The Journal of Experimental Biology 201, 609–622 (1998)
Printed in Great Britain © The Company of Biologists Limited 1998
JEB1321

EFFECTS OF SPEED ON THE HINDLIMB KINEMATICS OF THE LIZARD *DIPSOSAURUS DORSALIS*

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Accepted 18 November 1997: published on WWW 26 January 1998

Summary

Lizards are the most diverse extant lineage of vertebrates believed to have retained the sprawling limb posture of ancestral tetrapods and, although the sprinting speeds of lizards are well documented, quantitative analyses of limb movements are lacking. We therefore examined a wide range of steady running speeds to quantify variation in the kinematics of a morphologically generalized hindlimb in the lizard *Dipsosaurus dorsalis*. From speeds of 50 to 350cm s^{-1}, stride length, step length and stride frequency all had significant curvilinear increases from 13.3 to 39.4cm, from 8.9 to 12.8cm and from 3.9 to 8.6Hz, respectively, whereas duty factor (percentage of cycle when foot is on ground) decreased from 63 to 34% with increased speed. For five standardized speeds ranging from 50 to 250cm s^{-1}, analyses of variance detected highly significant (*P*<0.001) effects of speed on 27 out of a total of 46 kinematic variables. The height of the hip at the time of footfall increased significantly with increased speed, whereas the amount of pelvic rotation in the horizontal plane (mean 36°) per stride was unaffected by speed. The orientation of the long axis of the foot changed by nearly 50° with increased speed such that the foot was nearly straight forward at 250cm s^{-1}, and at high speeds the heel often did not touch the ground. The effective length of the limb at footfall nearly doubled with increased speed as a combined result of increased plantar flexion and knee extension and a more erect femur. The pervasive effects of speed on hindlimb kinematics observed for this species do not conform simply with previous generalizations of lizards as having plantigrade foot posture and sprawling limbs.

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

Introduction

Limb postures of vertebrates are commonly grouped into categories that are defined by examples rather than by quantitative criteria (Gatesy, 1991). For example, the limb posture of most extant birds and mammals is categorized as upright, whereas most extant amphibians and reptiles have a sprawling limb posture, which is generally regarded as the ancestral condition for tetrapodal vertebrates (Rewcastle, 1981; Hildebrand, 1985). In anterior view, limbs with upright posture appear to extend straight down from the hip so that the foot appears to be directly beneath the hip. In contrast, for hindlimbs with typical sprawling posture, the femur is nearly parallel to the ground, the knee is lateral to the hip, the ankle is below the knee and, thus, the ankle and foot are lateral to the hip. Hence, during locomotion, the upright limbs of endothermic vertebrates are largely confined to a parasagittal plane, whereas the sprawling limbs of ectothermic vertebrates have considerable movement in the horizontal (frontal) plane (Rewcastle, 1981). However, with the exception of Reilly and Delancey (1997), most of the scant kinematic data available for the limbs of ectothermic vertebrates are for a single speed or a range of relatively slow speeds. Thus, it is not entirely clear whether generalizations regarding sprawling limb posture for ectothermic vertebrates have been biased by the lack of quantitative kinematics at high speeds.

Lizards and salamanders are two major lineages of extant vertebrates with species that most closely resemble the sprawling limb posture of ancestral tetrapods (Ashley-Ross, 1994*a*). Although several species of lizards retain many aspects of the ancestral sprawling posture and limb movement (Brinkman, 1981), many species of lizards also have a variety of derived morphologies and locomotor behaviors not found in salamanders. For example, the length of the hindlimbs in many species of lizards is often much greater than that of the forelimbs, and this morphological specialization is associated with the specialized behavior of bipedal running (Snyder, 1952, 1954). Most species of lizards also appear to move with a greater range of velocities than those that can be elicited from salamanders. Hence, comparative studies of the kinematics of the limbs of lizards are especially useful for clarifying: (1) the nature of locomotion with sprawling limbs, (2) the extent to which morphological specializations are correlated with specialized locomotor behaviors, and (3) the extent to which different speeds are attained by altering the posture and movement of the limbs.

Several species of lizards have served as model systems for studying whole-animal locomotor performance such as sprinting speed (reviewed in Garland and Losos, 1994); however, the limb movements involved in rapid locomotion have not been studied quantitatively. For many species of lizards, the front limbs commonly do not contribute propulsive force at higher speeds; hence, understanding the function of the hindlimbs of lizards is especially important since they are used for all speeds of locomotion in all species of lizards. Snyder's (1952, 1954) qualitative analysis of the hindlimb movements of lizards focused primarily on bipedal species, and most additional studies of hindlimb movements in lizards have also been qualitative and for a minimal range of locomotor speeds (Brinkman, 1981). Even Reilly and Delancey's (1997) recent quantitative study of the hindlimb kinematics of a lizard was limited to different speeds of walking (duty factor >50 %). Some previous studies of the locomotor performance of lizards have also documented the stride frequency and/or stride length during sprinting (Huey, 1982; Huey *et al.* 1984; Marsh, 1988), but additional movement data are minimal. Although Losos and Sinervo (1989) and Losos (1990) correlated hindlimb morphology to the sprinting ability of *Anolis* lizards, no aspects of the limb movements involved in attaining maximal sprinting speed were quantified.

Locomotor performance is a complex result of morphology, physiology and behavior; therefore, the functional consequences of morphological variation are usually not apparent until the movements and behaviors of intact animals are documented. For example, if species of lizards with long limbs took short steps, then they might not move any faster than a species of lizard with short limbs that takes long steps. Hence, behavior can confound the relationship between morphology and performance, and the current lack of information on limb movements complicates our understanding of the relationship between limb morphology and locomotor performance.

The goal of the present study is to quantify the hindlimb kinematics of a lizard (*Dipsosaurus dorsalis*) with a generalized limb morphology over a broad range of speeds. Specifically, we determine the effects of speed on: (1) stride frequency and length, (2) step length, (3) effective limb length, (4) foot posture and (5) several additional variables describing the positions and amplitudes of movements of the hip, knee, ankle, metatarsals and fourth toe.

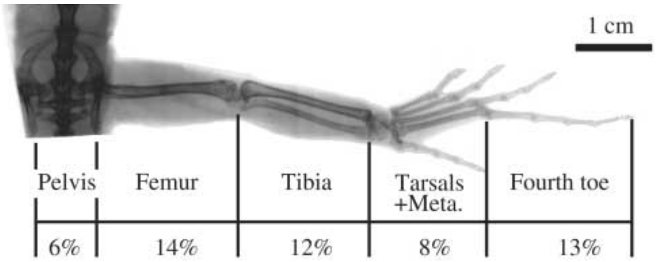

Fig. 1. Radiograph of a dorsal view of the right hindlimb of a desert iguana *Dipsosaurus dorsalis* with a snout–vent length of 12.0 cm. The relative lengths given below each anatomical location are percentages of hindlimb span, and they are mean values for the four individuals studied rather than for the single individual shown in the figure. As in many iguanian lizards, the lengths of the femur and tibia are similar, and the fourth toe is extremely long. Meta., metatarsals.

Materials and methods

Experimental subjects

We studied the desert iguana *Dipsosaurus dorsalis* (Baird and Girard), partly because its hindlimb morphology is fairly generalized for iguanian lizards. For example, *D. dorsalis* lacks the extreme elongation of the hindlimbs found in bipedal specialists (Snyder, 1954) or any of the specialized foot structures for prehension or clinging that are found in many arboreal specialists (Williams and Peterson, 1982; Peterson, 1984). Furthermore, as for 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 (Fig. 1). This species also runs reasonably well on a treadmill over a broad range of speeds, and considerable background information is available on its locomotor performance and muscle physiology (Gleeson, 1991).

We collected all lizards near Yuma, Arizona, 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. Video-taping sessions extended from approximately 1 week to 3 months after we had captured the lizards. After video-taping eight individuals, we selected four individuals that matched all the speeds required for a balanced experimental design for the primary statistical analysis. We chose four lizards that also had very similar size, as indicated by the following mean ± 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), tail length 21.5±1.1 cm (19.2–24.5) cm, and hindlimb span (HL span) 17.3±0.3 cm (16.8–17.7 cm). For these four individuals, we obtained the following mean ± s.e.m. values (% HL span): the width of the pelvis (between the acetabula) 5.5±0.2 %, and the lengths of the femur 14.2±0.1 %, tibia 12.4±0.1 %, foot (from heel to base of the fourth toe) 7.9±0.1 % and fourth toe 12.6±0.2 % (Fig. 1).

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 images s^{-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 30 s. Immediately before and after the lizards ran on the treadmill in preliminary trials using this protocol, we used a thermocouple and a Tegam 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 ranging from 50 to 250 cm s^{-1} at 50 cm s^{-1} intervals. Prior to video-taping, we painted key landmarks on the pelvis and hindlimb of each lizard in order to facilitate digitizing. 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. We concentrated on the following landmarks of the hindlimb: hip, knee and ankle, and the base, middle and tip of the long fourth toe (excluding the claw). We excluded the claw because its tapering tip was difficult to see on the video tapes.

