

EFFECTS OF INCLINE AND SPEED ON THE THREE-DIMENSIONAL HINDLIMB KINEMATICS OF A GENERALIZED IGUANIAN LIZARD (*DIPSOSAURUS DORSALIS*)

BRUCE C. JAYNE* AND DUNCAN J. IRSCHICK

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

*e-mail: jaynebc@email.uc.edu

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Summary

Lizards commonly move on steep inclines in nature, but no previous studies have investigated whether the kinematics of the limbs of lizards differ on inclined surfaces compared with level surfaces. Therefore, we examined how the kinematics of the hindlimb were affected by both incline (downhill 30°, level and uphill 30°) and different speeds of steady locomotion (50–250 cm s⁻¹) in the morphologically generalized iguanian lizard *Dipsosaurus dorsalis*. On the uphill surface, the strides of lizards were shorter and quicker than those at a similar speed on the level and downhill surfaces. A multivariate analysis revealed that the kinematics of locomotion on all three inclines were distinct, but several kinematic features of locomotion on the downhill surface were especially unique.

For example, downhill locomotion had the lowest angular excursions of femur rotation, and the knee and ankle were flexed more at footfall which contributed to a very low hip height. For *D. dorsalis*, changes in knee and ankle angles on the uphill surface were similar to those described previously for mammals moving up inclines, despite fundamental differences in limb posture between most mammals and lizards. Several features of the kinematics of *D. dorsalis* suggest that a sprawling limb enhances the ability to move on inclines.

Key words: lizard, *Dipsosaurus dorsalis*, kinematics, hindlimb, locomotion, incline.

Introduction

When moving in their natural habitats, most species of terrestrial animal commonly encounter surfaces of varying incline. Small animals especially must climb up and down obstacles in the environment which relatively large animals such as humans could simply step over. In every-day experience, humans commonly encounter the sensation of increased muscular effort being required to move up inclines and the need to use limbs as brakes to control the speed of downhill locomotion. Limited data for taxonomically diverse species have also found that the energetics, patterns of muscle activity and kinematics may change with the incline of the locomotor surface (Farley and Emshwiller, 1996; Full and Tullis, 1990; Margaria et al., 1963; Roberts et al., 1997; Sloniger et al., 1997; Smith and Carlson-Kuhta, 1995; Vilensky et al., 1994). Thus, there are good reasons to suspect that animals may alter their limb movement when traversing surfaces of varying incline, but quantitative kinematics for animals on inclines are extremely limited. Furthermore, previous data for locomotion on inclines are so fragmentary and include such phylogenetically and morphologically diverse taxa (arthropods, lizards, birds, humans and quadrupedal mammals) that inferences are likely to be tenuous regarding the effects of inclines on unstudied species with different size and limb posture. Hence, whether or not species with different limb designs respond similarly to inclines remains an open question.

Within the clade of tetrapodal vertebrates, limb posture varies considerably and, compared with the derived upright limbs of extant birds and mammals, the function of sprawling limbs that resemble those of ancestral tetrapods is poorly understood for extant ectothermic vertebrates such as salamanders and lizards. In vertebrates with sprawling hindlimbs, the femur is nearly parallel to the ground, the knee is lateral to the hip, and the ankle and foot are below the knee and hence are lateral to the hip (Ashley-Ross, 1994a,b; Edwards, 1977; Hildebrand, 1985; Rewcastle, 1981; Sukhanov, 1974). One consequence of sprawling limbs is that their movements are not co-planar; therefore, three-dimensional methods are needed to understand these movements completely. However, nearly all previous studies of the posture and kinematics of the hindlimb of ectothermic vertebrates (e.g. Ashley-Ross, 1994a,b; Brinkman, 1981; Fieler and Jayne, 1998; Gatesy, 1991; Reilly and Delancey, 1997a; Rewcastle, 1981; Sukhanov, 1974) have relied exclusively on two-dimensional measurements. One key characteristic that distinguishes the limb movements of ectothermic vertebrates from those of endotherms is substantial long-axis rotation of the femur, which can only be measured using three-dimensional methods (Ashley-Ross, 1994a; Barclay, 1946; Edwards, 1977; Peters and Goslow, 1983). However, measurements of femur rotation are only available

for a single species of ectothermic vertebrate (Brinkman, 1981). Besides being needed to quantify certain movements that are unique to vertebrates with sprawling limbs, three-dimensional methods are also required to measure the angle of the knee and other joints within the limb during locomotion. Thus, in contrast to the abundant data available for endothermic vertebrates, basic kinematic quantities such as the amount of knee flexion and extension are only available for a few species of ectothermic vertebrates and for a very limited set of conditions (Brinkman, 1981; Gatesy, 1990, 1991).

Lizards are a particularly good group of ectothermic tetrapods for studying locomotion and the effects of incline for three reasons. First, lizards are the most diverse group of extant ectothermic tetrapods. Second, specializations for climbing and an arboreal existence have evolved repeatedly within lizards (Peterson, 1984; Williams and Peterson, 1982). Third, even terrestrial species of lizards that lack apparent morphological specializations for climbing often encounter and traverse steep inclined surfaces in their natural habitat (Irschick and Jayne, 1998; Jayne and Ellis, 1998).

Limited data suggest that moving up inclined surfaces may affect many aspects of the locomotion of lizards, for example, the net cost of transport increases (Farley and Emshwiller, 1996; Taylor et al., 1972). The maximal velocities of some species of lizards also decrease significantly when they run up inclined surfaces both in laboratory tests (Carothers, 1986; Irschick and Jayne, 1998) and in nature (Jayne and Ellis, 1998), but the effects of incline on maximal velocity may be size-dependent (Huey and Hertz, 1982, 1984). For a bipedal species of lizard (*Callisaurus draconoides*) accelerating from a standstill, Irschick and Jayne (1998) found that stride length decreased and stride frequency increased when running up an incline compared with a level surface, but these kinematic quantities did not vary significantly for a second species of lizard (*Uma scoparia*). Consequently, the generality of the effects of incline on limb movements of lizards remains unclear. For example, decreased stride length when running uphill might occur only in bipedal specialists when accelerating or running near maximal speed. Furthermore, no study of lizard locomotion on an incline has quantified any aspect of limb movement beyond such basic quantities as stride length and frequency, and no study has quantified any kinematics of lizards running downhill.

Several studies of lizards (Fieler and Jayne, 1998; Reilly and Delancey, 1997b; Urban, 1965; White and Anderson, 1994) have documented how both stride length and frequency increase with increased speeds of steady locomotion, as is the case for most species of limbed animals. Fieler and Jayne (1998) also found that many additional kinematic quantities of the hindlimb changed with increased speed. Consequently, studies seeking to isolate the effects of inclines on the kinematics of running lizards should control for the potentially confounding effects of speed. Furthermore, an experimental design that varies both speed and incline is useful for clarifying whether incline and speed have any interactive effects on the kinematics.

The goal of this study was to quantify simultaneously the effects of incline and speed on the three-dimensional hindlimb kinematics of the lizard *Dipsosaurus dorsalis*. Specifically, we examine the effects of incline (uphill 30°, level and downhill 30°) and speed (50–250 cm s⁻¹) on (1) stride characteristics (e.g. stride length, step length), (2) linear displacements and effective lengths of the hindlimb, and (3) three-dimensional angles and lengths of the hindlimb. In addition to testing whether an incline affects the kinematics of the hindlimb of lizards, we were particularly interested in testing two alternative hypotheses regarding the distinctness of locomotion on inclines. If stride lengths of lizards are shorter on an inclined surface compared with those on a level surface, then one might predict that the effects of incline on kinematics could simply mimic those of decreased speed (and shorter stride length). Alternatively, strides of equal length on both a level and inclined surface could be kinematically distinct.

Materials and methods

Experimental subjects

We studied the desert iguana *Dipsosaurus dorsalis* (Baird and Girard) in part because the hindlimb morphology of this predominantly terrestrial species is generalized for iguanian lizards. For example, *Dipsosaurus dorsalis* lacks the extreme elongation of the hindlimbs found in bipedal specialists (Irschick and Jayne, 1998; Snyder, 1954) or any of the specialized toe structures for prehension that are found in many arboreal specialists (Irschick et al., 1996; Williams and Peterson, 1982). Furthermore, as in many iguanian lizards, the lengths of the femur and tibia in this species are nearly equal, the feet are large and the fourth toe is extremely long (Fieler and Jayne, 1998). This species also runs reasonably well on a treadmill over a broad range of speeds, and considerable information is available on its locomotor performance and muscle physiology (Gleeson, 1986; Marsh and Bennett, 1985, 1986). The forelimbs of *D. dorsalis* and many other species of lizards do not contact the ground during rapid bipedal running. Consequently, we concentrated on the kinematics of the hindlimb because it is used for all modes of locomotion in *D. dorsalis*; for many species of lizards, the hindlimbs are probably more important than the forelimbs for generating propulsive forces (Snyder, 1954; Sukhanov, 1974).

We collected all lizards near Yuma, Arizona, USA (Arizona permit number SP 611590), and transported them back to the University of Cincinnati for experiments. Lizards were caged individually or in pairs and maintained on a diet of lettuce, broccoli and a powdered mixture of Purina puppy chow and Kellogg Special K cereal. Within the cages, incandescent light bulbs were on for 12 h per day and allowed lizards to thermoregulate and attain their preferred body temperature of approximately 40 °C (Gleeson and Harrison, 1988), which also approximated the body temperatures during experiments. We video-taped animals within 1 week to 3 months after collecting them. After video-taping eight individuals, we selected four individuals that matched all the standardized speeds on all

three inclines as required for a balanced experimental design. We chose four lizards with very similar size, as indicated by the following mean \pm S.E.M. values (and ranges): mass 62 ± 3.2 g (60–69 g), snout–vent length (SVL) 12.2 ± 0.1 cm (11.9–12.5 cm). Fieler and Jayne (1998) provide additional body dimensions of these four individuals.

