

SIZE MATTERS: ONTOGENETIC VARIATION IN THE THREE-DIMENSIONAL KINEMATICS OF STEADY-SPEED LOCOMOTION IN THE LIZARD *DIPSOSAURUS DORSALIS*

DUNCAN J. IRSCHICK AND BRUCE C. JAYNE*

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

Although many studies have investigated how locomotor capacities change with size, few studies have examined whether different-sized individuals within a species have similar kinematics during locomotion. We quantified the skeletal limb morphology and the three-dimensional kinematics of the hindlimb of four sizes (4–66 g) of the lizard *Dipsosaurus dorsalis* moving steadily at both the walk–run transition (50 % duty factor) and at a moderately fast speed of 250 cm s⁻¹. We used analyses of variance to test whether limb movements changed with size and to determine whether size and speed had interactive effects on kinematics. The disproportionately long hindlimbs of smaller lizards partly contributed to their relatively greater (i.e. adjusted by snout–vent length) values of linear kinematic variables. Both relative linear and angular kinematics changed significantly with both size and speed, both of which had widespread interactive effects. By having more extension of the knee and ankle joints, and thus a

relatively higher hip height during stance, the slow-speed movements of small lizards displayed some of the characteristics of the fast-speed movements in larger lizards. Further, approximately one-fifth and two-fifths of the strides of the two smallest size classes were digitigrade at the lower and higher speeds, respectively, whereas the two largest size classes always had a plantigrade foot posture. Some of the most striking effects of size on kinematics were most evident at the lower of the two speeds. Unlike interspecific studies, which show that the limbs often become more crouched with decreased size, the more extended limbs of smaller lizards in this study suggest that variation in size alone cannot be the causal reason for differences in limb posture.

Key words: locomotion, kinematics, size, lizard, *Dipsosaurus dorsalis*, ontogeny, scaling, gait.

Introduction

An issue of general interest is how size affects both structure and function; size is particularly important for locomotor function because the entire mass of the animal is moved. Most insights regarding the scaling of structure and function for the locomotion of limbed vertebrates are from broad-scale comparisons of phylogenetically diverse mammals such as mice and horses (Alexander et al., 1981; Heglund et al., 1974; Taylor et al., 1980). Several generalities have emerged from the scaling literature for mammalian locomotion, such as a decreased mass-specific cost of transport with increased size (Taylor et al., 1982). However, the ability of such broad-scale comparisons to isolate the effects of size may be limited because phylogenetically diverse groups often differ qualitatively in their morphology and physiology. For example, the limbs of small mammals (mainly rodents) are more crouched than those of large mammals (mainly ungulates) (Biewener, 1983), but this trend might primarily reflect the qualitatively different limb structure of ungulates. Isolating the effects of size is facilitated by restricting the

phylogenetic diversity of a sample, which can be accomplished by studying more closely related taxa (i.e. do larger rodents have less crouched limbs than smaller rodents?) or studying ontogenetic variation within a single species.

Lizards are an excellent group for studying intraspecific scaling of locomotor function because the mass of adults and juveniles often varies considerably (as much as 50-fold) and the precocial neonates are capable of running rapidly (for a review, see Garland and Losos, 1994). Ontogenetic variation in maximal running speed, stride length and stride frequency have been documented for lizards (Garland, 1985; Marsh, 1988). However, as for most vertebrates, ontogenetic variation in kinematic quantities such as joint angles has not been studied for lizards. Consequently, predictions of the effects of intraspecific variation in size on kinematics must be inferred primarily from broad-scale interspecific studies while acknowledging that inter- and intraspecific scaling relationships can differ (Gould, 1971).

Comparing the locomotion of different-sized animals is

complicated because large animals generally move faster and change gaits at greater absolute speeds than small animals (Heglund et al., 1974). Hence, several studies have used gait transitions or preferred speeds to define an equivalent speed for facilitating comparisons among species of different sizes. For example, at the trot–gallop gait transition of mammals, stride frequency scales regularly with size (Heglund et al., 1974), and other quantities such as the mass-specific energetic cost per stride do not change with size (Heglund and Taylor, 1988). Peak muscle stress is constant at the preferred speeds of some mammals (Perry et al., 1988). Biewener (1990) suggested that similar skeletal stresses in mammals of varying size result from the more erect postures of larger mammals, which compensates for the scaling of bone diameters, and large bird species also have more erect limbs than small species (Gatesy and Biewener, 1991).

The interspecific studies of locomotion cited above suggest that larger individuals within a species will have a more erect limb and will change gaits at greater absolute speeds than smaller individuals. Several alternative hypotheses regarding the effects of size on kinematics are also plausible. For example, some interpretations of geometric similarity predict that linear and angular displacements should scale with linear anatomical dimensions with slopes of 1 and 0, respectively, when morphology scales isometrically as discussed by Richard and Wainwright (1995). When morphology does not scale isometrically, the anatomical lengths of different-sized individuals should still be sufficient for predicting linear displacements when angular displacements are equal. For example, one lizard with limbs twice as long as another would be expected to have twice the step length as another with equal joint angles.