Kinematics

For each stride, we divided stride length (cm) by stride duration (s) to calculate an average forward velocity. For each lizard at each speed, we selected four strides of steady-speed (±10 % of average forward velocity) locomotion for frame-by-frame motion analysis. We defined the *x*-axis as the horizontal dimension parallel to the overall direction of travel and the tread surface, the *y*-axis as the vertical dimension perpendicular to the tread surface, and the *z*-axis as perpendicular to the *x*–*y* plane. We used video analysis software (MeasurementTV, Datacrunch Inc., San Clemente, CA, USA) to digitize the *x*–*y* coordinates of the pelvis, knee, ankle, metatarsals and phalanx 2, and the toe tip of the long fourth toe, from the lateral view. We used the dorsal view to digitize the angles of the metatarsals and phalanges relative to the *x*-axis, and the *x* and *z* coordinates of the right and left sides of the pelvis and heel. From the coordinates, we calculated variables describing (1) whole-limb movements (2) hip and pelvic movements, (3) movements within the hindlimb, and (4) limb and foot posture.

Five variables described movements of the whole limb and attributes of the entire locomotor cycle. Stride length (STRIDEL) was the distance traveled along the *x*-axis between successive footfalls of the right hind foot, whereas step length (STEPL) was the distance traveled by the body along the *x*-axis while the foot touched the ground. Cycle duration (CYCLE) was the time between successive footfalls of the same foot, and stride frequency (FREQUENCY) was the inverse of CYCLE. Duty factor (DUTY) was the percentage of CYCLE when the foot was on the ground.

Three variables described movements of the hip and pelvis. For each stride, we calculated the mean height of the hip relative to the tread surface (HHEIGHT), and vertical hip excursion (VHIPEXCUR) equaled the difference between maximum and minimum heights of the hip within a stride. After we had calculated the angle of the pelvis relative to the *x*-axis from the dorsal view of each image, we calculated pelvic rotation (PROTATION) as the difference between the maximum and minimum values within each stride.

To describe movements within the hindlimb, we calculated six variables for each of five anatomical locations including the knee (KNEE), the ankle (ANKLE), the distal end of the fourth metatarsal (META) and the base of phalanx 2 (MIDTOE) and the tip of the fourth toe (TOETIP). We used one frame of reference that was relative to the locomotor (tread) surface and another that was relative to the hip of the lizard. To facilitate visualizing movements of the limb relative to the hip, the *x* and *y* coordinates of each limb location were standardized so that the hip was positioned at the origin in the *x*–*y* plane. Plots of these relative coordinates facilitated visualizing hindlimb movements because each of the resulting loops represented the path traveled by a limb element as seen in lateral view while the hip of the lizard remained stationary. For each such loop representing a single cycle, X_{min} and X_{max} described the most anterior and mostposterior positions relative to the hip, respectively. Positive and negative values of X indicate positions anterior and posterior to the hip, respectively. The total horizontal excursion relative to the hip (ΔX) equaled $X_{\mathrm{max}}–X_{\mathrm{min}}$. Similarly, we calculated the maximum height relative to the hip (Y_{max}) and the minimum height relative to the hip (Y_{min}), where positive and negative values indicate positions dorsal and ventral to the hip, respectively. The vertical excursion of each limb element (ΔY) equaled $Y_{\mathrm{max}}–Y_{\mathrm{min}}$. Hence, the names of the thirty variables describing movements within the limb all include a dimension and an anatomical location. For example, the variable ΔY ANKLE refers to the total vertical movement per stride of the ankle relative to the hip.

Eight variables described limb and foot posture. At footfall, we measured the effective limb length (LIMBL) of the entire limb as the straight line distance in lateral view from the hip to the most posterior portion of foot contact (Fig. 2). After determining LIMBL, we determined the contributions of the femur (FEMURL), the tibia (TIBIAL), the tarsals plus the fourth metatarsal (METAL) and the fourth toe (TOEL) (Fig. 2). We measured three additional variables from the

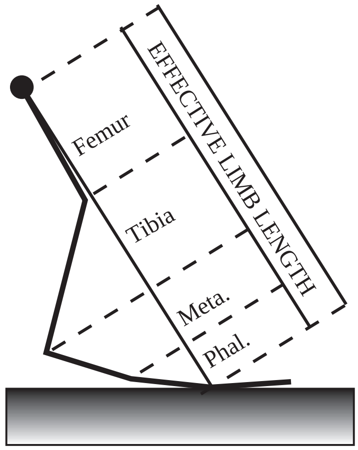

Fig. 2. Schematic diagram of the right hindlimb in lateral view at footfall. The straight-line distance from the hip to the most posterior point of foot contact equals the effective limb length (LIMBL), and we partitioned LIMBL into contributions from the femur, tibia, metatarsals (Meta.) and phalanges (Phal.).

dorsal views at the earliest time during the stance phase when heel height was at a minimum: the angles of the metatarsals (AMETA) and fourth toe (ATOE) relative to the *x*-axis, and the width of stride (WIDTH), which equaled the difference between the *z* coordinates of the right and left heels (at the earliest time of minimum heel height for each foot).

Statistical analyses

For statistical analysis, we performed two-way mixed-model analysis of variance (ANOVA) using SYSTAT version 5.0. Speed was the fixed factor (N=5), whereas individual was the random factor (N=4). For each ANOVA, four strides were analyzed for each individual. Following Zar (1996), we calculated F-tests for significant effects of speed by dividing its mean squares by the two-way interaction term. Forty-six ANOVAs were performed; hence, a Bonferroni correction for multiple comparisons would yield a P-value of approximately 0.001. Consequently, we emphasize results with P<0.001. However, because this is a very conservative correction that is quite likely to reject genuinely significant effects, we also provide the exact values of the F-tests to clarify the magnitude of the speed effects. We also calculated linear and quadratic least-squares regressions that predicted stride length and frequency from speed, and in these analyses we used combined data from the five standardized speeds and some faster (>270 cm s^{-1}) speeds that were not used in the ANOVAs.

Results

General description of limb movement

The hip (Figs 3B, 4B) and axial structures of the lizard moved forward with a constant speed as the limb oscillated relative to the hip. The hindlimb and hip also oscillated vertically relative to the tread surface with complicated, non-sinusoidal patterns (Figs 3A, 4A). The amplitudes of vertical oscillations of the hip were small compared with those of the limb elements. Consequently, the waveforms of vertical displacement of the limb elements relative to the tread (Figs 3A, 4A) and hip were fundamentally similar. In contrast, transforming the longitudinal displacements of the limb from a tread (Figs 3B, 4B) to a hip frame of reference created a different pattern of oscillation very similar to a sinusoid.

From immediately after footfall until the middle of the stance phase (Fig. 5, Fig. 3A at 75 ms; Fig. 4A at 20 ms), the height of the hip declined, and then it usually increased for the remainder of the stance phase. During the stance phase,