Experimental protocol

We obtained simultaneous dorsal and lateral views of lizards moving on a treadmill using a two-camera NAC HSV-500 high-speed video system operating at $250 \text{ images s}^{-1}$ (Fig. 1). For 30 min prior to each trial, we kept the lizards in thermally insulated boxes with hot water bottles at 40°C , and trials usually lasted less than 1 min. Immediately before and after the lizards ran on the treadmill in preliminary trials using this protocol, we used a thermocouple and a Teagam model 871A digital thermometer to measure cloacal temperatures, which ranged from 35 to 40°C . Over the course of several weeks, we video-taped lizards at five standardized speeds at 50 cm s^{-1} intervals ranging from 50 to 250 cm s^{-1} on each of three inclines: uphill 30° , level and downhill 30° . Our experiments included both walking (duty factor $>50\%$) and running (duty factor $<50\%$) on all inclines. Prior to video-taping, we painted landmarks (Fig. 1) on the pelvis and hindlimb of each lizard to facilitate digitizing the video images. After video-taping the lizards, we obtained radiographic images of anesthetized lizards from which we measured the length of the hindlimb bones. The pelvic landmarks painted on the surface of the lizards averaged 5 mm posterior and 5 mm dorsal to the hip joint; hence, before calculating the kinematic quantities, we transformed the coordinates of the pelvic landmarks to approximate the coordinates of the hip.

Kinematics

For each lizard at each speed and incline, we selected 2–4 strides of steady-speed ($\pm 10\%$ of mean forward velocity) locomotion for frame-by-frame motion analysis. An analysis of variance (ANOVA) verified that the speeds of the strides that we selected ($N=219$) did not vary significantly among individual lizards ($F_{3,159}=1.25$, $P>0.05$), among the different inclines ($F_{2,6}=0.10$, $P>0.05$) or for any of the two-way interaction terms involving individual, incline and speed. We used custom-designed video-analysis software (Stereo Measurement TV, written by Garr Updegraff, San Clemente, CA, USA; garru@uci.edu, garru@fea.net) to digitize all the two- and three-dimensional coordinates; kinematic quantities, including three-dimensional angles between two lines and several other variables, were calculated from the digitized coordinates using macros for Microsoft Excel version 7.0 (written by G. Updegraff and B. Jayne). For the two slowest and three fastest speeds, we digitized images every 8 and 4 ms, respectively, which provided an average of 32 images per stride (range 18–47 images). We digitized the three-dimensional coordinates of the following landmarks: the hip, knee and ankle, and the base, middle and tip of the long fourth toe (excluding the claw). We excluded the claw because its

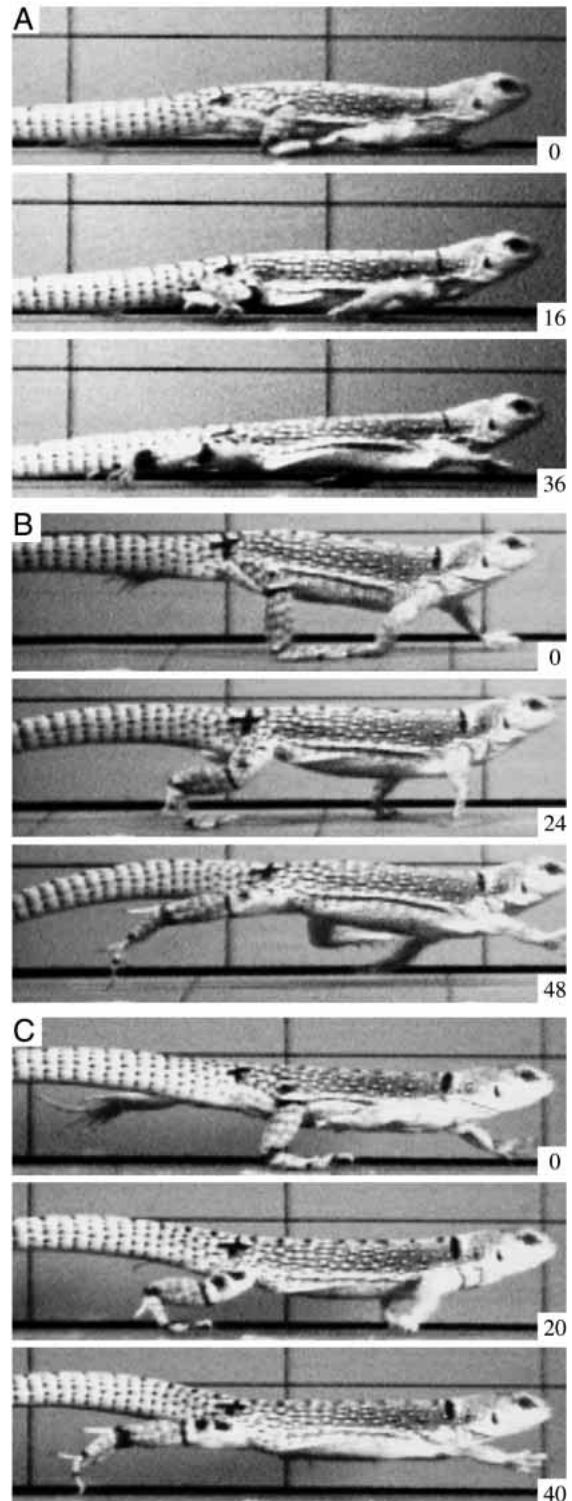


Fig. 1. Representative lateral views of a single *Dipsosaurus dorsalis* (snout–vent length 11.9 cm , mass 59.5 g) traveling at 250 cm s^{-1} on the downhill (A), level (B) and uphill (C) surfaces. The three images for each incline are at the times of hindlimb footfall, mid-stance and the end of stance. On each of the images, the vertical lines in the background are 10 cm apart, and the elapsed time after footfall (ms) is indicated in the lower right-hand corner. Video clips of the locomotion of *D. dorsalis* can be viewed on the world wide web at <http://www.biology.uc.edu/faculty/jayne/bruce.htm>.

tapering tip was difficult to see on the video tapes. In addition, we digitized four two-dimensional coordinates from a dorsal perspective: the right and left ankles, and the right and left hip points. The x axis was the horizontal dimension parallel to the overall direction of travel and the motion of the tread surface. The y axis was perpendicular to the tread surface, and the z axis was perpendicular to the x - y plane.

To facilitate visualization of the movements of the limb distal to the hip in three dimensions, we transformed all x , y and z coordinates so that the hip was located at (0,0,0) and positive values of x , y and z indicated anterior, dorsal and lateral, respectively. For these relative coordinates, we then determined the minimum (X_{\min} , Y_{\min} , Z_{\min}) and maximum (X_{\max} , Y_{\max} , Z_{\max}) values within each stride cycle, and the difference between the maximum and minimum (ΔX , ΔY , ΔZ) values indicated the total excursion along each orthogonal axis for each landmark of the limb during the entire stride cycle.

Three linear quantities described the height of the hip relative to the tread surface and one variable indicated the relative time at which the minimum occurred. In contrast to the distal portions of the limb, for the hip we used a three-dimensional coordinate system where the tread surface had a value of zero for the y coordinate. First, we measured hip height at the time of footfall ($Y_{\text{hip,footfall}}$). Second, hip height at footfall minus minimum hip height equaled the decrease in hip height during the stance (foot contact) portion of the cycle ($\Delta Y_{\text{hip,stance}}$). Third, maximum hip height minus minimum hip height yielded the total vertical oscillation of the hip for the entire stride cycle ($\Delta Y_{\text{hip,total}}$). To indicate where within the stance phase hip height was at a minimum, we calculated a fraction equal to the following: (time at which minimum hip height occurred minus time of footfall)/(stance duration). Two additional linear quantities measured effective limb lengths as the straight-line distances from the hip to the ankle in both three and two dimensions (x - y plane).

Six variables described movements of the whole limb and attributes of the entire locomotor cycle. Stride length was the distance traveled along the x axis between successive footfalls of the right hind foot, whereas step length was the distance traveled by the body along the x axis during stance of the right hindfoot. Stride width equaled the difference between the z coordinates of the left and right ankles at the times of footfall. Stride duration was the elapsed time between successive footfalls of the right hindlimb, and duty factor was the percentage of the cycle (stride) duration when the foot was on the ground. Mean forward velocity of each stride equaled stride length (cm) divided by stride duration (s).

Three-dimensional angles described angles of three joints within the hindlimb at footfall, at maximum flexion within the stance phase and at the end of stance, and one two-dimensional angle indicated the orientation of the fourth toe. The knee angle was the angle between the femur and the tibia such that smaller values between 0° and 180° indicate greater flexion of the joint. The ankle angle was the angle between the tibia and metatarsal on the dorsal side of the foot so that decreasing values between 0° and 180° indicate greater dorsiflexion of

the foot. Finally, the toe angle was the angle between the metatarsals and a straight line extending from the base to the tip of the fourth toe so that values greater than 180° indicate plantar flexion of the toe. To determine the amount of flexion that occurred in the first portion of the stance phase, we subtracted the minimum value during stance from the value at footfall, and similarly the amount of joint extension during stance equaled the value at the end of stance minus the minimum value during stance. The angle of toe orientation indicated the angle of the fourth toe relative to the x axis such that larger values between 0° and 90° indicate that the toe is oriented more laterally, and this angle was measured at footfall, at mid-stance and at the end of stance.

From a dorsal perspective, we also measured a two-dimensional angle to indicate the orientation of the pelvis. The angle between the x axis and a line connecting the left and right hips indicated the orientation of the pelvis, and the difference between maximum and minimum values of these angles indicated the amount of rotation of the pelvis (projected onto a horizontal plane). We could not directly measure the amount of pelvic roll about the longitudinal axis of the lizard because the right hip generally obscured the view of the left hip, which was needed to determine its y coordinate. We attempted to estimate the y coordinates of the left hip by shifting values of the right hip by half a cycle and then estimating the angle of pelvic roll using the difference between left and right hip y coordinates for each time. Although this method worked well for certain strides, these estimates gave unreliable results for many strides. Furthermore, an ANOVA did not detect any statistically significant effects of either speed ($F_{4,12}=2.9$, $P>0.05$) or incline ($F_{2,6}=0.6$, $P>0.05$) on these estimated values of pelvic roll. Therefore, not accounting for pelvic roll seems unlikely to confound an interpretation of the effects of speed and incline on other variables. Consequently, we preferred to determine certain movements of the femur relative to fixed planes of reference because these alternative methods corresponded better to visualization of the video images than did values obtained by attempting to correct for the amount of pelvic roll.

For each of the three angles that described the orientation of the femur, we determined both the maximum and minimum values attained during each stride cycle. The angle of femur retraction was a two-dimensional angle determined from a dorsal view of the femur and the line connecting the left and right hips such that values of 0° indicated when the femur was perpendicular to the longitudinal axis of the pelvis, and greater magnitudes of positive and negative values indicated greater amounts of retraction and protraction, respectively. The angle of femur rotation about its long axis was the three-dimensional angle between the plane containing the femur and the tibia and a vertical reference plane passing through the femur such that greater positive values indicated greater clockwise rotation of the right femur as seen in a right lateral view. The angle of femur depression was a three-dimensional angle between the femur and a horizontal plane passing through the right hip such that

positive and negative values indicated that the femur was below or above the horizontal reference plane, respectively.

