chameleons did not change significantly with incline.

Inclines commonly appear to affect the longitudinal position of the foot relative to where the limb articulates with the girdle. The most anterior and posterior positions of the ankle and foot of *C. calyptratus* occurred on the downhill and uphill surfaces, respectively. When *D. dorsalis* moves downhill, changes in femur retraction and rotation tend to position the foot more anterior relative to the hip than when moving on a level surface, and for faster speeds of uphill locomotion these movements contribute to a more posterior location of the foot

relative to the hip (Jayne and Irschick, 1999). Similarly, when cats move up and down inclines, the distal limb shifts posterior and anterior, respectively. Perhaps, the more posterior orientation of the distal limb facilitates pushing the body up inclines, whereas the more anterior position on downhill may facilitate the animal's deceleration (Carlson-Kuhta et al., 1998).

This research was supported by NSF grant IBN 9983003 to D. J. Irschick and B.C.J. The acquisition of a high-speed video system was supported by NSF grant BIR 9217409 to B.C.J. R. German, D. Gist, M. Maynard, and A. Horner provided valuable comments on early drafts of the manuscript.

References

- Abu-Ghalyun, Y., Greenwald, L., Hetherington, T. E. and Gaunt, A. S. (1988). The physiological basis of slow locomotion in chameleons. *J. Exp. Zool.* **245**, 225-231.
- Biewener, A. (1989). Scaling body support in mammals: Limb posture and muscle mechanics. *Science* **245**, 45-48.
- Carlson-Kuhta, P., Trank, T. V. and Smith, J. L. (1998). Forms of forward quadrupedal locomotion. II. A comparison of posture, hindlimb kinematics, and motor patterns for upslope and level walking. *J. Neurophysiol.* **79**, 1687-1701.
- Carothers, J. H. (1986). An experimental confirmation of morphological adaptation: toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution* **40**, 871-874.
- Cartmill, M. (1974). Pads and claws in arboreal locomotion. In *Primate Locomotion* (ed. F. A. Jenkins), pp. 45-83. New York: Academic Press.
- Cartmill, M. (1985). Climbing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 73-88. Cambridge: Belknap Press.
- Demes, B., Jungers, W. L. and Nieschalk, U. (1990). Size- and speed-related aspects of quadrupedal walking in slender and slow lorises. In *Gravity, Posture and Locomotion in Primates* (ed. F. K. Jouffroy, M. H. Stack and C. Niemitz), pp. 175-198. Florence: Il Sedicesimo.
- Farley, C. T. and Emshwiller, M. (1996). Efficiency of uphill locomotion in nocturnal and diurnal lizards. *J. Exp. Biol.* **199**, 587-592.
- Fielor, C. L. and Jayne, B. C. (1998). Effects of speed on the hindlimb kinematics of the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **201**, 609-622.
- Gatesy, S. M. (1991). Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *J. Zool. Lond.* **224**, 577-588.
- Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool. Lond.* **224**, 127-147.
- Goslow, G. E. and Jenkins, F. A. (1983). The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exanthematicus*). *J. Morphol.* **175**, 195-216.
- Higham, T. E., Davenport, M. S. and Jayne, B. C. (2001). Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards. *J. Exp. Biol.* **204**, 4141-4155.
- Huey, R. B. and Hertz, P. E. (1982). Effects of body size and slope on sprint speed of a lizard *Stellio (Agama) stellio*. *J. Exp. Biol.* **97**, 401-409.
- Huey, R. B. and Hertz, P. E. (1984). Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* **110**, 113-123.
- Irschick, D. J., Austin, C. C., Petren, K., Fisher, R. N., Losos, J. B. and Ellers, O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* **59**, 21-35.
- Irschick, D. J. and Jayne, B. C. (1998). Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Biol.* **201**, 273-287.
- Irschick, D. J. and Jayne, B. C. (1999a). A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. *Physiol. Biochem. Zool.* **72**, 44-56.
- Irschick, D. J. and Jayne, B. C. (1999b). Comparative three-dimensional

- kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.* **202**, 1047-1065.
- Jayne, B. C. and Ellis, R. V.** (1998). How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia*. *Anim. Behav.* **55**, 1115-1130.
- Jayne, B. C. and Irschick, D. J.** (1999). Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). *J. Exp. Biol.* **202**, 143-159.
- Jayne, B. C. and Irschick, D. J.** (2000). A field study of incline use and preferred speeds for the locomotion of lizards. *Ecology* **81**, 2969-2983.
- Jenkins, F. A.** (1974). *Primate Locomotion*. New York: Academic Press.
- Larson, S. G., Schmitt, D., Lemelin, P. and Hamrick, M.** (2000). Uniqueness of primate forelimb posture during quadrupedal locomotion. *Am. J. Phys. Anthropol.* **112**, 87-101.
- Larson, S. G., Schmitt, D., Lemelin, P. and Hamrick, M.** (2001). Limb excursion during quadrupedal walking: how do primates compare to other mammals? *J. Zool. Lond.* **255**, 353-365.
- Losos, J. B. and Irschick, D. J.** (1996). The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.* **51**, 593-602.
- Losos, J. B. and Sinervo, B.** (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* **145**, 23-30.
- Losos, J. B., Walton, B. M. and Bennett, A. F.** (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Funct. Ecol.* **7**, 281-286.
- Mattingly, W. B. and Jayne, B. C.** (in press). Resource use in arboreal habitats: structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, in press.
- Peterson, J. A.** (1984). The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zool. Lond.* **202**, 1-42.
- Reilly, S. M. and Delancey, M. J.** (1997). Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. *J. Exp. Biol.* **200**, 753-765.
- Reilly, S. M. and Elias, J. A.** (1998). Locomotion in *Alligator mississippiensis*: Kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. *J. Exp. Biol.* **201**, 2559-2574.
- Rewcastle, S. C.** (1983). Fundamental adaptations in the lacertilian hind limb: A partial analysis of the sprawling limb posture and gait. *Copeia* **1983**, 476-487.
- Roberts, T. J., Marsh, R. L., Weyland, P. G. and Taylor, C. R.** (1997). Muscular force in running turkeys: The economy of minimizing work. *Science* **275**, 1113-1115.
- Russell, A. P.** (2002). Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Int. Comp. Biol.* **42**, 1154-1163.
- Russell, A. P. and Bels, V.** (2001). Biomechanics and kinematics of limb-based locomotion in lizards: review, synthesis and prospectus. *Comp. Biochem. Physiol.* **131A**, 89-112.
- Schmitt, D.** (1994). Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. *J. Hum. Evol.* **26**, 441-457.
- Schmitt, D.** (1998). Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In *Primate Locomotion: Recent Advances* (ed. E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry), pp. 175-200. New York: Plenum Press.
- Smith, J. L., Carlson-Kuhta, P. and Trank, T. V.** (1998). Forms of forward quadrupedal locomotion. III. A comparison of posture, hindlimb kinematics, and motor patterns for downslope and level walking. *J. Neurophysiol.* **79**, 1702-1716.
- Strasser, E., Fleagle, J., Rosenberger, A. and McHenry, H.** (1998). *Primate Locomotion: Recent Advances*. New York: Plenum Press.
- Vilensky, J. A., Moore, A. M. and Libii, J. N.** (1994). Squirrel monkey locomotion on an inclined treadmill: implications for the evolution of gaits. *J. Hum. Evol.* **26**, 375-386.
- Zaaf, A., Van Damme, R., Herrel, A. and Aerts, P.** (2001). Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and a climbing gecko. *J. Exp. Biol.* **204**, 1233-1246.
- Zar, J. H.** (1996). *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.