We examined whether the three-dimensional kinematic patterns of the hindlimb of the lizard *Dipsosaurus dorsalis* differ with size and speed. The kinematics of lizards changes substantially with speed (Fieler and Jayne, 1998; Jayne and Irschick, 1999). Further, since incline and speed have interactive effects on kinematics (Jayne and Irschick, 1999), size and speed may also have interactive effects on kinematics. *D. dorsalis* is an excellent subject for studying how kinematics changes with size because one can obtain locomotion over a broad range of sizes and speeds (Marsh, 1988). Specifically, we addressed the following questions. (i) Do joint angles and size-adjusted linear kinematics change with size? (ii) Do speed and size have interactive effects on kinematics? (iii) Are differences in limb dimensions among size classes sufficient to explain any potential kinematic differences?

Materials and methods

Experimental subjects

We studied the desert iguana *Dipsosaurus dorsalis* (Baird and Girard) in part because of its generalized morphology (Fieler and Jayne, 1998) and because it has a large increase in mass through ontogeny (from 3 to 60 g). The forelimbs of *D. dorsalis* and of 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*, and for many species of lizards the hindlimbs are probably more important than the forelimbs for generating propulsive forces (Snyder, 1954; Sukhanov, 1974).

We examined four individuals in each of four size classes. Adults (data taken from Jayne and Irschick, 1999) had masses ranging from 54.3 to 65.6 g (mean 62.0 g). Subadult lizards had masses ranging from 26.1 to 35.9 g (mean 28.0 g). Intermediate lizards ranged from 9.5 to 14.0 g (mean 12.5 g), and juveniles ranged from 4.4 to 7.9 g (mean 5.9 g). Juvenile lizards were collected near Palm Springs, California (California permit number 802030-01), and all other lizards were from Yuma Arizona (Arizona permit SP 854176). After capture, all lizards were transported to the University of Cincinnati for experiments. Lizards were caged individually or in pairs and were fed either crickets or lettuce and broccoli sprinkled with a vitamin supplement. Within the cages, incandescent light bulbs were switched 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.

Morphological variables

To elucidate how shape scales with size, we measured snout–vent length (SVL), mass and 11 linear dimensions (see Table 1) using calipers (± 0.1 mm) to measure distances on life-size ventral-view radiographs of anesthetized specimens for which kinematic patterns were examined. For the hindlimb, we measured the distance from the heel to the distal end of the fourth metatarsal (see Table 1, tarsals and metatarsals), and the length of the fourth toe from its base to the base of the claw. We measured the length of the foot of the forelimb (see Table 1, forefoot) from the wrist to the base of the claw on the fourth toe. We also measured the width of the pelvis between the hip joints, and the trunk length equaled the longitudinal distance between the shoulder and hip joints.

Experimental protocol

We videotaped most animals within a few weeks after collecting them. We videotaped each individual until we obtained approximately four strides of steady-speed ($\pm 10\%$ of average forward velocity) quadrupedal locomotion at a duty factor of 50% and at a relatively fast speed (250 cm s^{-1}). For animals that do not have a conspicuous gait transition, such as lizards and birds (Gatesy and Biewener, 1991), a duty factor of 50% denotes the walk–run transition (Hildebrand, 1985) and, hence, is one metric for defining an equivalent speed. The fast speed of 250 cm s^{-1} was the highest speed that could be reliably obtained for all sizes. Hereafter, the 50% duty factor will be referred to as the slow speed and locomotion at 250 cm s^{-1} will be referred to as the fast speed.

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} . We used

procedures similar to those of Irschick and Jayne (1999) to regulate the temperature (35–40 °C) of the lizards. Paint marks on the pelvis and hindlimb facilitated digitization of the video images. The pelvic landmarks painted on the surface of the lizards were slightly posterior and dorsal to the hip joint for each of the size classes.

Kinematics

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, and kinematic quantities including three-dimensional angles between two lines and several other variables were calculated from coordinates with macros for Microsoft Excel version 7.0 (written by G. Updegraff and B. Jayne). For the subadult and adult lizards, locomotion at the slow speed was digitized every 8 ms, and all other locomotion was digitized at 4 ms intervals. For all strides combined, an average of 27 ± 1 (mean \pm S.E.M.) images per stride were digitized. We digitized the three-dimensional coordinates of the following landmarks: the pelvis, knee and ankle, and the base, middle and tip of the fourth toe (excluding the claw). We excluded the claw because its tapering tip was difficult to see on the video tapes. We also digitized four two-dimensional coordinates from a dorsal perspective: the right and left ankles, and the right and left pelvic landmarks. 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.

Before calculating the kinematic quantities, we transformed the coordinates of the pelvic landmarks to approximate the coordinates of the hip by correcting for the average vertical and horizontal distance from the pelvic landmarks to the hip joint for each size class. Three linear quantities described the height of the hip relative to the tread surface. 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 ($\Delta Y_{\text{hip,total}}$).

We calculated the x coordinate of the toetip at footfall and at the end of stance. Positive and negative x values were, respectively, the anterior and posterior distances relative to the hip. We calculated two- (x, y) and three-dimensional effective limb lengths as the straight-line distance from the hip to the most posterior portion of the plantar surface of the foot that contacted the treadmill at the time of footfall. Individual strides varied in foot posture. Hence, effective limb lengths for plantigrade (heel contacting the treadmill) and digitigrade (only phalanges contacting the treadmill) strides were the distances from the hip to the ankle and from the hip to the distal tip of the fourth metatarsal, respectively.