Statistical analyses

For all analyses, we used SYSTAT 5.0 (Wilkinson, 1992); $P < 0.05$ was the primary criterion for statistical significance for all analyses, but we emphasize findings for which P values were less than 0.001. In tabular summaries of statistics, we provide relevant details such as degrees of freedom and F -values to clarify the magnitude of statistical differences and the potential effects of multiple comparisons. For each kinematic variable, we performed a three-way ANOVA using incline, speed and individual as the factors. Incline and speed were both fixed variables, and individual was a random factor. The denominators for the F -tests on the main effects were the two-way interaction terms of the fixed effect and the individual factor (Zar, 1996). We were primarily interested in the incline, the speed and the incline by speed interaction term, so we present tabular summaries of F -values only for these three effects.

To evaluate whether locomotion on a particular incline was unique in a multivariate fashion, we used a subset of the kinematic variables in a discriminant function analysis with

each stride ($N=219$) as an individual data point and each incline ($N=3$) as the categorical variable. Most kinematic variables were significantly correlated with stride length. Thus, to examine the extent to which variation in stride length caused variation among inclines, we also performed multivariate analyses on residuals of variables that were regressed on stride length (linear least-squares regressions).

Results

General description of limb movement

Figs 2 and 3 illustrate lateral and dorsal views of the paths traveled by the different portions of the limb relative to the hip for locomotion on the different inclines. Linear displacements in all three dimensions during the stride cycle generally increased from the proximal to the most distal location within the hindlimb (Figs 2, 3). The most anterior position of the different portions of the hindlimb was generally at or just slightly before footfall (Fig. 2). Within a single stride, the most anterior (X_{\max}) and most posterior (X_{\min}) positions of the knee relative to the hip had extremely similar magnitudes, whereas for more distal portions of the limb, the magnitude of X_{\min} was commonly more than twice that of X_{\max} , and this contributed

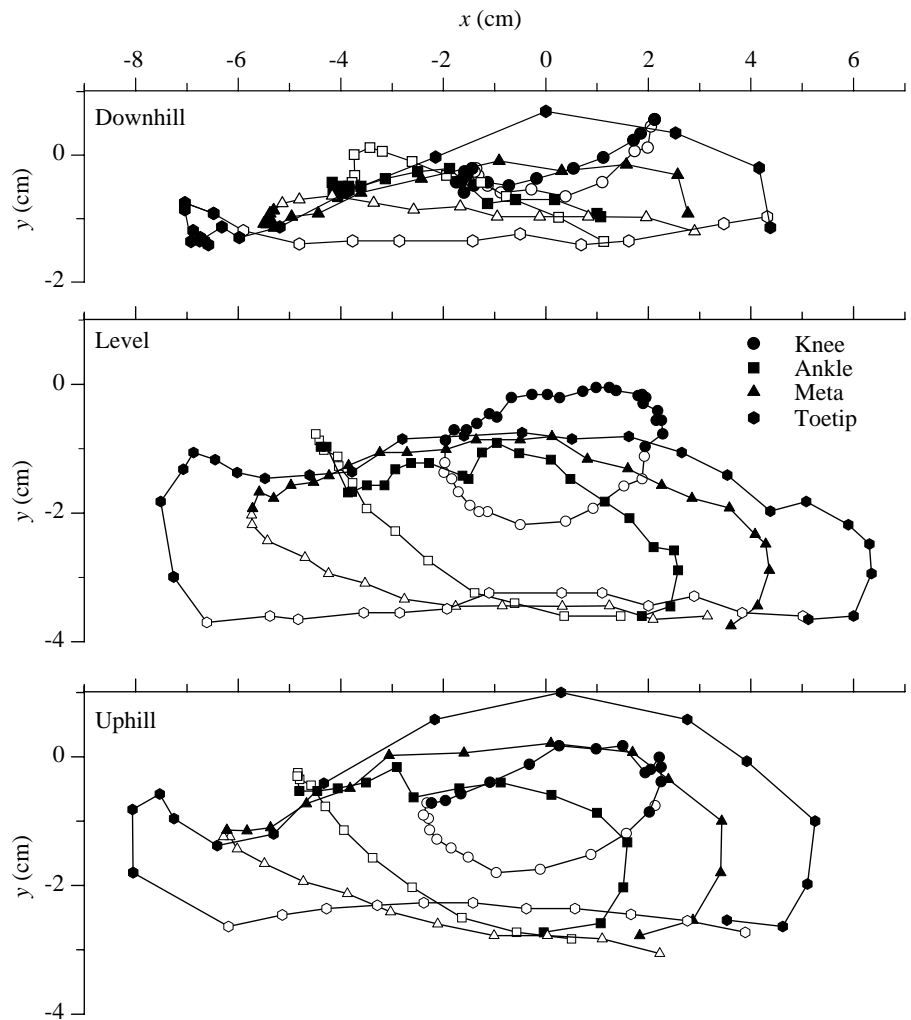


Fig. 2. Lateral (x versus y) views of paths made during one stride by the right knee, ankle, metatarsal (Meta) and toetip landmarks for locomotion on the downhill, level and uphill surfaces at 250 cm s^{-1} . The hip is located at $(0,0,0)$, and positive values of x , y and z indicate the forward, dorsal and lateral directions of travel, respectively. The open and filled symbols represent the stance and swing portions of the stride, respectively. The direction of overall movement in the loops is clockwise. The time between successive points is 4 ms.

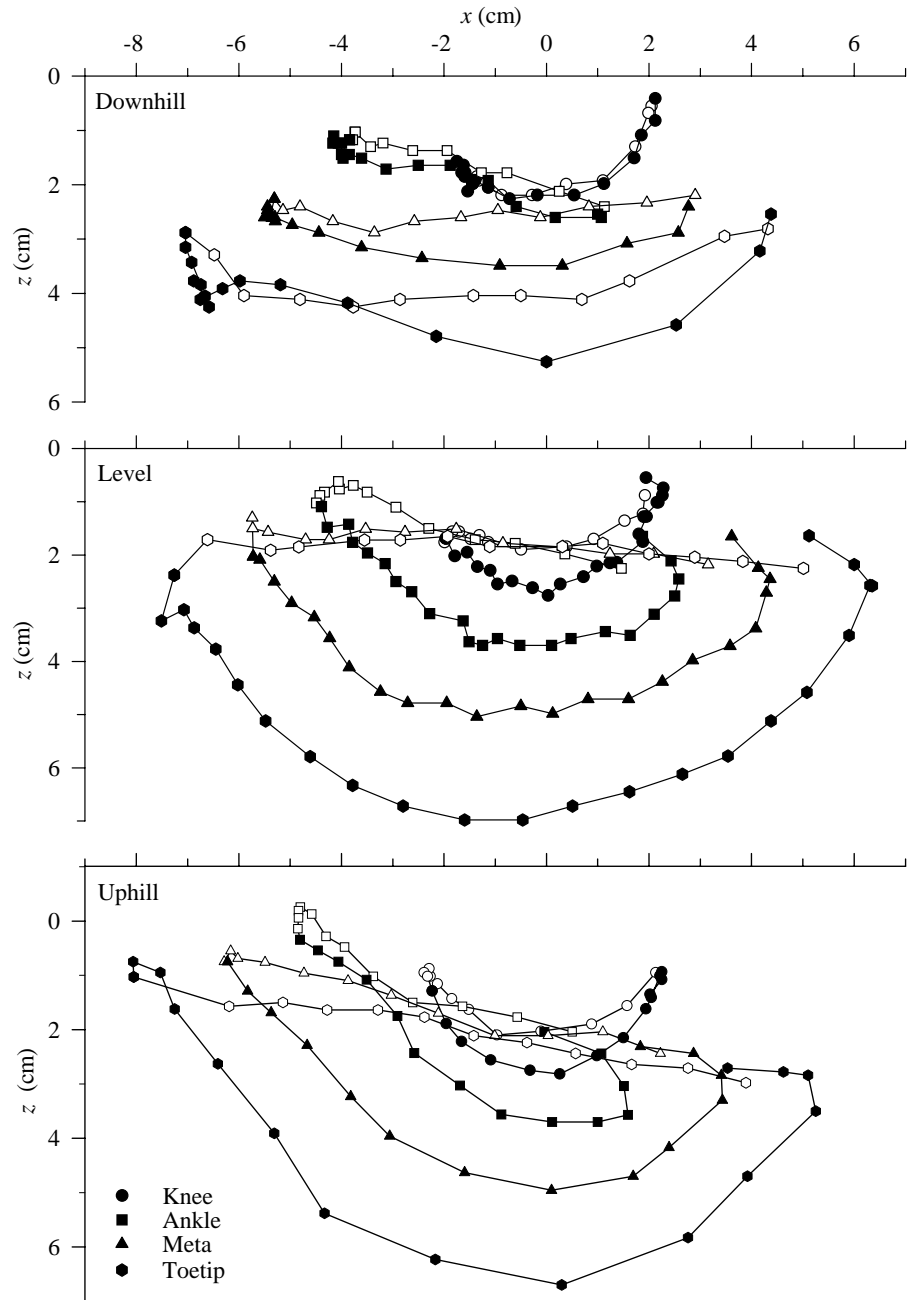


Fig. 3. Dorsal (x versus z) views of paths made by the right knee, ankle, metatarsal (Meta) and toetip landmarks for the same strides as shown in Fig. 2. All symbols, axes and sign conventions are explained in the legend to Fig. 2.

to the asymmetric appearance of the resulting loops (Fig. 2). The most ventral and dorsal locations of the limb relative to the hip occurred at approximately mid-stance and mid-swing, respectively. Z_{\max} generally occurred in the swing phase when all portions of the limb had a longitudinal position similar to that of the hip (Fig. 3). As indicated by the greater spacing between successive points, the fastest movements of the hindlimb occurred during the swing phase rather than during the stance phase.