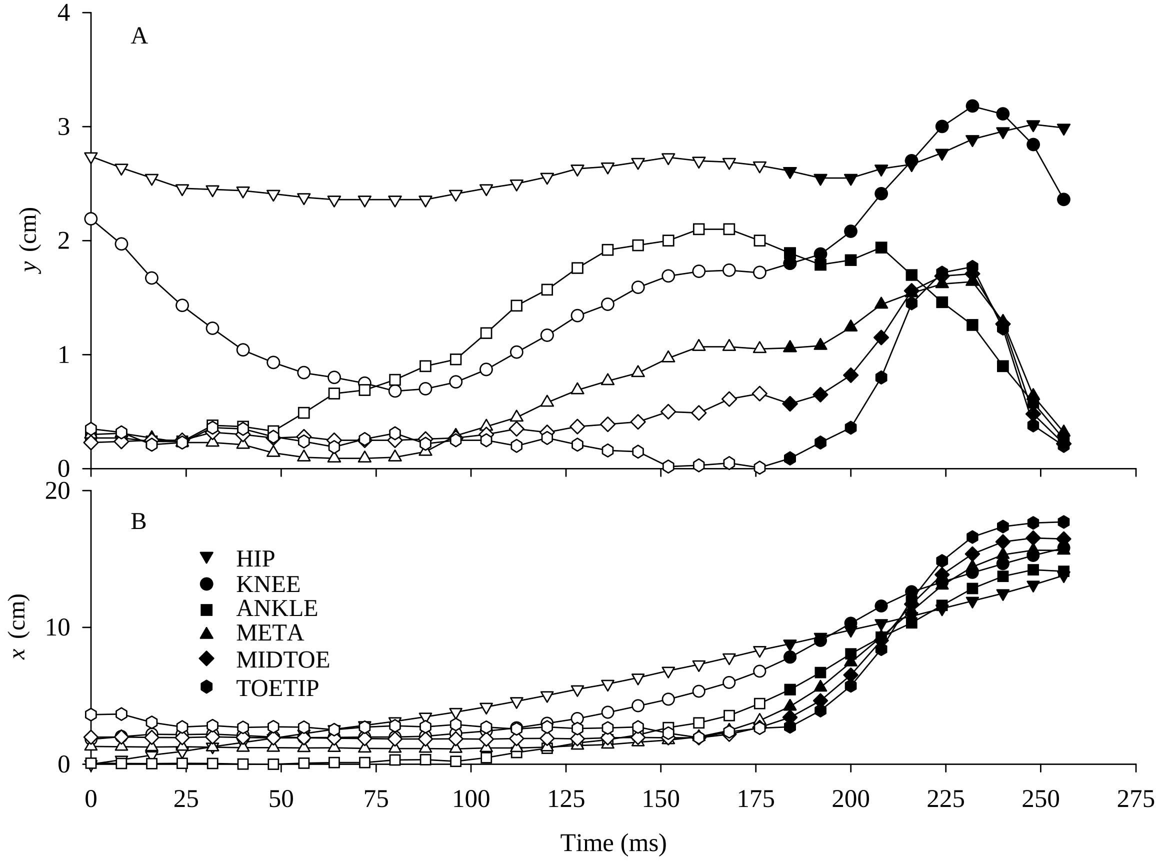

Fig. 3. Longitudinal (A) and vertical (B) displacements of the hip, knee, ankle, metatarsals (META) and the middle (MIDTOE) and the tip of the fourth toe (TOETIP) relative to the tread surface for one stride at a forward speed of 50 cm s^{-1}. Open and filled symbols represent the stance and swing portions of the stride, respectively. To enhance the clarity of the illustration, we used a low-bandpass filter with a cut-off frequency of 45 Hz on the raw data (sampled at 250 Hz). The time between successive points of the illustrated filtered data is 8 ms. The axes for Figs 3 and 4 are drawn to the same scale to facilitate comparison of the slopes of the graphs.

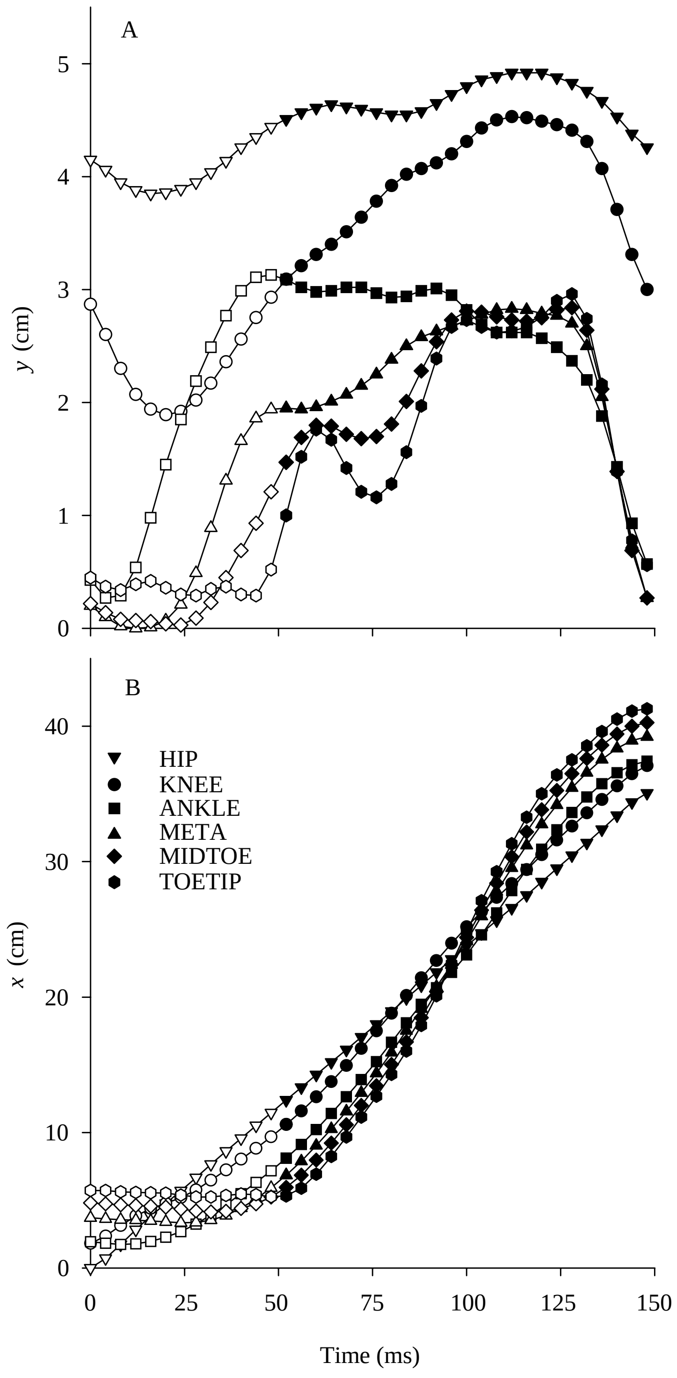

Fig. 4. Longitudinal (A) and vertical (B) displacements of the hip, knee, ankle and metatarsals (META), and the middle (MIDTOE) and tip of the fourth toe (TOETIP) relative to the tread surface for one stride at a forward speed of 250 cm s^{-1}. Open symbols represent the stance portion of the stride, and filled symbols represent the swing portion of the stride. Data were filtered as in Fig. 3, and the time between successive points is 4 ms. The axes for Figs 3 and 4 are drawn to the same scale to facilitate comparison of the slopes of the graphs.

changes in the heights of the hip and knee were nearly in phase, but the amplitude of vertical movements of the knee was nearly twice that of the hip (Figs 3A, 4A). After the ankle began to move up and away from the tread surface (Fig. 3A, 50 ms; Fig. 4A, 12 ms), a progression of movements lifted the foot from proximal to distal, such that the tip of the fourth toe had the last contact with the tread surface. Interestingly, elevation of the ankle began while the height of the knee was still decreasing relative to the tread surface, and the ankle was commonly as high or higher than the knee during late stance (Figs 3A, 4A, 5). During stance, the vast majority of longitudinal limb movements were oriented posteriorly. For ectothermic tetrapods, posterior and anterior movements of the knee caused by rotating the femur relative to the hip (as seen in dorsal view) are referred to as femoral retraction and protraction, respectively (Edwards, 1977).

At the start of the swing phase (Fig. 3A, 180 ms; Fig. 4A, 50 ms), the height of the ankle relative to the tread was near its maximum and equal to that of the knee, but for the remainder of the swing phase the height of the knee greatly exceeded that of the ankle. The height of the knee relative to the tread increased for approximately the first two-thirds of the swing phase and then decreased rapidly through the end of swing (Figs 3A, 4A). Maximal height of the hip generally occurred during the latter half of the swing phase (Figs 3A, 4A). During the final portion of the swing phase, the heights of all parts of the limb rapidly decreased as the foot approached the tread surface (Figs 3A, 4A).

Longitudinal movements of the limb during the swing phase were initially anterior but then reversed direction just prior to the end of swing. Thus, the swing and stance phases did not correspond exactly with the protraction and retraction of the limb, respectively. The velocities of movements relative to the hip increased from proximal to distal in the limb, and this was most conspicuous for the velocities of limb protraction during swing.

In addition to considering the components of movement in the x and y directions independently, the stick figures of the hindlimb (Fig. 5) facilitate visualization of the combined effects of vertical and longitudinal movements. Furthermore, plotting y *versus* x helps to visualize the paths (loops) traveled by the different portions of the hindlimb relative to the hip (Fig. 6). As indicated by the closer spacing between successive points, velocities in the x direction were generally lowest at the extreme anterior and posterior portions of the loops, which corresponded to the transition between stance and swing and between swing and stance, respectively. Rather than the loops of movement resembling a simple shape such as an ellipse, the loops generally lacked any simple pattern of overall symmetry about either a vertical or longitudinal axis. These loops also nicely illustrate the successive increases in longitudinal distance traveled proceeding from the proximal to the distal elements of the hindlimb.

Effects of speed

Modulating the frequency and amplitude of limb movements are two general mechanisms by which animals can modulate speed and, as shown in Fig. 7, both the length and frequency of the strides of *D. dorsalis* showed highly significant

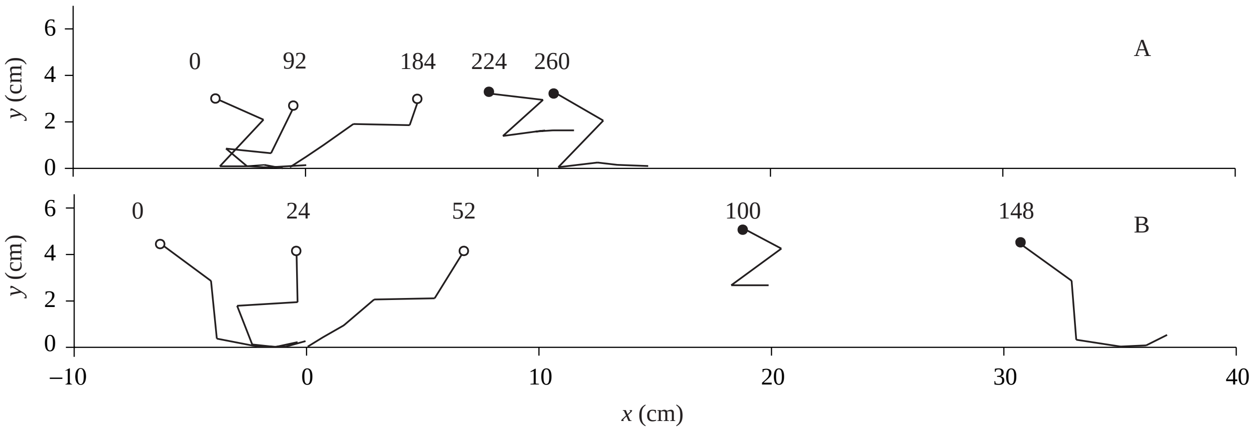

Fig. 5. Stick figures showing a lateral view of hindlimb movements relative to the treadmill for one stride at speeds of 50 cm s^{-1} (A) and 250 cm s^{-1} (B). From proximal to distal, the line segments represent the femur, tibia, metatarsals, the proximal two phalanges, and the distal two phalanges of the fourth toe. Stick figures include the beginning and end of stance and times at approximately mid-stance and mid-swing. Numbers above each stick figure indicate elapsed time (ms). The strides shown are for the same data in Figs 3 and 4. Open and filled circles indicate the hip during stance and swing, respectively.