Six variables described movements of the whole limb and attributes of the entire locomotor cycle. Stride length was the

x distance traveled between successive footfalls of the right hind foot, whereas step length was the x distance traveled by the body during the stance phase 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. The average forward velocity of each stride equaled stride length (cm) divided by stride duration (s).

Six three-dimensional angles described angles of the knee, ankle and toe joints within the hindlimb at footfall and at the end of stance, and one two-dimensional angle indicated the orientation of the fourth toe at footfall. 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. The angle of toe orientation at footfall 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.

Six angular excursions describe the amounts of flexion and extension that occurred in the early and later portions of the stance phase, respectively. To determine the amount of flexion in early stance, 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.

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 the maximum and minimum values of these angles indicated the amount of rotation of the pelvis (projected onto a horizontal plane). We could not reliably 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 (Irschick and Jayne, 1999; Jayne and Irschick, 1999). Consequently, we determined certain movements of the femur relative to fixed planes of reference.

For each of 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

To examine scaling relationships of morphology, we performed linear least-squares regressions among each of the \log_{10} -transformed variables and \log_{10} -transformed snout–vent length (SVL). To examine the scaling of simple kinematic variables (stride length, step length and stride duration) for both speeds, we averaged the values of each of these variables for each individual at each speed and plotted the resulting values against the corresponding SVL of each lizard. To examine differences among both size classes and speed for the kinematic variables, we performed three-way analyses of variance (ANOVAs) using size, speed and individual as factors. Size and speed were fixed and crossed, and individual was a random factor nested within size. We were primarily interested in the size, speed and size by speed interaction terms. For certain linear variables that were likely to increase with size (e.g. stride length), we performed ANOVAs on relative (i.e. size-adjusted) values, which were calculated by dividing the value of the variable by the SVL of the corresponding lizard.

To examine whether the size classes were distinct in multivariate kinematic space, we performed a discriminant function analysis (DFA) on 20 variables that included relative linear, timing and angular variables. This analysis does not control for the potentially confounding effects of non-isometric scaling of limb dimensions. Thus, we performed a second DFA that only examined angular variables, which have no necessary causal relationship with limb dimensions. Each combination of size and speed formed a single group (i.e. adult lizards at the slow speed), resulting in a total of eight groups ($N=8$).

Some kinematic variables did not appear to change linearly with size, and hence the entire data set was not well suited for alternative statistical analyses such as analysis of covariance. To facilitate our multivariate analyses, we also chose four narrow and non-overlapping size ranges of lizards, but this choice also made our sample suboptimal for performing analysis of covariance and certain regression analyses. We do provide some scaling equations using mean values per individual for some kinematic variables used commonly in other studies (stride and step length, etc.). However, our primary focus was not to describe the empirical relationships between each kinematic variable and size. Instead, we used three-way analyses of variance (ANOVAs) as the most practical way of providing a uniform method for testing the effects of size and speed while simultaneously accounting for variation within individuals.

Values are presented as means \pm S.E.M.

Results

Morphology

The most proximal elements of both girdles (femur and humerus) had scaling coefficients that were not significantly different from isometry (Table 1). From proximal to distal within both the hindlimb and forelimb, progressively more distal elements had stronger negative allometry, as shown by the slopes being significantly less than 1. Overall, small lizards had relatively long tails and distal limb dimensions and relatively short trunks compared with larger lizards (Fig. 1).

Whole-stride and linear kinematics

At the slow speed, a two-way ANOVA (factors: size and individual nested within size) confirmed that duty factors (grand mean 50.1%) did not differ significantly with size ($F_{3,12}=0.1$, $P>0.25$) and that the forward speed (u) for the smallest to largest size classes had mean values of 99 ± 5 , 115 ± 4 , 117 ± 4 and 119 ± 9 cm s^{-1} , respectively, which also did not differ significantly with size ($F_{3,12}=1.7$, $P>0.10$). For the fast speed, values of forward speed (grand mean 249 cm s^{-1})

Table 1. Scaling relationships of morphology with snout–vent length for *Dipsosaurus dorsalis*

Dependent variable	Slope	y intercept	r^2
Mass (g)	3.099 ± 0.085	-1.606 ± 0.080	0.99
Tail length (cm)	$0.801\pm 0.063^*$	0.468 ± 0.060	0.92
Femur length (cm)	1.033 ± 0.026	-0.725 ± 0.024	0.99
Tibia length (cm)	$0.777\pm 0.047^{**}$	-0.504 ± 0.044	0.95
Tarsal and metatarsal length (cm)	$0.674\pm 0.042^{**}$	-0.598 ± 0.392	0.95
Fourth toe length (cm)	$0.561\pm 0.042^{**}$	-0.277 ± 0.039	0.93
Total hindlimb length (cm)	$0.767\pm 0.024^{**}$	0.080 ± 0.023	0.99
Humerus length (cm)	1.021 ± 0.045	-0.874 ± 0.043	0.97
Ulna length (cm)	$0.743\pm 0.044^{**}$	-0.702 ± 0.041	0.95
Forefoot length (cm)	$0.658\pm 0.056^{**}$	-0.522 ± 0.053	0.91
Pelvic width (cm)	0.999 ± 0.025	-0.993 ± 0.024	0.99
Trunk length (cm)	$1.111\pm 0.023^{**}$	-0.301 ± 0.023	0.99

Values are coefficients \pm S.E. ($N=16$ lizards).