Fig. 4 illustrates how angles within the hindlimbs vary during the stride cycle. After footfall, the knee flexes briefly, whereupon it extends for the remainder of stance until it is maximally extended in the very early portion of the swing phase (Fig. 4). After attaining maximal extension, the knee

once again flexes and is then briefly extended again just slightly before the next footfall (Fig. 4). Dorsiflexion of the foot occurs immediately after footfall until the ankle attains a minimal angle near mid-stance, and this time of minimum ankle flexion was consistently after that of the knee during the stance phase (Fig. 4). The times of footfall, the greatest angle of the pelvis relative to the x axis (not shown in Fig. 4), the greatest amount of femur protraction (Fig. 4, most negative value) and the greatest counterclockwise rotation of the right femur about its long axis (Fig. 4, minimum value) were nearly simultaneous. Soon after footfall, the femur is retracted and rotated clockwise about its long axis until maximum amplitudes of these movements are attained just slightly before or at the end of stance. The rates of femur retraction and

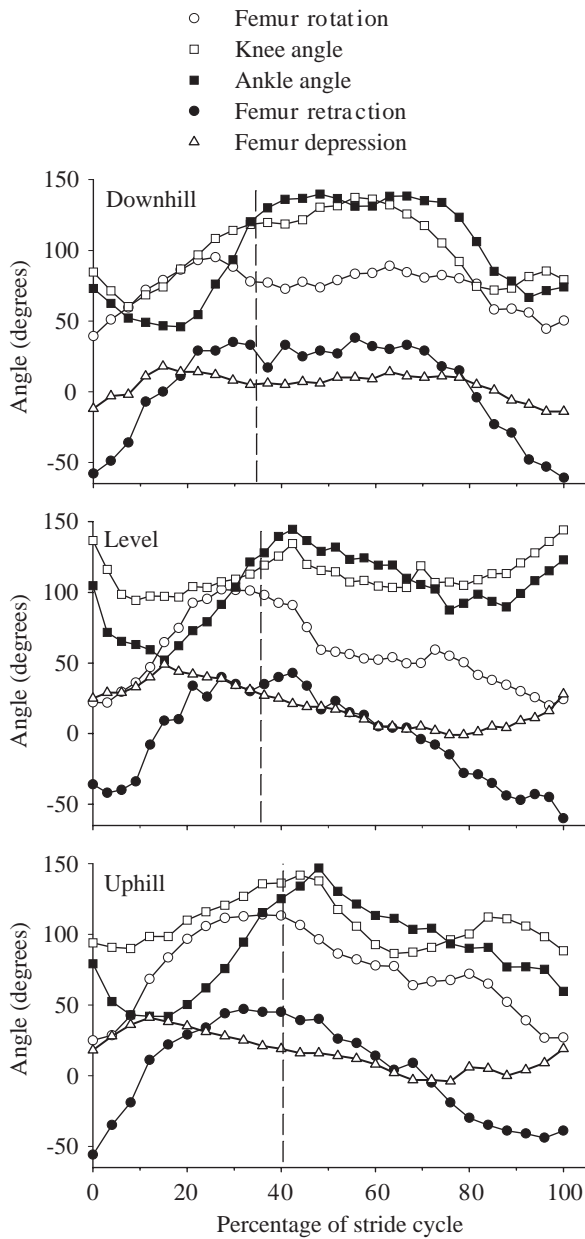


Fig. 4. Values of the angles of femur retraction, femur rotation, femur depression and of the knee and ankle joints *versus* time (as a percentage of the stride cycle) for a single stride on the downhill, level and uphill surfaces for an individual lizard traveling at 250 cm s⁻¹. The dashed line indicates the end of stance, and footfall occurs at time 0%.

clockwise rotation and the rates of femur protraction and counterclockwise rotation are strikingly similar to each other (Fig. 4).

Effects of incline and speed

Whole-stride characteristics

Both incline and speed had highly significant and interactive effects on stride length (Table 1). Stride length increased significantly with speed on each surface, but values were similar at slow speeds and then diverged with increased speed

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

Dependent variable	ANOVA effect		
	Incline (2,6)	Speed (4,12)	Incline × Speed (8,24)
Stride length [‡]	36.3**	247.3**	4.6*
Step length [‡]	45.7**	17.9**	1.5
Stride width	10.5*	7.1*	1.1
Stride duration [‡]	68.3**	191.1**	3.2*
Duty factor	5.1	80.7**	0.8
Y _{hip} footfall [‡]	133.5**	10.1**	3.0*
ΔY _{hip} stance [‡]	22.6**	3.2	1.0
ΔY _{hip} total [‡]	11.3**	0.7	2.0
Two-dimensional effective length (footfall)	74.7**	31.1**	2.4*
Three-dimensional effective length (footfall)	12.5*	16.9**	3.1*

*P<0.05, **P<0.001.

Degrees of freedom are given in parentheses.

‡ indicates use in the discriminant function analysis.

Y_{hip}footfall, hip height at the time of footfall; ΔY_{hip}stance, change in hip height during stance; ΔY_{hip}total, total vertical oscillation of the hip for entire stride cycle.

such that uphill values became shorter relative to those of the other surfaces (Fig. 5A). Similarly, step length increased significantly with increased speeds, and the shortest steps generally occurred on the uphill surface (Table 1; Fig. 5B). Stride width changed significantly with both speed and incline (Table 1) such that wider strides generally occurred both on the downhill surface and with increased speed (Fig. 5C). Neither step length nor stride width increased as rapidly with increased speed as did stride length (Fig. 5A–C). Stride duration decreased significantly with increased speed, and uphill stride durations were significantly shorter than those for the other surfaces (Table 1; Fig. 5D). Duty factor also decreased with increased speed but, unlike stride duration, it was not significantly affected by incline (Table 1; Fig. 5E).

Linear measurements

Most linear measurements varied substantially among the three inclines (Figs 1–3). Table 2 summarizes the results of ANOVAs for each minimum and maximum position and the excursions in each of the three dimensions. Table 2 is arranged to facilitate recognition of how the effects of both incline and speed depended on the particular dimension and portion of the limb. For example, none of the most anterior positions (X_{max}) of any of the landmarks on the hindlimb was significantly affected by incline, whereas incline significantly affected the most posterior positions (X_{min}) of all landmarks on the limb. The longitudinal excursion (ΔX) of the knee showed highly significant variation among inclines (Table 2) such that the

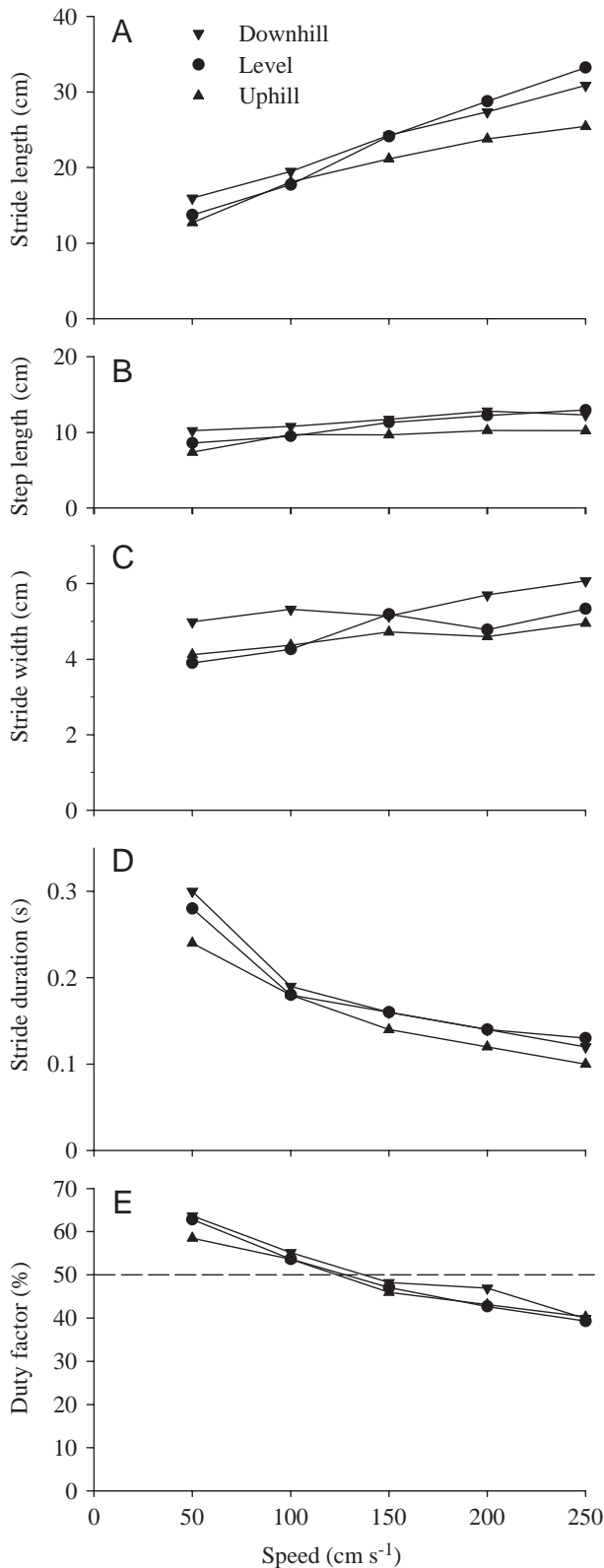


Fig. 5. Mean values of stride length (A), step length (B), stride width (C), stride duration (D) and duty factor (E) versus speed. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. The dashed line in E denotes the walk-run transition. Table 1 summarizes the results of statistical comparisons among inclines and speeds.

smallest values occurred consistently for downhill locomotion. None of the longitudinal variables of the knee was significantly affected by speed, whereas for the more distal portions of the limb most longitudinal positions and excursions showed highly significant increases with increased speed. The effect of incline was most pronounced on Y_{\min} for all parts of the hindlimb (Table 2), for which mean values for downhill locomotion were usually only half the values for level locomotion and for uphill locomotion. The magnitude of Y_{\min} also showed highly significant increases with increased speed, whereas Y_{\max} , which occurs during the swing phase, was unaffected by speed. Hence, the significant effects of both incline and speed on ΔY for all parts of the hindlimb were primarily a result of the more ventral location of the limb during stance rather than of changes in both the ventral and dorsal locations of the limb during each stride. In the lateral dimension, the most conspicuous variation among inclines and speeds was generally for Z_{\max} rather than for Z_{\min} or ΔZ , and, for most parts of the limb, Z_{\max} showed the smallest values for downhill locomotion and for decreased speeds of locomotion within each incline. Several of the linear positions and excursions also showed significant interactive effects of speed and incline (Table 2).