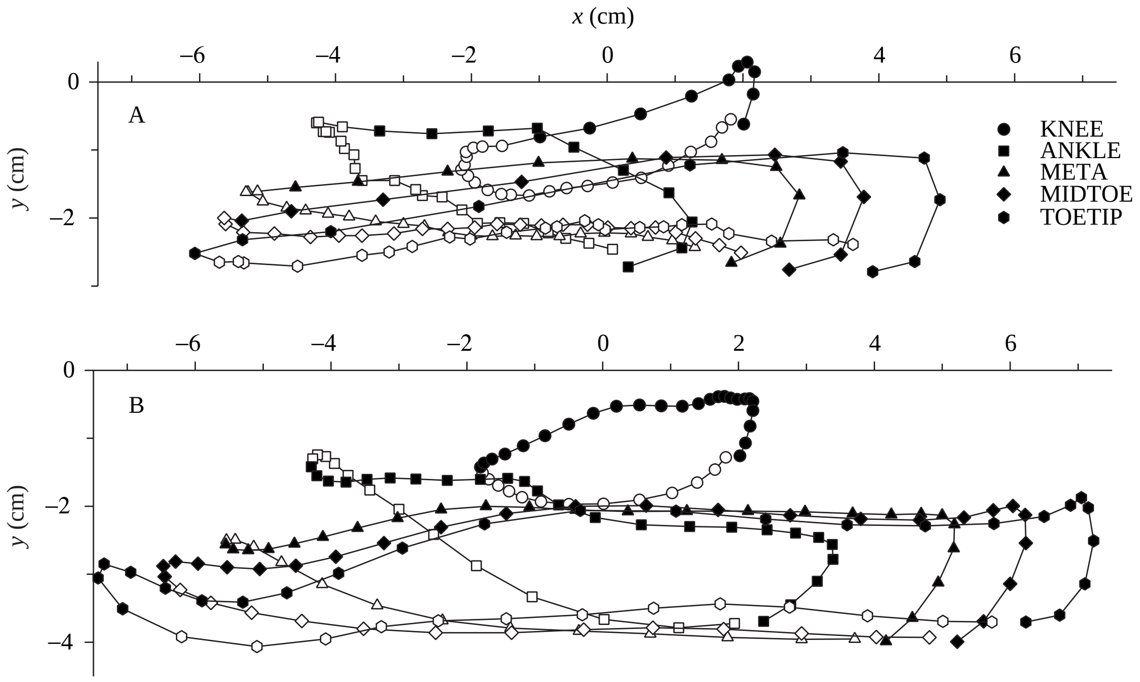

Fig. 6. A lateral view of the paths traveled relative to the hip of the KNEE, ANKLE, META, MIDTOE and TOETIP landmarks for speeds of 50 cm s^{-1} (A) and 250 cm s^{-1} (B). The hip is located at (0,0). The open symbols represent the stance portion of the stride, and the filled symbols represent the swing portion of the stride. The direction of overall movement in the loops is clockwise. In A and B, the times between successive points are 8 and 4 ms, respectively.

curvilinear increases as speed increased. For 50, 200 and 350 cm s^{-1}, values of stride length (Fig. 7A) and frequency (Fig. 7B) predicted from the regressions were 13.3, 28.8 and 39.4 cm and 3.9, 7.0 and 8.6 Hz, respectively. Hence, the rate of increase in stride frequency diminished more rapidly with increasing speed than that of stride length. For 50, 200 and 350 cm s^{-1}, values of step length (Fig. 7A) and duty factor (Fig. 7C) predicted from the regressions were 8.9, 12.2, 12.8 cm and 63, 42 and 34 %, respectively.

For the remainder of the results, we restricted our statistical analyses to the five standardized speeds ranging from 50 to 250 cm s^{-1}, for which we able to obtained a balanced experimental design suitable for analysis of variance (ANOVA). All of the following *F*-tests for the significance of speed effects that are indicated parenthetically in the text had d.f.=4,12.

From 50–250 cm s^{-1}, speed had highly significant effects on all five variables describing whole-limb movements and

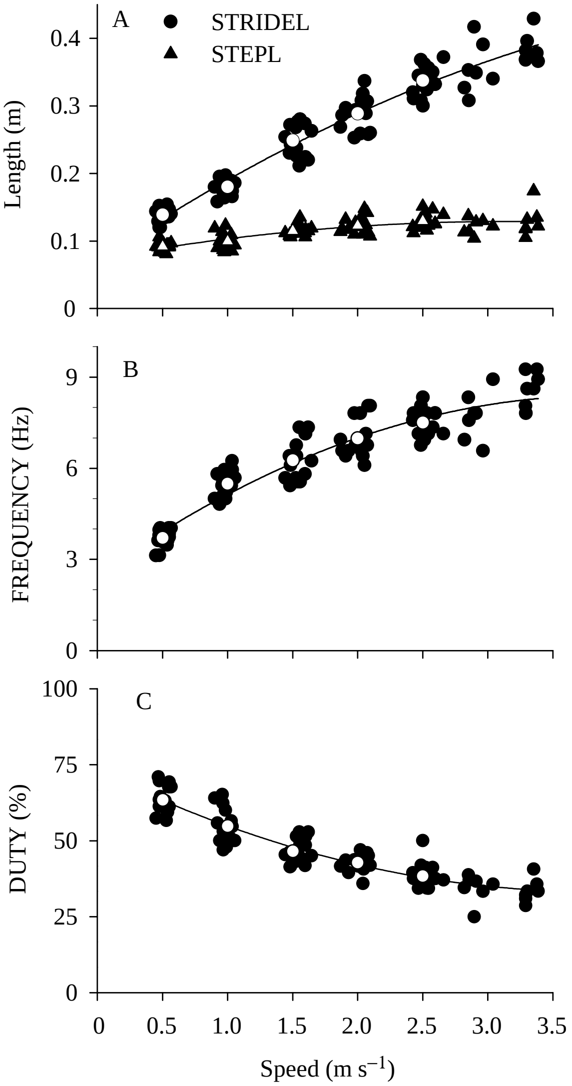

Fig. 7. Plots of the regressions for (A) stride length, STRIDEL (circles), and step length STEPL (triangles), (B) stride frequency, FREQUENCY, and (C) duty factor, DUTY, *versus* forward velocity, *V*. The total of 94 strides shown includes those from the five standardized speeds and 14 strides from speeds greater than $2.7\,\mathrm{m\,s^{-1}}$. Filled symbols indicate individual observations, whereas open symbols indicate mean values for the five standardized speeds used in the ANOVAs. $\mathrm{STRIDEL}=0.071+0.130V-0.011V^2$ ($r^2=0.94$, $P<0.001$). $\mathrm{STEPL}=0.074+0.035V-0.0056V^2$ ($r^2=0.59$, $P<0.001$). $\mathrm{FREQUENCY}=2.50+2.989V-0.360V^2$ ($r^2=0.88$, $P<0.001$). $\mathrm{DUTY}=73.1-21.0V+2.78V^2$ ($r^2=0.85$, $P<0.001$).

attributes of the entire locomotor cycle. Stride frequency ($F=66.0$, $P<0.001$) and stride length ($F=260.0$, $P<0.001$) both increased with increased speed (Fig. 7). Despite the significant ($F=24.6$, $P<0.001$) effects of speed on step length, the increase in step length was relatively small compared with that of stride length (Fig. 7A). Cycle duration decreased ($F=104.4$, $P<0.001$) with increasing speed from a mean value of 0.27 s at $50\,\mathrm{cm\,s^{-1}}$ to 0.13 s at $250\,\mathrm{cm\,s^{-1}}$. Duty factor also decreased significantly ($F=53.3$, $P<0.001$) with increased (Fig. 7C).