Asterisks indicate significant deviations from isometry; $*P<0.05$, $**P<0.001$ (two-tailed t -tests, d.f.=15).

$P<0.001$ for the slopes of all regressions.

All independent and dependent variables were \log_{10} -transformed.

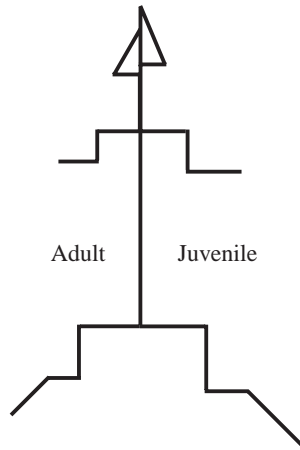


Fig. 1. A stick figure showing the average head and limb dimensions of a juvenile (snout–vent length, SVL 5.7 cm) and adult (SVL 12.2 cm) *Dipsosaurus dorsalis* scaled to the same trunk length. From proximal to distal, the line segments within the forelimb are the humerus, ulna and forefoot, and those of the hindlimb are the femur, tibia, tarsals+metatarsals and fourth toe.

did not differ significantly with size ($F_{3,12}=1.1, P>0.25$), and the duty factors for the smallest to largest size classes had mean values of $31.2\pm 0.8, 33.9\pm 0.9, 36.7\pm 1.2$ and $36.4\pm 1.4\%$, respectively, which also did not differ significantly with size ($F_{3,12}=2.0, P>0.10$).

For the smallest to largest size classes, the average Froude numbers $Fr [Fr=u(gL)^{-1/2}$, where g is the gravitational constant and L is hip height at footfall] were $2.6\pm 0.1, 2.6\pm 0.1, 2.5\pm 0.1, 2.6\pm 0.2$ (slow speed) and $5.7\pm 0.2, 5.1\pm 0.1, 4.9\pm 0.1, 4.3\pm 0.1$ (fast speed), respectively. At the slow speed, the Froude numbers did not vary significantly with size ($F_{3,12}=0.2,$

$P>0.75$), whereas at the high speed, the Froude numbers decreased significantly with increased size ($F_{3,12}=6.3, P<0.01$).

The occurrence of strides with digitigrade foot posture increased with increased speed and decreased size (Fig. 2). At the slow speed, the percentages of strides that were digitigrade at footfall from the smallest to the largest size class were 25, 19, 0 and 0%, and the corresponding values for the fast speed were 44, 44, 0 and 0%, respectively.

Table 2 summarizes the scaling relationships of stride length and duration, step length and duration and hip height at footfall with two linear measurements of lizard size. For the slow-speed data, the slopes of the scaling relationships between snout–vent length and all these kinematic variables were significantly less than 1, whereas only step duration and stride duration had slopes significantly different from 1 when total hindlimb length was the independent variable. The slopes of the scaling equations for the slow-speed data were always lower than the corresponding slopes for the high-speed data.

Relative stride length (divided by SVL) and relative step length both increased significantly with increased speed (Table 3; Fig. 3A,B). Speed and size had significant interactive effects on relative step length as a result of the values for slow and fast speed diverging with increased size. As size increased, lizards tended to have greater relative stride widths and to take slower strides (Fig. 3C,D).

Relative hip height at footfall increased significantly with increased speed and decreased significantly with increased size (Table 3; Fig. 4A). The total vertical oscillations of the hip increased significantly with increased speed (Fig. 4B). Vertical oscillations of the hip during the stance phase decreased with increased speed, but were unaffected by size (Fig. 4C). The relative effective limb lengths (two- and three-dimensional) increased significantly with increased speed in a similar

Table 2. Scaling relationships of selected linear and timing kinematic variables with snout–vent length and total hindlimb length for *Dipsosaurus dorsalis*

Dependent variable	Slow speed			Fast speed		
	Slope	y intercept	r^2	Slope	y intercept	r^2
(A) Snout–vent length (cm)						
Stride length (cm)	0.745±0.078	0.509±0.074	0.86	0.757±0.071	0.702±0.067	0.88
Step length (cm)	0.745±0.069	0.208±0.065	0.89	0.988±0.090	0.020±0.085	0.89
Stride duration (s)	0.496±0.085	1.300±0.080	0.70	0.660±0.084	1.598±0.079	0.81
Step duration (s)	0.497±0.085	1.601±0.080	0.70	0.892±0.086	2.281±0.081	0.88
$Y_{\text{hip,footfall}}$ (cm)	0.519±0.145	0.186±0.137	0.47	0.717±0.095	0.253±0.089	0.80
(B) Total hindlimb length (cm)						
Stride length (cm)	0.976±0.094	0.429±0.075	0.88	0.979±0.093	0.629±0.074	0.88
Step length (cm)	0.973±0.083	0.129±0.066	0.90	1.304±0.095	0.095±0.076	0.93
Stride duration (s)	0.624±0.117	1.334±0.094	0.66	0.844±0.113	1.654±0.091	0.79
Step duration (s)	0.622±0.118	1.632±0.095	0.66	1.170±0.099	2.380±0.079	0.90
$Y_{\text{hip,footfall}}$ (cm)	0.708±0.178	0.266±0.142	0.53	0.922±0.126	0.317±0.101	0.79

$P<0.005$ for the slopes of all regressions.