Hip height at footfall ($Y_{\text{hipfootfall}}$) showed highly significant differences (Table 1) among inclines and speeds such that mean downhill values (range 1.3–1.7 cm) were substantially smaller than all other mean values (range 2.1–3.6 cm) and hip height increased less with increased speed on the downhill surface compared with values for the other surfaces (Fig. 6A). In contrast to hip height at footfall, the mean values of total change in hip height per stride (Y_{hiptotal}) (range 5–9 mm) did not change significantly with increased speed, but values did differ significantly with incline such that the greatest values were consistently observed for locomotion on the level surface at the faster speeds (Table 1; Fig. 6B). The decrease in hip height during the first portion of stance ($Y_{\text{hipstance}}$) (Fig. 6C) differed significantly among the inclines ($F_{2,6}=22.6$, $P<0.05$; Table 1) such that the mean values for downhill locomotion (range 2.4–4.7 mm) were consistently smaller than those of the other surfaces (range 4.5–7.1 mm). Although speed did not have a statistically significant effect on $\Delta Y_{\text{hipstance}}$, the lowest mean values for all inclines occurred at the fastest speed (Fig. 6C). The time of minimum hip height within the stance phase did not differ significantly among inclines ($F_{2,6}=1.8$) or speeds ($F_{4,12}=0.2$); however, mean values for the downhill surface were consistently smaller than those for the other inclines at similar speeds. The mean values (pooled across all speeds) of the time at which minimum hip height occurred for the downhill, level and uphill surfaces were $39\pm 3\%$, $50\pm 3\%$ and $54\pm 3\%$ (means \pm S.E.M.) of stance duration, respectively.

Both two- and three-dimensional effective limb lengths had significant incline, speed, and incline by speed interaction terms (Table 1), and the changes with speed and incline were extremely similar to those of hip height (Fig. 6A,D,E). Three-dimensional values of effective limb length diminished but did

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

Anatomical location	Kinematic variable								
	X _{min}	X _{max}	ΔX	Y _{min}	Y _{max}	ΔY	Z _{min}	Z _{max}	ΔZ
Incline (2,6)									
Knee	16.8*	1.3	33.5**	99.8*	47.3**	30.2**	14.8*	23.9*	3.2
Ankle	25.2*	3.8	5.1	71.8**	2.6	45.3**	4.0	5.3*	16.7*
Metatarsal	12.6*	3.3	5.4*	145.3**	13.1*	38.1**	10.1*	15.4*	36.1**
Toetip	9.4*	2.2	4.0	114.4**	15.2*	29.1**	0.3	14.4*	4.6
Speed (4,12)									
Knee	2.5	0.7	3.2	24.6**	3.2	8.7*	0.7	4.0*	3.1
Ankle	3.3*	21.5**	19.2**	16.9**	1.3	69.1**	6.8*	37.9**	14.1**
Metatarsal	6.1*	26.5**	26.5**	14.8**	2.2	34.2**	0.6	23.5**	22.3**
Toetip	13.7**	34.0**	43.1**	14.3**	1.5	38.8**	6.8*	15.0**	24.2**
Incline × Speed (8,24)									
Knee	3.8*	1.1	2.6*	2.9*	2.0	2.6*	4.2*	2.5*	2.7*
Ankle	2.2	4.1*	2.6*	3.9*	2.1	2.6*	4.3*	3.0*	1.1
Metatarsal	1.7	4.3*	3.1*	3.5*	2.2	6.0**	2.3*	2.7*	1.4
Toetip	1.9	4.3*	3.4*	2.8*	1.7	3.3*	2.8*	2.4*	1.4

* $P < 0.05$, ** $P < 0.001$.
ANOVA effects and degrees of freedom are given above each group of rows indicating different locations within the hindlimb.

not eliminate the differences among inclines compared with those values obtained using two-dimensional calculations.

Angles within the limb

Mean values of the knee angle at footfall varied from 71° to 130° and were significantly affected by incline so that, within a speed, the rank order from smallest to greatest was generally downhill, uphill and level (Table 3; Fig. 7A). The knee angle at footfall also increased significantly with increased speed, and the significant incline by speed interaction term indicates a greater tendency for level values to increase with speed than for values for the downhill and uphill surfaces. The knee angle at the end of stance did not change significantly with speed, but it did vary significantly among inclines such that downhill locomotion consistently had the lowest values (Table 3; Fig. 7A). The amount of knee flexion during stance showed significant effects of incline ($F_{2,6}=23.1$, $P < 0.05$), speed ($F_{4,12}=6.9$, $P < 0.05$) and incline by speed ($F_{8,24}=3.6$, $P < 0.05$) such that values were similar among inclines at low speeds, did not change with speed for uphill locomotion, and changed most rapidly with increased speed for locomotion on the level surface (Fig. 7B). The mean values of the amount of knee extension during stance were remarkably similar for uphill and downhill locomotion compared with those for level locomotion (Fig. 7B), and the differences among inclines were not statistically significant ($F_{2,6}=0.3$). The amount of knee extension during stance showed a small but statistically significant decrease with increased speed ($F_{8,24}=3.9$). The angle of the knee at the end of stance only differed significantly among inclines, with the mean values for the downhill surface often being 10–20° less than those for the level and uphill surfaces (Table 3; Fig. 7A).

The mean values for the angle of the ankle at footfall and at the end of stance varied from 68° to 107° and from 104° to 135°, respectively (Fig. 7C), and neither of these variables was significantly affected by incline, but both increased significantly with increased speed (Table 3; Fig. 7C). The amount of ankle flexion during stance did not change significantly with speed ($F_{8,24}=0.6$), but it did differ significantly among inclines ($F_{2,6}=13.3$, $P < 0.05$), with mean values of 32±1°, 46±1° and 32±1° (means ± S.E.M.) for downhill, level and uphill locomotion, respectively (Fig. 7D). The amount of ankle extension during stance did not vary significantly either with speed ($F_{8,24}=1.1$) or among inclines ($F_{2,6}=1.4$).

The angles of the toe at footfall and the end of stance differed significantly among inclines (Table 3), with downhill locomotion consistently showing the highest values at each speed (Fig. 7E). The amounts of toe flexion during stance showed significant effects of incline ($F_{2,6}=14.8$, $P < 0.05$), speed ($F_{4,12}=7.0$, $P < 0.05$) and incline by speed ($F_{8,24}=2.4$, $P < 0.05$) such that mean values for downhill locomotion were smallest and changed little with speed values (range 15–24°), whereas mean values for the level surface were generally largest and increased the most with increased speed (range 15–55°).

The orientation of the fourth toe at footfall was not affected by incline, but it did decrease significantly with increased speed, indicating that the toe pointed anteriorly during locomotion at higher speeds (Table 3; Fig. 8A). In contrast to the time of footfall, at mid-stance the orientation of the toe differed significantly among inclines ($F_{2,6}=7.5$, $P < 0.05$) such that the mean values of the toe orientation were most lateral (42–73°) for every speed on the downhill surface and most

nearly straight forward (15–18°) for the three fastest speeds on the level. At the end of stance, the orientation of the toe also differed significantly among inclines (Table 3) with the

greatest mean values for faster speeds on the downhill surface (>160°), indicating that the toe was pointing nearly straight backwards.

Angles of the pelvis and femur

The mean amounts of pelvic rotation varied from 36 to 52° and were significantly greater on the uphill surface than on either the downhill or level surfaces (Table 3; Fig. 8B). Pelvic rotation did not vary significantly with speed (Table 3), but the lowest mean values for both the uphill and downhill surfaces were at the two fastest speeds (Fig. 8B).

The mean maximum angle of femur retraction ranged from 38° to 55° and, although this angle was not significantly affected by either speed or incline (Table 3), the smallest mean value at each speed was that for downhill locomotion (Fig. 9A). The mean minimum angles of femur retraction varied from -45° to -65° and differed significantly among inclines such that the greatest (most negative retraction angle) and smallest amounts of protraction occurred on the downhill and uphill surfaces, respectively (Table 3; Fig. 9A). The minimum angles of femur retraction also decreased significantly with speed (Table 3). Mean angular excursions

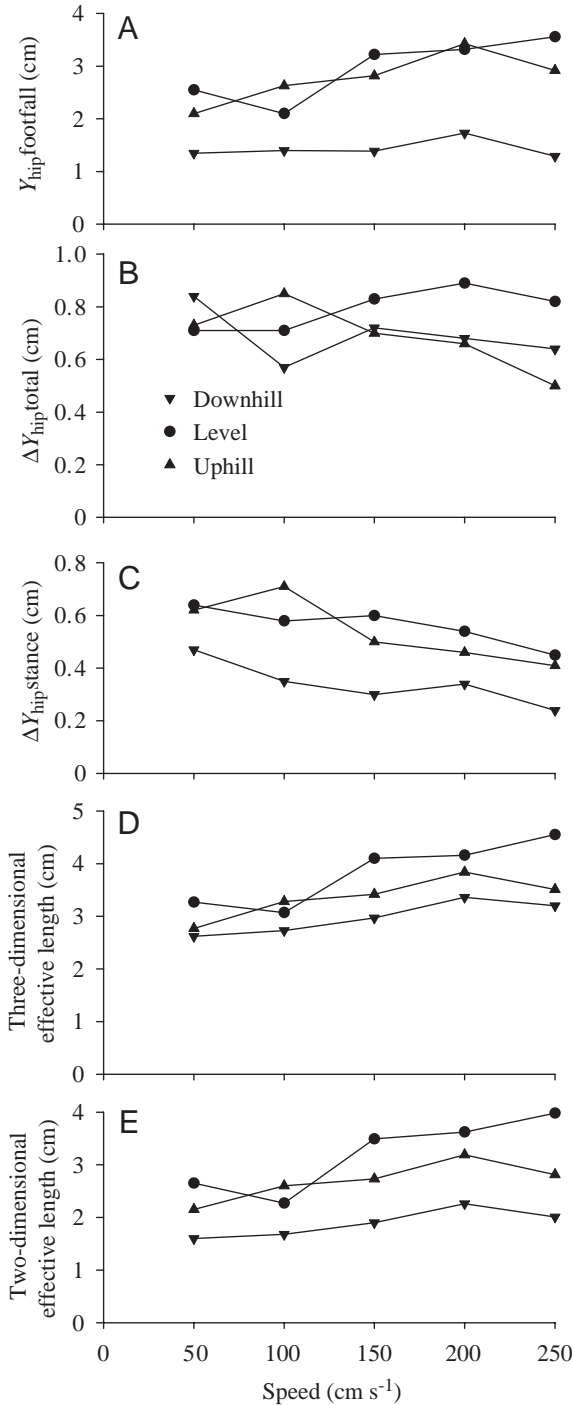


Fig. 6. Mean values of hip height at footfall ($Y_{hip}^{footfall}$) (A), the total change in Y_{hip} for the entire stride cycle (ΔY_{hip}^{total}) (B), the change in Y_{hip} during stance (ΔY_{hip}^{stance}) (C), and three-dimensional (D) and two-dimensional (E) effective limb lengths at footfall. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 1 summarizes the results of statistical comparisons among inclines and speeds.