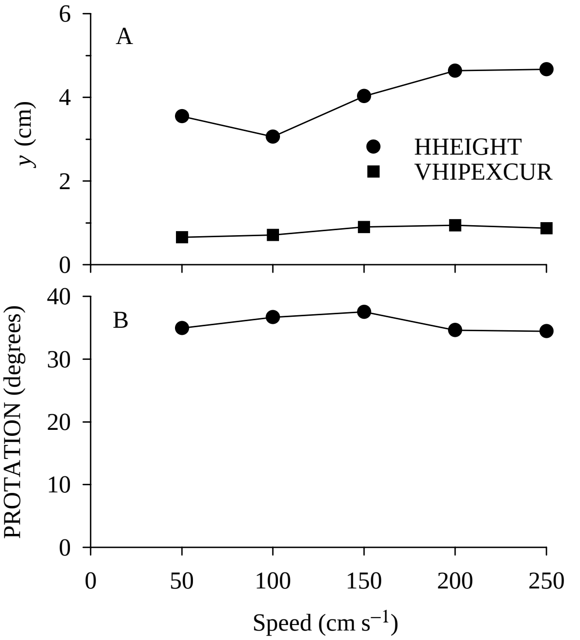

Fig. 8. Mean values of kinematic variables for each of the five standardized speeds used in the ANOVAs for (A) mean hip height, HHEIGHT, and vertical hip excursion, VHIPEXCUR, and (B) pelvic rotation (PROTATION) in the horizontal plane.

Table 1. *Summary of* F*-values (d.f.=4,12) testing for speed effects in the two-way ANOVAs performed separately for each variable describing the hindlimb position and movements relative to the hip*

Landmark	$X_{\max}$	$X_{\min}$	$Y_{\max}$	$Y_{\min}$	ΔX	ΔY
KNEE	0.8	2.2	14.1**	6.3*	2.0	3.0
ANKLE	16.8**	1.2	1.9	12.7**	13.5**	23.3**
META	15.0**	5.2*	6.9*	12.1**	14.7**	16.9**
MIDTOE	18.7**	5.4*	5.7*	12.1**	21.2**	13.5**
TOETIP	13.9**	5.7*	4.5*	12.4**	15.0**	11.7**

*$P<0.05$; **$P<0.001$.

$X_{\max}$, $X_{\min}$ and ΔX are the most anterior and posterior positions relative to the hip, respectively, and $\Delta X=X_{\max}-X_{\min}$.

$Y_{\max}$, $Y_{\min}$ are the most dorsal and ventral positions relative to the hip, respectively, and $\Delta Y=Y_{\max}-Y_{\min}$.

Only one of the three variables for the hip and pelvis varied significantly with speed. Mean height of the hip (Fig. 8A, HHEIGHT) had a significant ($F=6.7$, $P<0.05$) increase of 1.1 cm with increased speed. In contrast, the amplitude of the vertical oscillations of the hip (Fig. 8A, VHIPEXCUR) did not change significantly ($F=3.2$) with speed, and its grand mean was 0.82 cm. The amount of pelvic rotation per stride (Fig. 8B, PROTATION) also did not change significantly ($F=0.5$) with speed, and its grand mean approximated 36 °.

Twenty-four of the total of 30 variables describing limb positions and movements relative to the hip varied significantly ($P<0.05$) with speed, and 17 of these variables had highly significant ($P<0.001$) speed effects (Table 1). The proportion

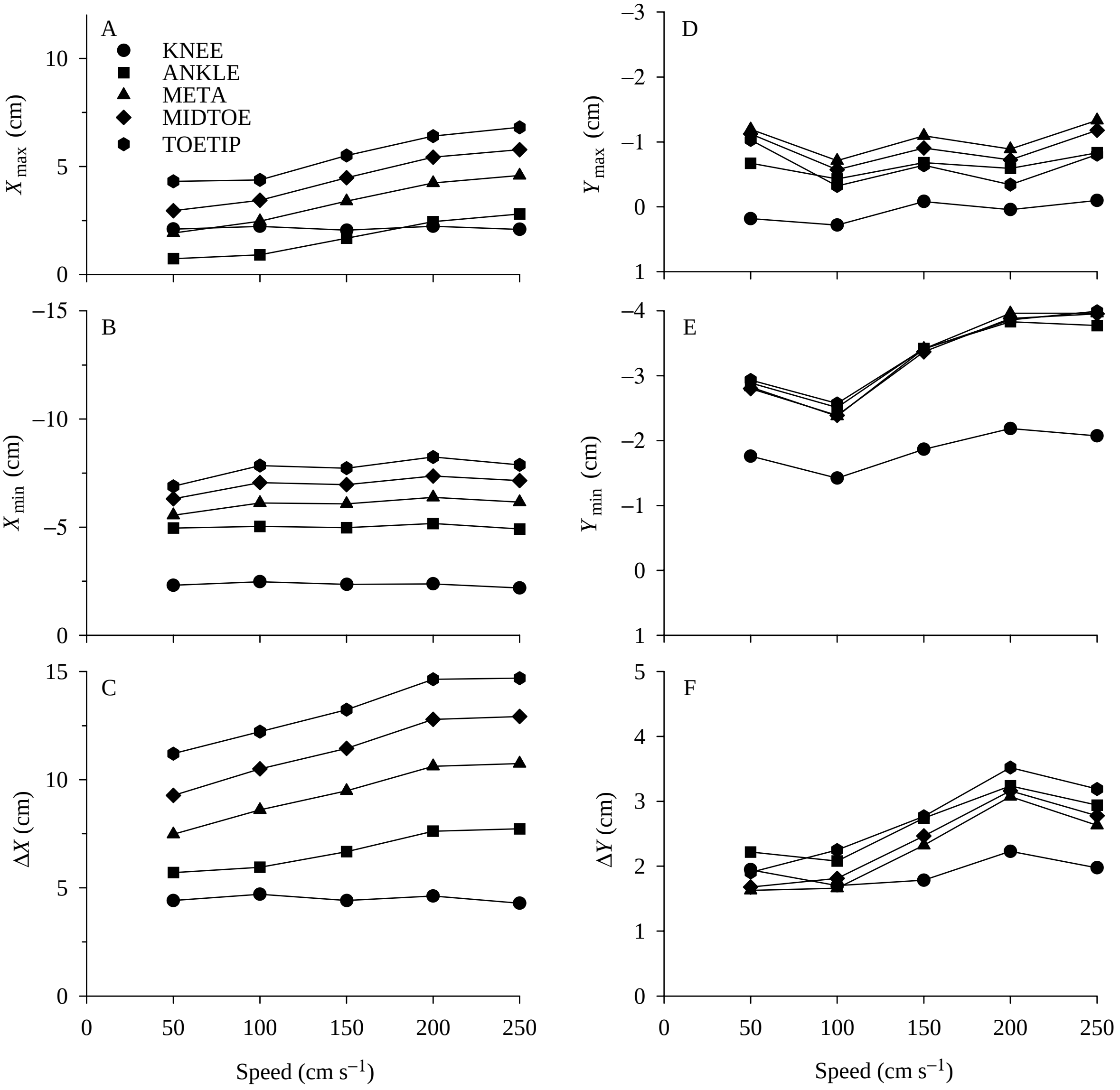

Fig. 9. Mean values of positions and movements of the KNEE, ANKLE, META, MIDTOE and TOETIP landmarks, relative to the hip. (A) Maximum anterior position ($X_{\max}$), (B) maximum posterior position ($X_{\min}$), (C) horizontal excursion ($\Delta X=X_{\max}-X_{\min}$), (D) maximum height ($Y_{\max}$), (E) minimum height ($Y_{\min}$) and (F) vertical excursion ($\Delta Y=Y_{\max}-Y_{\min}$).

of the kinematic variables that changed significantly with speed for each location within the limb also generally increased from proximal to distal (Table 1). For all locations of the limb that were distal to the knee (ANKLE, META, MIDTOE, TOETIP), the most anterior position relative to the hip during a stride ($X_{\max}$) increased with increased speed (Fig. 9A). For example, at the slowest and fastest speeds, the tip of the toe extended anterior to the hip by an average amount of 4.3 and 6.8 cm, respectively. A noteworthy result was that at lower speeds the ankle did not attain as great an anterior position relative to the hip as did the knee, whereas at faster speeds the ankle had a greater anterior position relative to the hip than that of the knee (Figs 5, 6, 9A). In contrast to $X_{\max}$, little conspicuous (Fig. 9B) or statistically significant (Table 1) variation occurred with speed for the most posterior position of the limb elements relative to the hip ($X_{\min}$), and the few apparent changes in this quantity were only between 50 and 100 cm s^{-1} (Fig. 9B). The total (per stride) longitudinal movements relative to the hip (ΔX) had highly significant variation with speed for all parts of the limb that were distal to the knee (Table 1). For the portions of the limb distal to the knee, the overall pattern of change in ΔX with increased speed was generally similar to that of $X_{\max}$ (Fig. 9A,C; Table 1). Within every speed, the rank order of the mean values of ΔX was from proximal to distal (Fig. 9C). The most dorsal location of the knee within the stride cycle ($Y_{\max}$) had a highly significant increase with increased speed, but this quantity lacked a clear pattern of change with speed for the more distal locations of the limb (Fig. 9D; Table 1). The most ventral locations of the limb elements relative to the hip ($Y_{\min}$) varied significantly (Table 1) with speed as values increased conspicuously from 100 to 200 cm s^{-1} (Fig. 9E). The significant pattern of variation with speed for the total dorsoventral movement relative to the hip (ΔY) was generally congruent with that of $Y_{\rm min}$ (Fig. 9E,F). As can be seen most readily from the plots of the paths traveled by the limb elements relative to the hip (Fig. 6), the effects of increased speed on the amounts of change in the longitudinal positions and movements of the limb relative to the hip were larger than those in the dorsoventral direction.