All independent and dependent variables were log₁₀-transformed.

Values are coefficients ± s.e. $N=16$ lizards.

$Y_{\text{hip,footfall}}$, hip height at footfall.

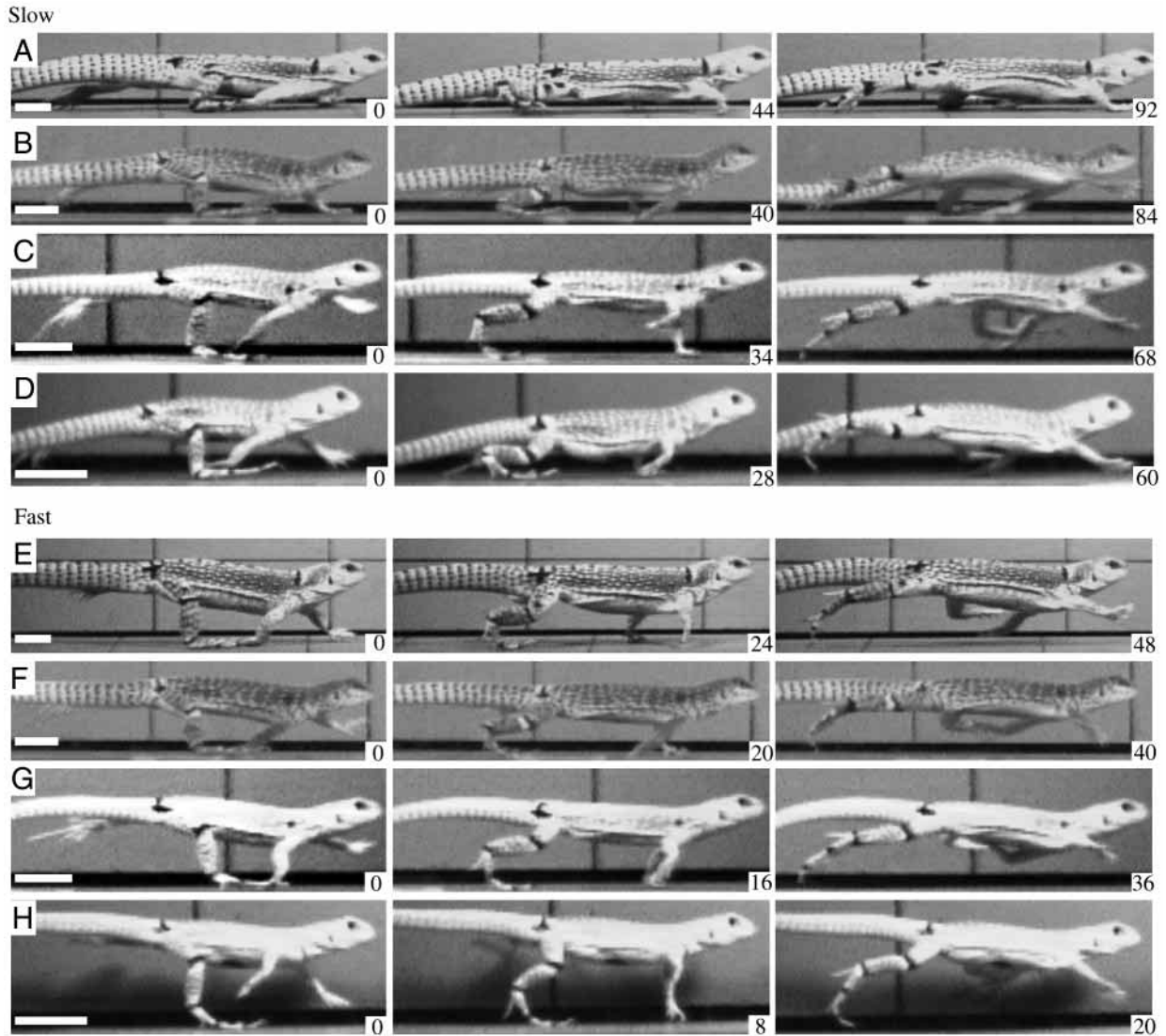


Fig. 2. Representative lateral views of single adult (A,E) (snout–vent length, SVL 11.9 cm, mass 59.5 g), subadult (B,F) (SVL 9.8 cm, mass 26.1 g), intermediate (C,G) (SVL 7.7 cm, mass 11.8 cm) and juvenile (D,H) (SVL 5.9 cm, mass 6.8 g) *Dipsosaurus dorsalis* with approximate duty factors and speeds of 50% (A–D) and 250 cm s^{-1} (E–H), respectively. The three images within each row are at the times of footfall (left), mid-stance (centre) and the end of stance (right). Scale bars, 2 cm. The elapsed times after footfall (ms) are indicated in the lower right-hand corners. Video recordings of the locomotion of *D. dorsalis* can be found at <http://www.biology.uc.edu/faculty/jayne/videos.htm>.

manner (Fig. 4D) and tended to decline with increased size ($0.08 > P > 0.05$).

The relative anterior position of the toetip (X_{toetip}) at footfall decreased significantly with increased size (Table 3; Fig. 5A), whereas the relative anterior position of the ankle (X_{ankle}) did not change significantly with size (Fig. 5C). At footfall, the relative anterior positions of the toetip and ankle were greater with increased speed. Both the relative posterior position of the toetip and ankle at the end of stance increased significantly with increased size (Fig. 5B,D).