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

Dependent variable	ANOVA effect		
	Incline (2,6)	Speed (4,12)	Incline × Speed (8,24)
Knee (footfall)‡	12.6*	17.2**	3.5*
Knee (end stance)‡	14.1*	1.2	2.1
Ankle (footfall)‡	4.2	8.1*	2.3
Ankle (end stance)‡	2.7	3.9*	1.1
Toe (footfall)	9.0*	2.2	1.6
Toe (end stance)	40.3**	0.7	4.0*
Toe orientation (footfall)	1.4	29.9**	1.5
Toe orientation (end stance)	9.8*	3.0	3.3*
Pelvic rotation‡	5.6*	2.5	1.4
Maximum femur retraction‡	3.3	2.0	1.0
Minimum femur retraction‡	14.3*	8.2*	1.8
Retraction excursion	1.3	8.1*	0.5
Maximum femur depression‡	68.7**	18.7**	2.7*
Minimum femur depression‡	29.1**	0.9	2.2
Depression excursion	12.6*	6.7*	2.0
Maximum femur rotation‡	59.2**	9.2*	1.1
Minimum femur rotation‡	14.8*	6.6*	1.0
Rotation excursion	50.4**	13.1**	1.1

* $P < 0.05$, ** $P < 0.001$; degrees of freedom are given in parentheses. ‡ indicates use in the discriminant function analysis.

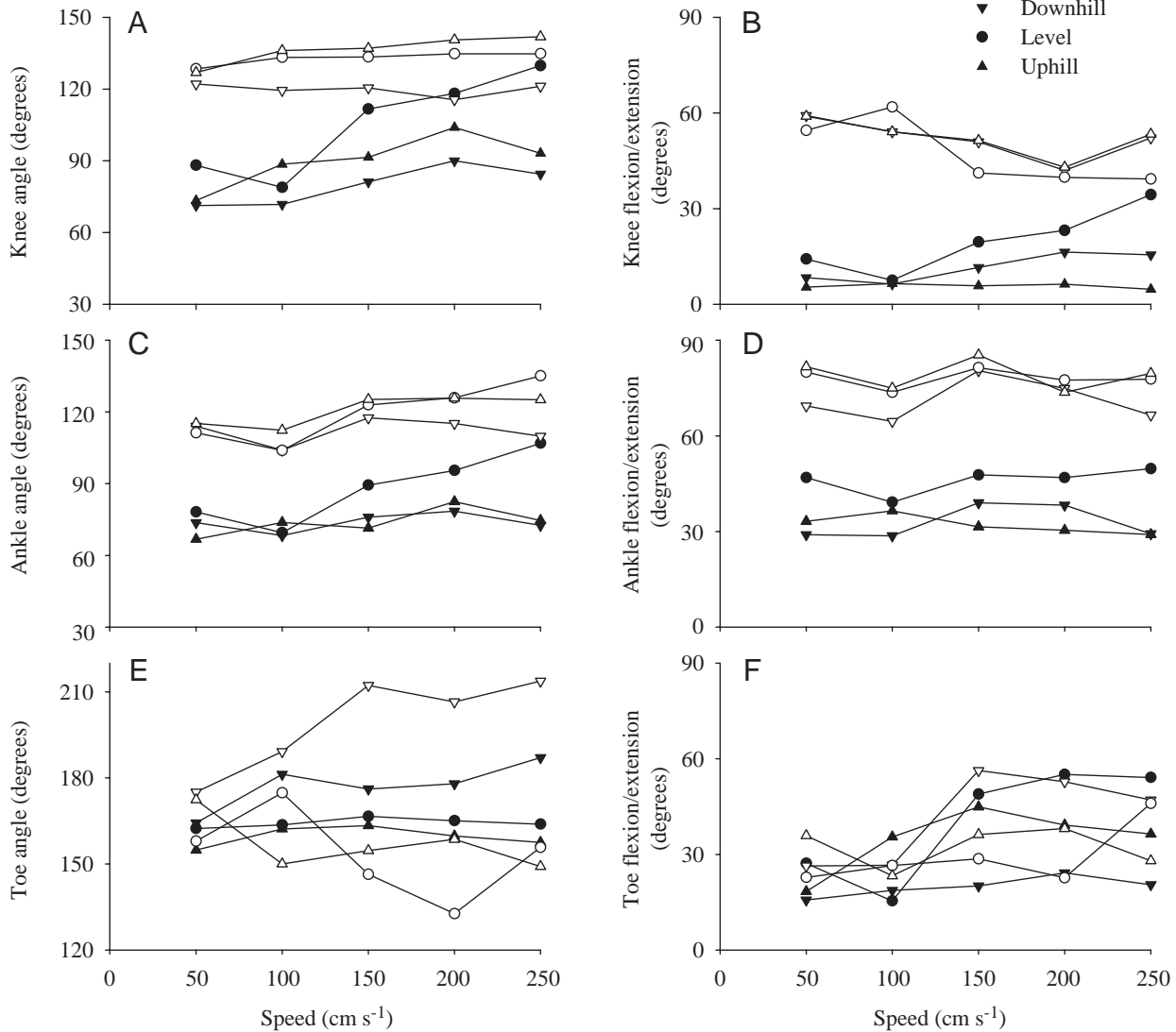


Fig. 7. Mean values of the three-dimensional angle of the knee (A), ankle (C) and toe (E) at the end of stance (open symbols) and at footfall (filled symbols), as well as the amounts of flexion (filled symbols) and extension (open symbols) during stance for the knee (B), ankle (D) and toe (F) *versus* speed. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 3 summarizes the results of statistical comparisons among inclines and speeds. The amounts of flexion and extension during stance (B,D,F) often differ from each other because additional amounts of flexion and extension often occur during the swing phase of the locomotor cycle.

from the position of greatest protraction to greatest retraction did not differ significantly among inclines, but increased significantly with increased speed, and the increase with speed (range 91–111°) was remarkably similar for all inclines (Table 3; Fig. 10A).

The maximum and minimum values of femur depression showed highly significant variation among inclines (Table 3) such that downhill locomotion consistently had the lowest mean values for each variable for each speed, whereas these quantities were extremely similar for locomotion on the level and uphill surfaces (Fig. 9B). For all speeds of downhill locomotion, the mean values of maximum (range 17–21°) and minimum (range –14° to –21°) femur depression were effectively constant. Maximal values of femur depression were

approximately 40° for the three fastest speeds of uphill and level locomotion. The total angular excursions from maximum to minimum femur depression differed significantly with both speed and incline (Table 3) and, for data pooled across all speeds, the smallest mean values occurred for the downhill locomotion ($35.8 \pm 0.8^\circ$); the mean values for the level ($41.2 \pm 2.1^\circ$) and uphill ($43.8 \pm 2.5^\circ$) surfaces were extremely similar (means \pm S.E.M.) (Fig. 10B).

The minimum, maximum and total angular excursion of femur rotation differed significantly among inclines and changed significantly with increased speed (Table 3; Figs 9C, 10C). Mean values of maximum femur rotation were lowest for the downhill surface for all speeds (range 78–92°), whereas the lowest mean values of minimum femur rotation were those

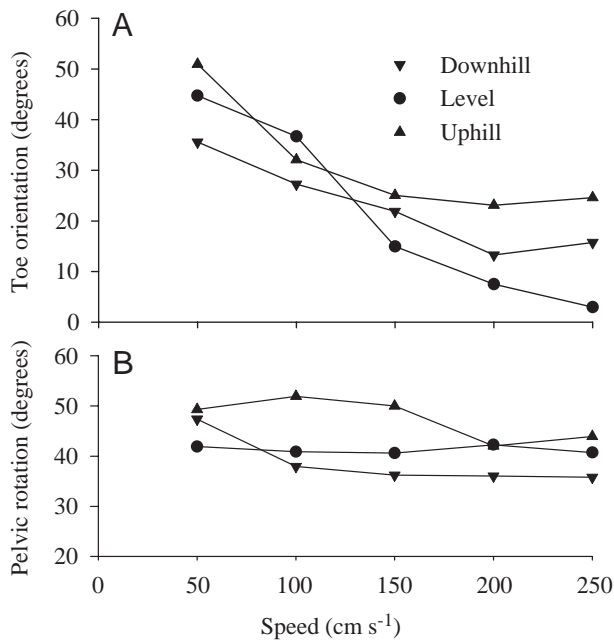


Fig. 8. Mean values of toe orientation at footfall (A) and the angle of pelvic rotation (B) versus speed. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 3 summarizes the results of statistical comparisons among inclines and speeds.

for the level surface (range 11–24°). At the highest speeds on the level surface, the plane containing the femur and tibia was nearly perpendicular to the tread surface at footfall (Fig. 1B). The mean values of the total angular excursion at each speed (Fig. 10C) were always lowest for downhill locomotion (range 48–66°), and those for the level surface were usually highest (range 75–105°). On all inclines, the amount of rotation generally increased with increased speed (Fig. 10C).

Multivariate analyses

Both discriminant functions (DFs) were highly significant (test of residual roots, DF1, $\chi^2=540$, d.f.=34, $P<0.001$; DF2, $\chi^2=129$, d.f.=16, $P<0.001$), and the overall test was highly significant (Wilks' $\lambda=0.075$, $F_{34,400}=31.3$, $P<0.001$). The first DF neatly separated downhill strides, which had higher values than both uphill and level strides (Fig. 11). The two variables that loaded highest with DF1 were $Y_{\text{hip}}^{\text{footfall}}$ and the maximum angle of femur depression (Table 4); hence, downhill strides had the lowest hip heights at footfall and the least femur depression during stance. The three variables for DF2 that best discriminated uphill from level strides (Table 4) were minimum femur rotation near the beginning of stance and the angles of the knee and ankle at footfall, such that strides on the level surface had more extended knee and ankle joints, and the plane through the femur and tibia was most nearly vertical.