Seven of the eight variables describing the effective lengths of limb elements and foot posture changed significantly with speed. Effective limb length at footfall (LIMBL) increased significantly (F=16.0, P<0.001) with increased speed, ranging from a mean value of 3.0 to 5.1 cm (Fig. 10A). The contributions of the femur (FEMURL), tibia (TIBIAL) and metatarsals (METAL) to the total effective limb length (LIMBL) all increased significantly with increased speed (F=20.6, P<0.001; 5.6, P<0.05; and 7.4, P<0.05; respectively). Furthermore, at the fastest speed, the mean value of FEMURL (2.26 cm) closely approximated the anatomical length of the femur (mean 2.46 cm), which suggests that the femur was nearly parallel to the sagittal plane. The toe did not contribute to the effective length of the limb because the distal portions of the metatarsals always contacted the ground at the moment of footfall for the five standardized speeds (Fig. 10A).

The angles of the both the metatarsals (Fig. 10B, AMETA) and phalanges (APHALANX) had highly significant decreases with increased speed with F-values of 26.6 (P<0.001) and 18.6 (P<0.001), respectively. Hence, at the fastest speeds, the long axis of the foot was pointed nearly straight forward (mean AMETA 5 °), whereas at the slowest speeds it pointed laterally with a mean angle of 50 ° (Fig. 10B). The extent of plantarflexion during foot contact also increased with increased speed. For example, the heel touched the ground at some point during the stance phase for all 48 strides observed with speeds of 150 cm s^{-1} or slower, whereas 19 %, 13 % and 24 % of the strides lacked heel contact at speeds approximating 200 cm s^{-1} (N=16), 250 cm s^{-1} (N=17) and greater than 270 cm s^{-1} (N=17), respectively. Foot posture at the time of footfall also changed considerably with speed: the heel did not touch the ground for only one of the 48 strides with speeds of less than 150 cm s^{-1}, whereas 31 % and 59 % of the strides at 250 cm s^{-1} and greater than 270 cm s^{-1} lacked heel contact at footfall.

To clarify how erect the limbs of *D. dorsalis* were, we determined the angle of the femur relative to the horizontal plane {=arcsine[$(Y_{\rm hip}-Y_{\rm knee})\times(\text{femur length})^{-1}$]}, where 0 ° indicates that the femur is in a horizontal plane and 90 ° indicates that the femur is pointing down, perpendicular to a horizontal plane. For our study, $Y_{\rm max}$ and $Y_{\rm min}$ of the knee indicate when depression of the femur (and knee) is least and greatest, respectively. The angles of femoral depression based on mean values of $Y_{\rm max}$ of the knee (Fig. 9D), ranged from only −5 ° to 1 °, indicating that for at least part of the swing phase the femur was nearly parallel to a horizontal plane. In contrast, angles of femoral depression based on the mean values of $Y_{\rm min}$ for the knee (Fig. 9E) ranged from 35 ° at 100 cm s^{-1} to 63 ° at 200 cm s^{-1}. Femoral adduction properly refers to the angle between the femur and the pelvis as seen from an anterior (two-dimensional) view. Values of $Y_{\rm min}$ of the knee were generally coincident with mid-stance when the x coordinates of the knee and hip were the same; hence, at mid-stance, the angles of femoral depression and adduction would be the same if the pelvis were parallel to a horizontal plane. Assuming symmetry of left and right hip movements, then the angle of the pelvis relative to the horizontal plane equals the arcsine of the difference between the height of the right hip and values of the right hip which have been shifted by one-half cycle (to approximate left hip height) divided by the distance between the left and right pelvic landmarks (13 mm). For speeds of 50

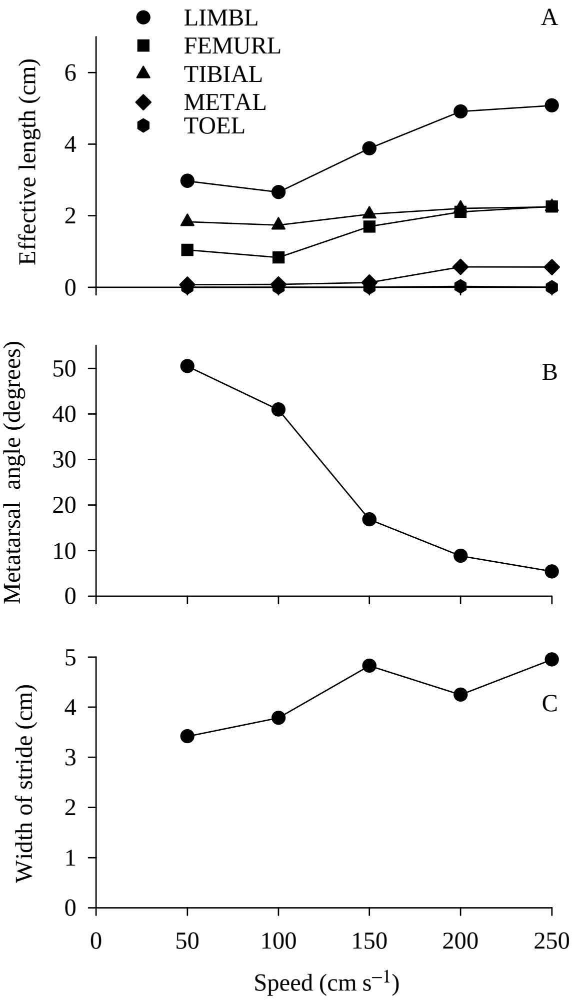

Fig. 10. Mean values of (A) effective limb length at footfall (LIMBL) and the contributions (FEMURL, TIBIAL, METAL and TOEL) of different elements of the limb (femur, tibia, metatarsals and the fourth toe, respectively) to effective limb length. (B) The angle of the metatarsals relative to the x-axis at the earliest time in the stance phase with maximum foot contact with the ground. A value of 0 ° indicates that the long axis of the metatarsals is pointing straight forward. (C) Width of stride is the lateral distance between the right and left feet at the times when the feet are completely touching the ground.

and 250 cm s^{-1}, based on the values of hip height in Figs 3 and 4, the angle of the pelvis relative to the horizontal plane at mid-stance approximated 12 ° and 42 °, respectively. Consequently, increased amounts of pelvic roll at higher speeds probably contributed to the more erect position of the femur relative to the horizontal plane. Calculating the exact angles of femoral adduction during early and late stance requires three-dimensional methods that are beyond the scope of this study.

Despite the increased erectness of the femur with increased speed, the width of strides (WIDTH) increased significantly (F=13.5, P<0.001) with increased speed (Fig. 10C), with mean values ranging from 3.4 to 5.0 cm. Increased values of WIDTH at greater speeds partly reflect the greater lateral distances that the lizards travel during the suspended phase between left and right hind footfalls. WIDTH was also not simply a constant proportion of stride length, as indicated by mean values of WIDTH/stride length of 25 % and 15 % for 50 and 250 cm s^{-1}, respectively.

Some additional trends with increased speed were apparent for aspects of x and y movement which we did not quantify. For example, we plotted x and y (in both fixed and hip frames of reference) *versus* time for 50 and 250 cm s^{-1} using the same x and y scales to facilitate visual comparisons of velocities (slopes). Throughout the stance phase, the speeds of limb retraction were greater for faster speeds of locomotion. During stance, the maximal speeds of foot (landmarks from ANKLE to TOETIP) elevation relative to the hip were also faster for the faster speeds. Interestingly, despite the fivefold difference in speed, the maximal speeds of limb protraction during swing and limb depression during the latter portion of swing were very similar.

Discussion

Comparative hindlimb kinematics

Of all extant groups of vertebrates, salamanders are generally considered the best model for understanding the ancestral condition of tetrapodal vertebrates. Consequently, studies of salamanders have figured most prominently in clarifying how sprawling vertebrate limbs function (Edwards, 1977; Ashley-Ross 1994*a*,*b*). For vertebrates with sprawling limbs, pelvic rotation and femoral retraction and rotation can all contribute substantially to the forward movement of the animal, whereas these movements contribute little to the propulsion of vertebrates with erect limbs (Edwards, 1977). Lateral bending of the vertebral column contributes to rotation of the pelvic girdle within the horizontal plane. Femoral retraction refers to the amount of posterior rotation of the distal femur relative to the hip (as seen in a projection onto a horizontal plane). Femoral rotation refers to rotation of the femur about its long axis. Femoral rotation causes antero-posterior movements of the foot *via* a 'double crank' mechanism described in more detail elsewhere (Ashley-Ross, 1994*a*; Edwards, 1977). Brinkman (1981) suggested that large amounts of femoral rotation in salamanders and lizards might actually differentiate ancestral *versus* derived step cycles of tetrapods better than an upright limb because the knee of primitive mammals is often quite lateral to the hip but little femoral rotation occurs in the step cycle of these animals. Understanding the function of sprawling vertebrate limbs is thus facilitated by examining the extent to which various species of salamanders and lizards may be used interchangeably as models.