Angular variables

At the slow speed, adults had significantly lower knee and ankle angles at footfall than the other size classes, but this

difference diminished at the high speed (Table 4; Fig. 6A,C). Both the knee and ankle angles at footfall had highly significant increases with increased speed (Fig. 6A,C). Knee angle at the end of stance also increased significantly as size increased (Fig. 6B). At the slow speed, the ankle angle at the end of stance decreased significantly with increased size, and the difference between slow and fast speeds increased with increased size (Fig. 6D). The toe angle at footfall decreased significantly with increased size, with values of the largest size class being approximately 8° less than the other size classes (Fig. 6E). The most conspicuous trend for the toe angle at the end of stance was the regular increase with increased size at the fast speed (Fig. 6F).

Knee flexion during early stance increased significantly with

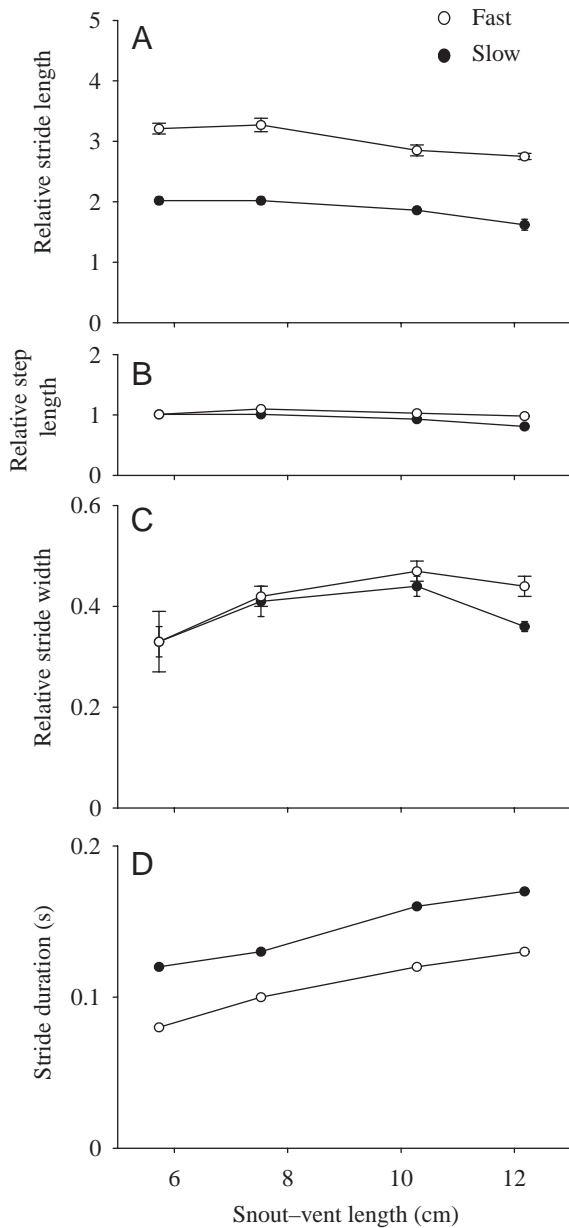


Fig. 3. Mean values of relative (divided by snout-vent length) stride length (A), relative step length (B), relative stride width (C) and stride duration (D) versus mean snout-vent length. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively. Table 3 summarizes significant differences among size classes and speeds. Values are means \pm S.E.M. Some of the standard errors are smaller than the symbols.

increased speed, but this difference diminished as size increased (Table 4; Fig. 7A). In contrast, knee extension during late stance increased significantly with increased size (Fig. 7B). Ankle flexion during early stance was affected by neither size nor speed (Fig. 7C). Small lizards had a very large decrease in ankle extension with increased speed compared with large lizards (Fig. 7D). Toe flexion decreased with increased size at the slow speed, but size and speed had