Strides from each of the inclines had high classification probabilities from the discriminant function analysis, as indicated by only 16 of 219 strides being misclassified. Only one downhill stride was misclassified, whereas the remaining

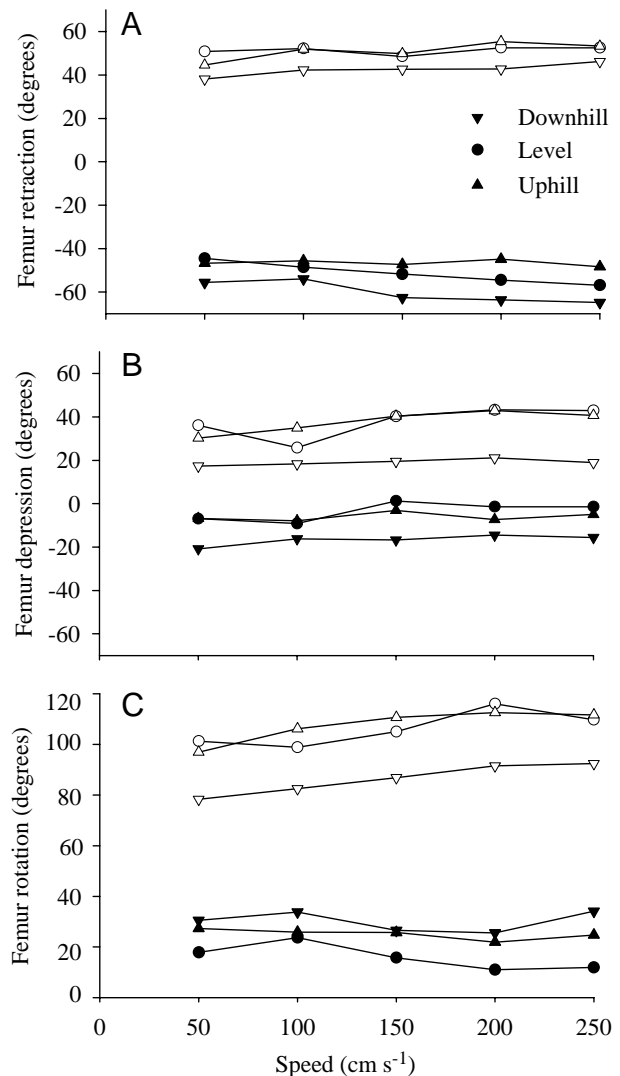


Fig. 9. Mean minimum (filled symbols) and maximum (open symbols) values during the entire stride cycle for the angles of femur retraction (A), femur depression (B) and femur rotation (C) versus speed. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 3 summarizes the results of statistical comparisons among inclines and speeds.

15 misclassified strides involved locomotion on the uphill or level surfaces. Using residual values of kinematic variables (calculated from regressions with stride length) had little effect on a similar discriminant function analysis, as indicated by a total of 25 misclassified strides, for which only one misclassification involved downhill values. Therefore, strides on different inclines were distinct even after the effects of stride length had been removed.

Discussion

Effects of incline

Our observations contradict the hypothesis that variation in kinematics on inclines is primarily a result of variation in stride

length, with correlated changes in several additional kinematic variables. Because incline and speed commonly had interactive effects on kinematics, if the same three inclines had been used for observations at only a single speed, fundamentally different conclusions might have been obtained regarding the locomotor response to inclined surfaces. Within a particular incline, the changes in kinematics with increasing speed often had discontinuities rather than being simple linear increases. For locomotion of *D. dorsalis* on a level surface, Fieler and Jayne (1998) suggested that the decrease in hip height near 100 cm s^{-1} may be the result of a gait transition since duty factors approximated 50% between 100 and 150 cm s^{-1} . Interestingly, with increased speeds on both the uphill and downhill surfaces, discontinuities in kinematic quantities were less evident compared with those observed for level surfaces (see Figs 6D, 7A).

Many species of lizards frequently move with apparent ease up and down steep inclines in their natural habitats, and many clades of lizards have evolved behavioral and morphological

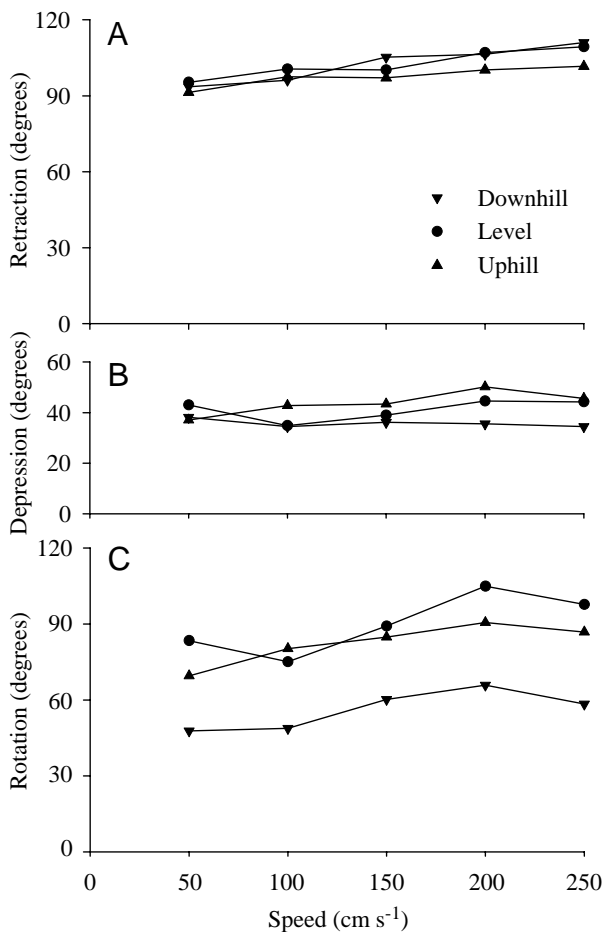


Fig. 10. Mean values of angular excursions during the entire stride cycle for the femur during retraction (A), depression (B) and rotation (C) versus speed. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 3 summarizes the results of statistical comparisons among inclines and speeds.

specializations for climbing (Irschick et al., 1996; Williams and Peterson, 1982). Perhaps certain attributes of limb posture and movement of ectothermic tetrapods facilitate movement on inclined surfaces. Movements commonly used to differentiate ectothermic from endothermic vertebrate locomotion include pelvic rotation resulting from lateral axial bending, femur retraction and femur rotation (Ashley-Ross, 1994a; Barclay, 1946; Carrier, 1987; Edwards, 1977; Rewcastle, 1981; Ritter, 1992).

Pelvic rotation and femur retraction both occur on the horizontal plane; hence, both these movements could contribute to forward propulsion without contributing to vertical displacement relative to the locomotor surface. Consequently, one might expect lizards to rely more on pelvic rotation and femur retraction on inclines compared with locomotion on level surfaces. Pelvic rotation did differ significantly among surfaces such that the greatest amounts generally occurred on the uphill surface. Increased amounts of pelvic rotation were not simply a generalized response to inclined surfaces because downhill locomotion consistently showed the lowest values. Instead, the greater amounts of pelvic rotation for uphill locomotion may reflect an increased importance of the axial structures in contributing to the propulsive forces needed to travel uphill compared with those for moving on level and downhill surfaces. Although the initial (minimum) angle of femur retraction differed significantly among inclines, the angular excursions indicating the total amount of femur retraction per stride (Fig. 10A) were striking for their lack of significant variation among inclines.

Unlike pelvic rotation and femur retraction, rotation of the femur creates a component of movement that is perpendicular

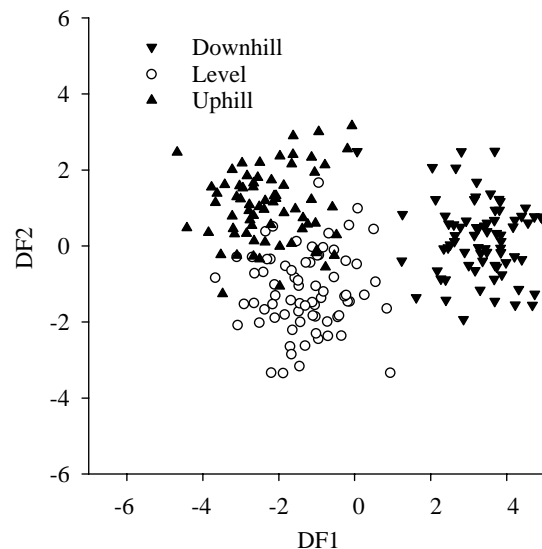


Fig. 11. Discriminant function 1 (DF1) versus discriminant function 2 (DF2) from a discriminant function analysis of 17 kinematic variables. Each point is for an individual stride. Circles, upside-up triangles and upside-down triangles represent locomotion on the level, uphill and downhill surfaces, respectively. Table 4 provides the canonical loadings for both discriminant functions.

Table 4. Loadings from a discriminant function analysis on 219 strides of uphill, downhill and level locomotion

Variable	DF1	DF2
Stride length	0.07	-0.23
Step length	0.16	-0.32
Stride duration	0.06	-0.11
$Y_{\text{hipfootfall}}$	-0.42	-0.33
$\Delta Y_{\text{hipstance}}$	-0.05	-0.12
$\Delta Y_{\text{hiptotal}}$	0.02	-0.27
Knee angle (footfall)	-0.17	-0.45
Knee angle (end stance)	-0.23	0.02
Ankle angle (footfall)	-0.07	-0.44
Ankle angle (end stance)	-0.09	-0.05
Pelvic rotation	-0.12	0.22
Minimum femur retraction	-0.28	0.15
Maximum femur retraction	-0.14	-0.06
Minimum femur depression	-0.34	-0.39
Maximum femur depression	-0.49	-0.26
Minimum femur rotation	0.21	0.63
Maximum femur rotation	-0.35	-0.11

Substantial loadings (≥ 0.4) are marked in bold type.

Canonical correlations for DF1 and DF2 were 0.93 and 0.68, respectively.

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

to the locomotor surface because of the changing angle of the crus relative to the locomotor surface. The total amount of femur rotation (Fig. 10C) showed highly significant variation among inclines. Furthermore, the diminished amounts of femur rotation on both the inclined surfaces compared with the level surface are consistent with kinematics on inclined surfaces being modified to decrease the vertical oscillations relative to the locomotor surface. Besides reduced vertical oscillation, the reduced height of the animal should also contribute to stability on inclines by keeping the center of mass close to the surface.