To facilitate interspecific comparisons of hindlimb kinematics of ectothermic tetrapods, Table 2 summarizes the animal sizes and speeds used for previous studies of hindlimb kinematics of one species of salamander (Ashley-Ross, 1994*b*) and three species of lizards (Brinkman, 1981; Jayne *et al.* 1990; Reilly and Delancey, 1997). Ashley-Ross (1994*b*) found that out of a total of 21 kinematic variables describing the hindlimb movements of *Dicamptodon tenebrosus*, only stride length, stride duration and step duration changed significantly or showed strong trends with increased speed. For the lizard *Varanus exanthematicus*, Jayne *et al.* (1990) found statistically significant changes in stride length, stride duration, step length, step duration and duty factor with increased speed. Reilly and Delancey (1997) found that only five of 38 kinematic variables of the lizard *Sceloporus clarkii* changed significantly with speed and concluded that increased stride frequency was the primary mechanism for increasing speed. In our study of *Dipsosaurus dorsalis*, 37 of 46 kinematic variables had significant (P<0.05) changes with increased speed and 27 variables had such low P-values (<0.001) that a correction for multiple comparisons would not alter the conclusions. Thus, compared with *D. tenebrosus* and *S. clarkii*, speed had profound effects on the kinematics of *D. dorsalis*. Differences in statistical power may have contributed to the different conclusions of these studies regarding the effects of speed, but below we consider in more detail some of the other factors contributing to these apparent differences among taxa with sprawling limbs.

Theoretical considerations convincingly show how increased amounts of pelvic rotation can enhance step length and thus speed (Ashley-Ross, 1994*b*; Edwards, 1977). Furthermore Ashley-Ross (1994*b*) found that, as *Dicamptodon tenebrosus* increased speed, pelvic rotation nearly doubled (from 39 ° to 73 °). Illustrations in Brinkman (1981) indicate that pelvic rotation in a walking *I. iguana* approximates 75 °. Neither Reilly and Delancey (1997) nor our study detected statistically significant effects of speed on the amounts of pelvic rotation, and the mean values for *S. clarkii* and *D. dorsalis* were 41 ° and 36 °, respectively. Future comparative work is necessary to resolve whether the amounts of pelvic rotation are statistically different among different species of lizards, but the available data present the intriguing possibility that pelvic rotation is important for modulating speed in salamanders but not in lizards.

For both *Dicamptodon tenebrosus* (Ashley-Ross, 1994*b*) and *S. clarkii* (Reilly and Delancey, 1997), the maximum angles of femur protraction and retraction do not change significantly with speed, and within a particular stride the maximum angular protraction of the femur is consistently less than the maximal angular retraction of the femur. For *D. dorsalis*, the amounts of femur protraction and retraction are proportional to values of $X_{\max}$ and $X_{\min}$ for the knee, which did not change significantly with speed and were approximately equal to each other. In contrast to the knee, values of $X_{\max}$ for more distal portions of the limb in *D. dorsalis* did change significantly with speed. Furthermore, at low speeds, the unequal distal values of $X_{\max}$ and $X_{\min}$ in *D. dorsalis* resemble the asymmetry in the amounts of femur protraction and retraction found by Reilly and Delancey (1997) for *S. clarkii*. Lateral views of additional species of lizards also commonly show asymmetry in the amplitudes of anterior *versus* posterior movements of the limb relative to the hip (Snyder, 1952, 1962; Sukhanov, 1974). However, for *D. dorsalis*, asymmetry in the longitudinal movements of the limb diminishes with increased speed.

Comparing the amounts of femoral rotation between different species of lizards and salamanders is complicated by the fact that these movements do not occur within a single plane. For salamanders, Edwards (1977) proposed that femoral rotation is the second most important contributor to forward propulsion after limb retraction, whereas Ashley-Ross (1994*a*) suggested that that femoral rotation contributes little to forward propulsion since it can occur only during a limited portion of the stance phase. However, neither Edwards (1977) nor Ashley-Ross (1994*b*) directly measured femoral rotation. Brinkman (1981) used dorsal view X-rays of *I. iguana* to estimate femoral rotation on the basis of the changing width of the distal part of the femur, and he obtained a value approximating 70 ° during the stance phase. Lateral views suggest that both *S. clarkii* (Reilly and Delancey, 1997) and *D. dorsalis* (Fig. 5) also have considerable amounts of femoral rotation during stance, but three-dimensional analyses are needed to determine the amount and importance of this movement in sprawling-limbed tetrapods.

Pelvic rotation, limb retraction and femoral rotation are all movements that can theoretically increase stride length and thus speed, but another mechanism for modulating speed is simply changing the frequency of strides. In contrast to our findings for *D. dorsalis* as well as those of Ashley-Ross (1994*b*) and Jayne *et al.* (1990), Reilly and Delancey (1997) suggested that *S. clarkii* modulates speed primarily by modulating the frequency and speed of limb movement. However, Reilly and Delancey (1997) found that the stride length of *S. clarkii* ranged from 8.0 to 15.0 cm and changed significantly with speed. Furthermore, step lengths can be calculated from tabular summaries in Reilly and Delancey (1997) and, when analyzed similarly to the values for stride length, step lengths of *S. clarkii* also increase significantly with increased speed. Thus, all previously studied lizards and salamanders modulate speed with a combination of changes in the frequency and amplitude of whole-limb movements.

Brinkman (1981) suggested that the kinematics of *I. iguana* and salamanders differed in three major respects. (1) At the beginning of stance in salamanders, the foot is anterior to the knee, whereas in *I. iguana* the foot is either below or posterior to the knee. (2) During stance in salamanders, the metatarsals are directed anteriorly, whereas in lizards they are directed laterally. (3) In salamanders, the foot rolls off the substratum passively and does not dorsiflex until the end of retraction, whereas in *I. iguana* the foot is actively plantarflexed at the end of protraction and actively dorsiflexed at the beginning of protraction. For *D. dorsalis,* the foot was commonly anterior to the knee at footfall and the metatarsals pointed forward during rapid locomotion (Figs 5B, 10B); therefore, points 1 and 2 are not general differences between salamanders and lizards. Similar to Brinkman's (1981) findings for *I. iguana*, considerable dorsiflexion of the foot in *D. dorsalis* occurs during the first half of femoral protraction (Fig. 5A, 184 *versus* 224 ms; Fig. 5B, 52 *versus* 100 ms). In addition, plantarflexion of the foot may occur during limb protraction (Fig. 5B, 100–148 ms), but this was not obvious during all speeds in *D. dorsalis* (Fig. 5A, 224–260 ms). Although the kinematics of *D. dorsalis* seem to be consistent with the active plantarflexion during stance, electromyograms are needed to clarify the extent to which these movements are active.

In the light of the conspicuous changes in the hindlimb kinematics that we found in *D. dorsalis*, speed has the potential to confound interspecific comparisons. The fastest speed studied by Reilly and Delancey (1997) was 44 % of the maximum sprinting speed of *S. clarkii*, and the fastest speed of *Dicamptodon tenebrosus* analyzed kinematically was 32 % of the fastest speed observed (Ashley-Ross, 1994*a*,*b*). Our fastest standardized speed (250 cm s^{-1}) approximates 60 % of the values reported for the maximal running speed of *D. dorsalis* (Marsh, 1988). Thus, many of our observations for *D. dorsalis* were for relatively faster speeds than those of previously studied ectothermic tetrapods (Table 2).

Table 2. *Comparisons of selected studies on the speed and hindlimb kinematics of ectothermic vertebrates*

Species	Mean *SVL* (cm)	Speed (cm s^{-1})	Frequency (Hz)	DUTY (%)	Reference
Dicamptodon tenebrosus	8.8	4–19	0.7–2.1	72–58	Ashley-Ross (1994*b*)
Iguana iguana	57	35	0.9–1.4	67	Brinkman (1981)
Varanus exanthematicus	30	27–138	0.6–1.8	75–58	Jayne *et al.* (1990)
Sceloporus clarkii	9.1	27–83	3.8–6.1	60–54	Reilly and Delancey (1997)
Dipsosaurus dorsalis	12.2	50–250	3.7–7.5	68–38	Present study

SVL is snout–vent length; DUTY is step duration as a percentage of stride duration.