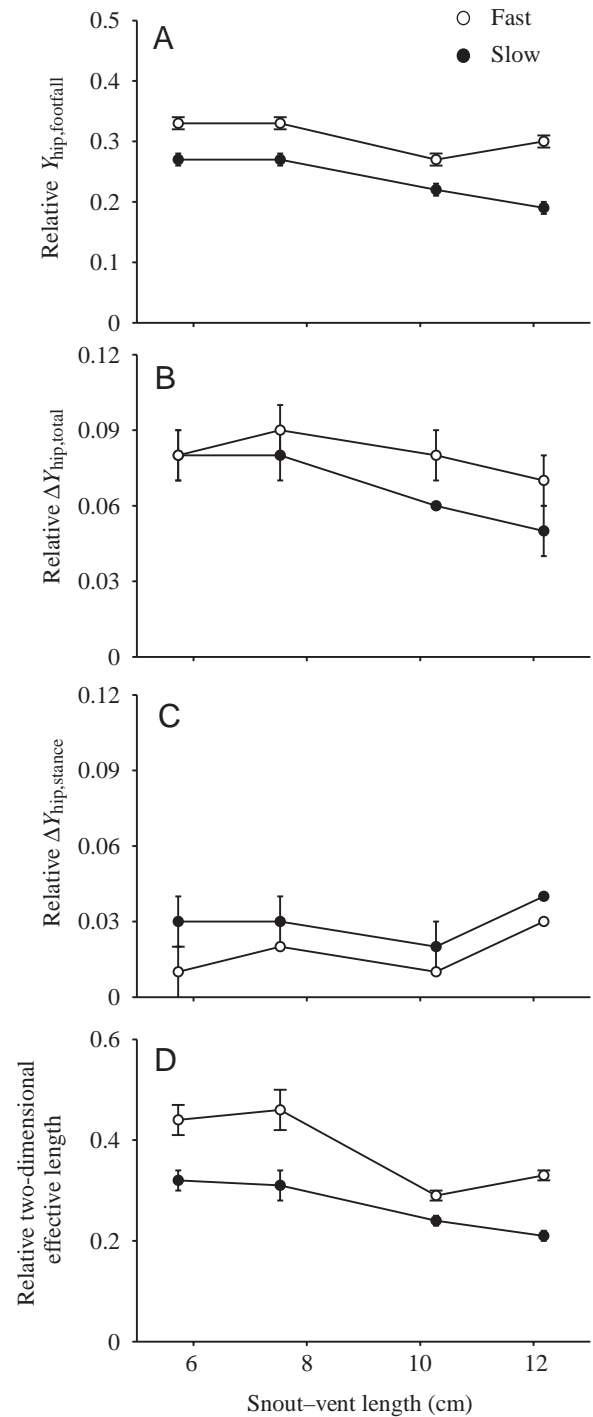


Fig. 4. Mean relative (divided by snout-vent length) values of hip height Y_{hip} at footfall (A), total change in Y_{hip} for the entire stride cycle (B), change in Y_{hip} during stance (C) and two-dimensional effective limb length at footfall (D). Values are means \pm S.E.M. Table 3 summarizes significant differences among size classes and speeds. Some of the standard errors are smaller than the symbols. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively.

significant and complicated interactive effects (Fig. 7E; Table 4). At the fast speed, toe extension increased linearly

Table 3. *F*-values from three-way ANOVAs performed separately on each kinematic variable describing whole-stride measurements and relative linear measurements

Dependent variable	Size, d.f.=3,12	Speed, d.f.=1,12	Size×speed, d.f.=3,12
Relative stride length	4.8*	328.9**	0.9
Relative step length	2.4	24.7**	4.6*
Relative stride width	3.6*	0.9	0.2
Stride duration	24.1**	135.7**	0.7
Relative $Y_{\text{hip,footfall}}$	5.5*	28.6**	0.6
Relative $\Delta Y_{\text{hip,stance}}$	1.7	12.0*	0.4
Relative $\Delta Y_{\text{hip,total}}$	2.3	3.9*	0.3
Relative 2-D effective length (footfall)	3.4	55.7**	2.2
Relative 3-D effective length (footfall)	3.3	40.8**	1.5
Relative $X_{\text{toetip,footfall}}$	8.1*	60.3**	4.3*
Relative $X_{\text{toetip,endstance}}$	11.0**	1.7	6.0*
Relative $X_{\text{ankle,footfall}}$	0.9	94.7**	8.8*
Relative $X_{\text{ankle,endstance}}$	107.5**	0.4	3.0

Y_{hip} , hip height; X_{toetip} , anterior–posterior position of toetip; X_{ankle} , anterior–posterior position of ankle; d.f., degrees of freedom.

All linear variables were divided by snout–vent length.

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

with increased size, and the effect of speed was reversed for small compared with large lizards (Fig. 7F).

Maximum femur retraction increased significantly with increased size but was unaffected by speed (Table 5; Fig. 8A). In contrast, minimum femur retraction decreased significantly with decreased speed but was unaffected by size (Fig. 8B). Maximum femur depression had a significant size by speed interaction such that the largest lizards had the greatest difference between the slow and fast speed (Fig. 8C). Minimum femur depression was unaffected by either size or speed (Fig. 8D). For the small lizards, maximum femur rotation was lower at the fast speed, whereas for the large lizards, this angle was higher at the the fast speed (Fig. 8E). Minimum femur rotation was significantly lower for the faster speed (Fig. 8F).

Pelvic rotation showed no significant difference among size classes, but decreased significantly as speed increased (Table 5; Fig. 9A). At the slow speed, lizards oriented their fourth toes on their hindlimb more laterally as size increased, whereas all lizards oriented their fourth toe nearly straight forward at the fast speed (Fig. 9B).