The caudofemoralis muscle of ectothermic vertebrates has an origin and insertion such that it contributes to both retraction and rotation of the femur (Ashley-Ross, 1995; Gatesy, 1991; Reilly and Delancey, 1997a,b). Thus, one might expect femur rotation and retraction to be tightly coupled. The timing of changes in angles is strikingly similar for both femur rotation and femur retraction within individual strides (Fig. 4). Hence, femur rotation and retraction are temporally coupled. However, the amount of femur rotation on the downhill surface was significantly smaller than that for the other surfaces, whereas the amounts of femur retraction were very similar on all surfaces. Therefore, the amplitudes of femur retraction and femur rotation can be decoupled when *D. dorsalis* moves on different inclines. Among different inclines, the minimum angles of femur retraction and rotation (indicating the limb position near the beginning of stance) varied in a fashion which further suggests that these two types of movement can be decoupled for animals moving on different surfaces. Since the

value of femur rotation at the beginning of stance was positive (i.e. the ankle is posterior to the vertical plane passing through the femur), *D. dorsalis* is able to decrease its hip height at footfall by having a greater initial rotation of the femur, and this has little apparent adverse effect on the ability of the animal to propel itself in part *via* femur retraction. Some lizards might have negative initial angles of femur rotation; hence, the general mechanism for decreasing hip height in animals with sprawling limb posture would be to have initial values of femur rotation that deviated more from zero (indicating that the lower leg is perpendicular to the locomotor surface). This mechanism of decreasing hip height by rotation of the femur would not work for most species of endothermic vertebrates where the limbs are nearly confined to a parasagittal plane.

The 'sprawling' posture of many ectothermic vertebrates is commonly viewed as a design inferior to that of the 'upright' limbs of endothermic vertebrates (for a review, see Gatesy, 1991). However, an apparent advantage of a 'sprawling' limb is that femur rotation can decrease hip height on inclined surfaces, and movements such as pelvic rotation and femur retraction can decouple longitudinal from vertical movements. Therefore, even generalized lizards such as *D. dorsalis* have behavioral mechanisms for adjusting hip height and minimizing vertical oscillations on inclined surfaces. This combination of limb posture and behavioral mechanisms may help to explain why so many lizards climb well and why so many clades of lizards have invaded arboreal habitats.

Comparisons with other vertebrates

Three recent studies have clarified the effects of incline on the movements and function of the hindlimb of endothermic vertebrates. On level surfaces, joint angles within the hindlimbs of cats (Smith and Carlson-Kuhta, 1995) and squirrel monkeys (Vilensky et al., 1994) decrease during early stance, and measurements of strain in the gastrocnemius muscle of turkeys also suggest some initial compliance of the limb during early stance (Roberts et al., 1997). For all three of these species moving on an uphill surface, the joints were more flexed at footfall and the joints flexed more during early stance compared with locomotion on a level surface (Roberts et al., 1997; Smith and Carlson-Kuhta, 1995; Vilensky et al., 1994). For both cats and squirrel monkeys, the angles of the knee and ankle at the end of stance were greatest for locomotion on the steepest uphill surface (Smith and Carlson-Kuhta, 1995; Vilensky et al., 1994). Similarly, for these two species, the longitudinal positions of the foot relative to the hip at both the beginning and end of stance were shifted posteriorly on the uphill surface, whereas the locations of the foot relative to the hip at both the beginning and end of stance were shifted anteriorly on the downhill surface (Smith and Carlson-Kuhta, 1995; Vilensky et al., 1994). Hip height of cats was lowest for the steepest downhill surface, intermediate for the uphill surface and greatest for the level surface (Smith and Carlson-Kuhta, 1995).

Thus, despite profound differences in limb posture among lizards, birds and mammals, the limited kinematic data had

some common features. For example, similar to all the endothermic taxa above, the limbs of *D. dorsalis* and *I. iguana* (Brinkman, 1981) flex during early stance. Certain kinematic features of *D. dorsalis* on inclined surfaces also closely paralleled those of endothermic vertebrates. For *D. dorsalis* on the downhill surface, the femur is protracted more and retracted less, resulting in an anterior shift in the location of the knee relative to the hip. On the downhill surface, smaller values of the knee angle (Fig. 7A) and the angle of femur rotation (Fig. 9C) at the end of stance also contributed to more anterior positions of the ankle relative to the hip. For *D. dorsalis* on the uphill surface, the femur was protracted the least (Fig. 9A), which shifts the location of the foot posteriorly. For *D. dorsalis*, the rank order of hip height on downhill, level and uphill surfaces was similar to that of the cat. However, unlike the cat, for which the amounts of knee and ankle flexion were greatest for downhill locomotion, these quantities for *D. dorsalis* were greatest on the level surface.

Previous kinematic data for three-dimensional joint angles of ectothermic tetrapods are limited to two species (*Iguana iguana* and *Alligator mississippiensis*) moving on level surfaces. Brinkman (1981) quantified the movements of a moderate-sized lizard (*I. iguana*, snout–vent length 57 cm) walking slowly (speed 0.35 m s^{-1} , duty factor 67%). For *I. iguana*, the angular excursion of femur retraction ranged from 140° to 165° . The amount of femur rotation about its long axis approximated 70° , and the beginning of femur rotation lagged behind the beginning of femur retraction (Brinkman, 1981). From the beginning to the end of stance, the angle of the knee of *I. iguana* changed from 55° to 155° . Gatesy (1991) studied small alligators (*A. mississippiensis*, total length 50–70 cm) walking slowly (speed $0.10\text{--}0.15 \text{ m s}^{-1}$, duty factor 67%). From the beginning to the end of stance, the angle of the knee of *A. mississippiensis* changed from 90° to 130° , and at footfall, mid-stance and the end of stance, the angles of the ankle approximated 90° , 45° and 140° , respectively. For both *I. iguana* and *A. mississippiensis*, the ankle flexed during early stance before extension began (Brinkman, 1981; Gatesy, 1991). For *I. iguana*, the knee flexed during early stance, whereas *A. mississippiensis* lacked any conspicuous flexion of the knee during early stance. Although Peters and Goslow (1983) did not provide values of femur rotation for the salamander *Ambystoma tigrinum*, they found that the femur generally began to rotate only after flexion of the knee during early stance brought the lower leg perpendicular to the femur.

For the slowest speed of locomotion of *D. dorsalis* on the level surface, the angular excursions of femur rotation were similar to the value for *I. iguana*, but the amount of femur rotation for *D. dorsalis* also increased by nearly 30° with increased speed. For all speeds and inclines, the knee of *D. dorsalis* flexed during early stance. This amount of knee flexion was slight ($<10^\circ$) and nearly constant on the uphill surface, whereas the amount of knee flexion during stance for both the level and downhill surfaces was substantial and increased considerably with increased speed (Fig. 7B). In contrast to the observations of Peters and Goslow (1983) for

A. tigrinum, rotation of the femur of *D. dorsalis* generally began immediately after footfall and was coincident with femur retraction (Fig. 4). The similar patterns of knee flexion in *I. iguana* and *D. dorsalis* may reflect their close phylogenetic affinity compared with the distantly related crocodylians. However, the limited number of ectothermic tetrapod taxa for which joint angles have been quantified and the effects of different locomotion speeds both have great potential to confound interspecific comparisons such as those discussed above.

Morphological versus effective limb length

Long hindlimbs are frequently considered to enhance sprinting speed, and several comparative studies of lizards have found positive correlations between maximal speed and the anatomical length of the hindlimb relative to body size (Bauwens et al., 1995; Losos, 1990; Miles, 1994). However, the distance from the hip to the nearest point of contact with the ground (effective limb length) depends on the orientation and flexion of elements in the limb. The only available data for the effective limb length of lizards are those of Fieler and Jayne (1998), who found that effective limb lengths at footfall for *D. dorsalis* moving slowly could be as low as 58% of the combined lengths of the femur and tibia. Furthermore, most studies that have previously calculated effective limb lengths of vertebrates have used two-dimensional projections onto a vertical (sagittal) plane (Farley et al., 1993; Fieler and Jayne, 1998; Gatesy and Biewener, 1991). Changes in effective limb length during stance and vertical oscillations of the center of mass (near the hip of lizards) both figure prominently in biomechanical models of limb function such as the mass-spring model (Alexander, 1989; Farley et al., 1993; McMahon et al., 1987).

For *D. dorsalis* on inclined surfaces, the lower height of the hip and the tendency of the ankle to be located more nearly lateral to the hip can greatly reduce effective limb length when it is calculated in an x - y plane. For example, for the downhill, uphill and level surfaces, the mean values of three-dimensional effective limb length at footfall for 50 cm s^{-1} were 2.62, 2.77 and 3.27 cm, respectively; at 250 cm s^{-1} , the mean values were 3.20, 3.51 and 4.55 cm, respectively. When expressed as a percentage of the three-dimensional values, for the downhill, uphill and level surfaces, the mean values of two-dimensional effective limb length at footfall for 50 cm s^{-1} were 61%, 77% and 81%, respectively; for 250 cm s^{-1} , the mean values were 63%, 80% and 83%, respectively. For this sample of *D. dorsalis*, the mean value of the length of the femur plus that of the tibia was 4.56 cm. Consequently, the mean values of two- and three-dimensional effective limb lengths for downhill locomotion at 50 cm s^{-1} are only 35% and 57%, respectively, of the anatomical length of the relevant portions of the hindlimb.

The effects of incline on effective limb length and performance of lizards may vary because of interspecific differences in morphology or kinematics. For example, Irschick and Jayne (1998) found that the long-limbed bipedal

specialist *Callisaurus draconoides* showed decreased maximal speed and stride length when running up a 30° incline, whereas a shorter-limbed sympatric species (*Uma scoparia*) was affected minimally by an inclined surface. The hindlimbs of many lizards that frequently climb on flat surfaces, such as *Anolis* species, geckos and certain sceloporines, appear dorsoventrally flattened in a fashion similar to that observed for *D. dorsalis* on inclines in this study. The effects of incline on limb movements within the morphologically generalized *D. dorsalis* may therefore parallel some of the evolutionary transitions from a terrestrial to a climbing specialist that uses flat surfaces. However, another type of climbing specialization found in lizards is the ability to use narrow perches (e.g. some *Anolis* species). Narrow perches force the feet to be more medial, and a more medial location of the ankle will often decrease the effective limb length. Furthermore, movements such as femur retraction may be less effective for movement on narrow perches than extension of joints within the limb. Thus, future comparative studies of perch specialists and flat-surface climbers will provide a test of whether limb movements and function are fundamentally different for these two types of movement on inclined surfaces.

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