Animals with similar Froude numbers are often considered to be moving at physiologically similar speeds (e.g. Farley *et al.* 1993). The Froude number is equal to the speed of locomotion divided by the square root of the gravitational constant times a characteristic length. Previous studies have used different characteristic lengths to calculate Froude numbers. We used mean values of effective limb length at footfall, mean hip height and anatomical limb length to calculate the Froude numbers of *D. dorsalis*, which were 0.87, 0.79 and 0.54, respectively, at 50 cm s^{-1} and 3.40, 3.51 and 2.72, respectively, at 250 cm s^{-1}. The transition between a walk and run for many quadrupedal mammals occurs when Froude numbers are between 2 and 3 (Alexander and Jayes, 1983), which agrees well with the Froude numbers (1.68–2.43) of *D. dorsalis* near the walk–run transition (150 cm s^{-1}). Using Froude numbers calculated from values of mean hip height for *D. dorsalis* in the scaling equations of Alexander and Jayes (1983) for non-cursorial mammals predicts relative stride lengths (stride length divided by hip height) of 4.0 and 4.7 at 50 and 250 cm s^{-1}, respectively, whereas the experimentally observed values were 3.9 and 7.2, respectively. Thus, compared with the locomotion of many species of mammals with similar Froude numbers, *D. dorsalis* has unusually long strides at higher speeds. Unfortunately, Froude numbers are not available for previous kinematic studies of salamanders and lizards (Table 2). Furthermore, the discrepancies between values calculated for slow speeds of *D. dorsalis* using anatomical lengths rather than kinematic quantities indicate the difficulty of estimating Froude numbers of other species of lizards and salamanders retrospectively.

The lack of running (duty factor <50 %) in previous studies (Table 2) may also have contributed to the contrasting conclusions that speed had widespread effects on the kinematics of *D. dorsalis* but not on that of *Dicamptodon tenebrosus* (Ashley-Ross, 1994*b*) or *S. clarkii* (Reilly and Delancey, 1997). For *D. dorsalis*, the transition from a walk to a run occurred between 100 and 150 cm s^{-1}, and some kinematic quantities (Figs 8A, 9E, 10A) had discontinuities near the walk–run transition rather than showing simple linear increases with speed. The difference between a walk and a run also affects the ability to determine the contributions of different movements such as limb retraction and pelvic rotation to stride length. During a walk, at least one foot within a girdle always contacts the ground and, hence, calculating the relative contributions of different limb movements during stance (step) provides insights into the relative importance of movements to forward progression (Ashley-Ross, 1994*a*). However, because neither foot touches the ground during the suspended phase of running in *D. dorsalis*, stride length is not simply the sum of the left and right step lengths (Fig. 5). For example, at 250 cm s^{-1}, the mean stride length of *D. dorsalis* was 33.8 cm, whereas twice the step length was only 26.0 cm (Fig. 7A). Therefore, the amplitudes of limb movements during the step are inadequate for predicting stride length, and the speed and force of limb movements become important determinants for stride length during running. Exactly which aspects of muscle physiology limit locomotor speed by constraining stride length and/or frequency are still not well understood (Marsh and Bennett, 1985; Marsh, 1988; Swoap *et al.* 1993).

Finally, when making interspecific comparisons, one should keep in mind the considerable diversity in the morphology, behavior and habitats of different species of lizards. For example, *S. clarkii* belongs to a clade of lizards with many species that frequently climb rocks (Miles, 1994). Thus, the lack of noticeable femoral adduction reported for *S. clarkii* (Reilly and Delancey, 1997) may reflect behavioral and/or morphological specializations of climbing forms that facilitate keeping the center of gravity close to the locomotor surface. Effectively all of the individuals of *D. dorsalis* that we encountered while collecting were on the ground, and this species is not very closely related to *S. clarkii* (Etheridge and de Queiroz, 1988). These differences in species phylogenetic relationships, behavior, habitat and morphology emphasize the need for comparative studies to test the robustness of generalizations regarding the function of the limb in ectothermic vertebrates.

Limb and foot posture

Although lizards are generally characterized as having sprawling limb posture and plantigrade foot posture, we found variation with speed that does not conform simply to this generalization. For example, the femur of *Dipsosaurus dorsalis* became strikingly more upright with increased speed, as indicated by some angles of femoral depression differing by more than 60 ° from the expectation for a ‘sprawling’ limb. Discussions of the sprawling limb posture of lizards are often not clear about whether the posture being referred to is for animals that are moving or at rest, and our results emphasize the importance of accounting for whether an animal is moving as well as the speed of movement.

Qualitative categories of erect and sprawling may have limited utility for describing what is actually a continuum of variation in limb posture (Gatesy, 1991). Sprawling and erect limb postures are often defined by examples and illustrations rather than by strict quantitative criteria, and mammals and birds are two clades of vertebrates that are commonly used to illustrate erect limbs. However, even though the limb movements of many species of mammals and birds are largely confined to a parasagittal plane, within these groups limb postures vary considerably as a result of different longitudinal locations of the hip and more distal joints of the limb. For example, Gatesy (1990) emphasized that the femur of birds is often nearly horizontal because the knee is substantially anterior to the hip. Crocodilians are often considered to have semi-erect limb posture, and Gatesy’s (1990) illustration suggests that the toes of the hind foot can also be oriented quite anteriorly. Although mammals such as elephants and certain ungulates have limbs resembling a column perpendicular to the ground (Hildebrand, 1985), both the longitudinal and lateral positions of the knee relative to the hip vary considerably among mammalian species (Jenkins, 1971). Hence, limb posture may vary with speed within a single species as well as among species within clades that are categorized as having either erect or sprawling limbs.

In addition to changes in the orientation of the femur, the foot posture of *D. dorsalis* changed substantially with increased speed. At fast speeds, the long axis of the fourth toe and metatarsal was nearly parallel to the direction of forward travel. If the tip of the foot of a tetrapod is oriented laterally, then plantarflexion of the foot while it is touching the ground will contribute minimally to forward propulsion and will tend to push the body of the animal towards the contralateral side (Brinkman, 1981). In contrast, for a foot that points forward, a greater proportion of the forces generated by plantarflexion will facilitate propelling the animal upwards and forwards. Consequently, the forward orientation of the foot of *D. dorsalis* at high speeds suggests that plantarflexion assumes a greater role in the production of propulsive force than during locomotion at low speeds.

Recent studies of the lower leg of vertebrates have clarified some of the implications of foot posture for both mechanics and muscle function. For example, for the human foot during the stance phase, the location of the ground reaction forces moves from the heel towards the tips of the toes (Carrier *et al.* 1994). Consequently, the length of the out lever and the gear ratio of the human foot increase from early to late stance (Carrier *et al.* 1994). Furthermore, changes in the foot position of running humans appear to lengthen the gastrocnemius muscle initially but then, as the stance phase continues, the gastrocnemius shortens with progressively faster speeds such that the maximum speed of muscle shortening is nearly coincident with the highest gear ratio at the end of stance (Carrier *et al.* 1994). Prestretching muscle is one mechanism for enhancing the mechanical power output of muscle. The relevance of the power output of a muscle depends on whether the muscle is being used to perform mechanical work or to generate high isometric forces to facilitate elastic recoil of stretched tendons (Roberts *et al.* 1997). At the fastest speeds observed for *D. dorsalis* ($>300\,\mathrm{cm\,s^{-1}}$), not only did the foot land in a digitigrade posture, but the foot commonly remained in a digitigrade posture throughout the stance phase, and the amount of ankle flexion appeared relatively small. Such minimal amounts of flexion at the ankle are consistent with the expectations of the limb acting more as a spring; however, the strongest evidence of vertebrate limbs acting as springs is for animals much larger than *D. dorsalis* (reviewed in Alexander, 1988; Biewener and Bertram, 1991). Thus, the changing foot postures of *D. dorsalis* with increased speed seem likely to affect both the gearing and muscle function of the limb, and the relatively enormous size of the feet (Fig. 1) seems likely to exaggerate some of these effects.

As indicated by effective limb lengths, which nearly doubled with increased speed, the combination of the limb dimensions and movements give *D. dorsalis* a remarkable capacity to modulate the length of the limb behaviorally during different speeds of locomotion. Rather than viewing the large feet of many species of lizards only as a mechanism for enhancing the stability of an animal with a ‘sprawling’ gait, it is useful to emphasize the probable dynamic role these structures have for attaining rapid running speeds. Most studies correlating morphology to sprinting performance in lizards have used total limb length (reviewed in Garland and Losos, 1994). However, when Miles (1994, Table 10.7) used multiple regressions of within-limb dimensions to account for interspecific variation in sprinting speeds of lizards, the length of the metatarsus was highly significant but the lengths of the femur and tibia were not significant. The congruence between our kinematic analysis, which suggests a prominent role of the foot in attaining rapid speeds, and the correlative comparative analysis of performance (Miles, 1994) highlights how kinematics and comparative tests of performance can complement each other for determining the predictive value of morphology for performance.

NSF grants IBN 9514585 and BIR 9217409 to B.C.J. provided support for research and acquisition of the high-speed video system. We are grateful to R. German, G. Uetz and D. Irschick for their comments on earlier drafts of this manuscript. S. Reilly generously sent us copies of his manuscripts while they were in press. We are grateful to T. Flam for help with collecting lizards, and T. Haffey and C. Clements for help with experiments and animal care. We would also like to thank R. German and M. Maunz for their help with radiography.

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