Multivariate analyses

The discriminant function analysis including duty factor and

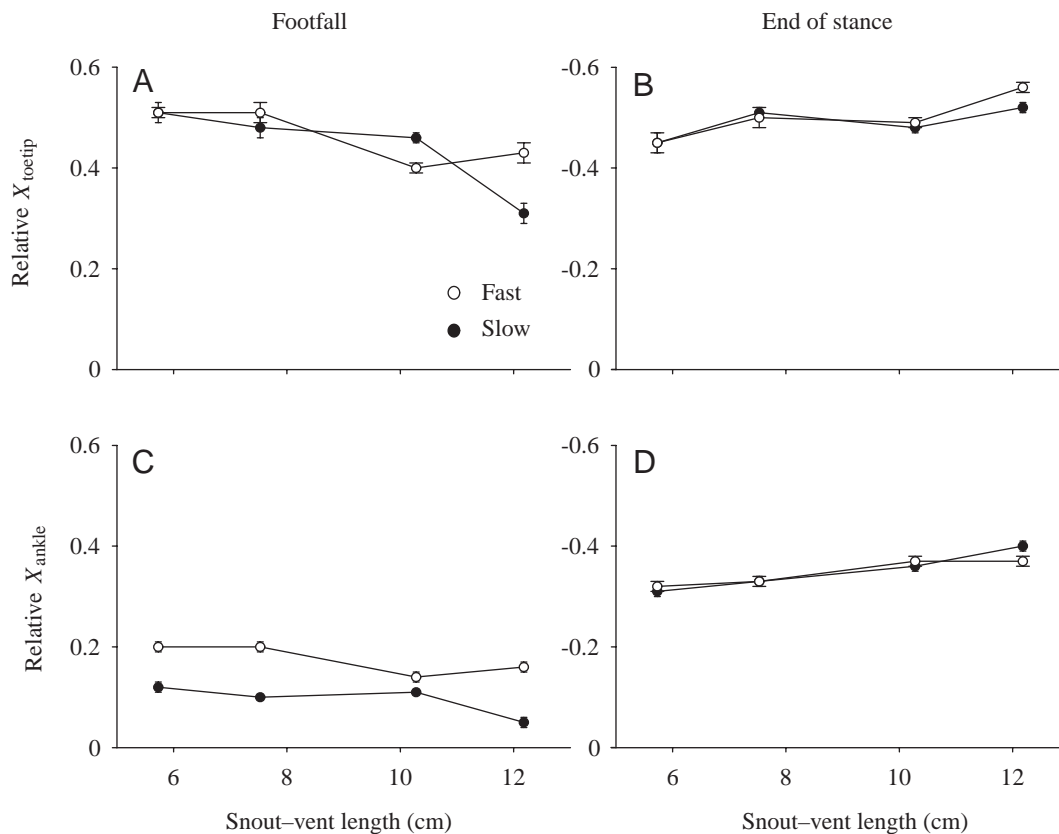


Fig. 5. Mean relative (divided by snout–vent length) values of the anterior–posterior position of the toe tip X_{toetip} (A,B), and ankle X_{ankle} (C,D) at footfall (A,C) and at the end of stance (B,D). Values are means \pm S.E.M. Table 3 summarizes significant differences among size classes and speeds. Some of the standard errors are smaller than the symbols. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively.

Table 4. F-values from three-way ANOVAs performed separately on each kinematic variable describing angular measurements of the knee, ankle and toe joints

Dependent variable	Size, d.f.=3,12	Speed, d.f.=1,12	Size×speed, d.f.=3,12
Knee angle (ff)	2.3	95.9**	3.9*
Knee angle (es)	15.9**	1.4	1.4
Ankle angle (ff)	1.5	95.9**	4.0*
Ankle angle (es)	0.7	50.3**	8.2*
Toe angle (ff)	16.3**	0.6	1.2
Toe angle (es)	5.3*	3.5*	3.9*
Knee flexion	1.1	61.2**	5.8*
Knee extension	10.4*	3.8	1.1
Ankle flexion	0.3	3.4	2.5
Ankle extension	1.6	5.6*	4.6*
Toe flexion	9.7*	6.2*	15.0**
Toe extension	3.4	1.7	14.8**

ff, footfall; es, endstance.

All measures of flexion and extension are during stance.

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

both angular and relative linear variables was highly significant overall (Wilks' $\lambda = 0.001$, $F_{140,641} = 8.0$, $P < 0.001$), and the first five discriminant functions (DFs) were significant (canonical correlations 0.96, 0.90, 0.81, 0.74 and 0.55, respectively) and explained 99% of the variance. The first and second DFs primarily divided the eight categories on the basis of speed and

Table 5. F-values from three-way ANOVAs performed separately on each kinematic variable describing angles of the femur, pelvis and toe

Dependent variable	Size, d.f.=3,12	Speed, d.f.=1,12	Size×speed, d.f.=3,12
Maximum femur retraction	7.6*	0.3	0.4
Minimum femur retraction	3.1	9.5*	1.0
Maximum femur depression	1.3	4.4*	3.7*
Minimum femur depression	0.9	0.9	0.7
Maximum femur rotation	5.6*	0.4	3.9*
Minimum femur rotation	1.4	31.8**	1.2
Pelvic rotation	2.2	6.6*	1.3
Toe orientation (ff)	2.5	19.2**	6.6*

Abbreviations are as in Table 4.
* $P < 0.05$, ** $P < 0.001$.

size, respectively (Fig. 10A). Slow locomotion had high positive values of DF1, and larger lizards had high negative values of DF2. The third DF primarily separated the subadult slow locomotion from the other groups (Fig. 10B). Of the total number (122) of strides, 94% were correctly classified into their pre-designated categories of size and speed. The major attributes (substantial loadings, Table 6) of the locomotion of larger lizards were low values of the relative x position of the toetip at footfall, and high values of knee angle at the end of stance, maximum femur retraction and maximum femur

Table 6. Loadings from discriminant function analyses of 20 kinematic variables for the locomotion of juvenile, intermediate, subadult and adult *Dipsosaurus dorsalis* at slow and high speeds

Variable	All kinematics			Angular kinematics		
	DF1	DF2	DF3	DF1	DF2	DF3
Duty factor	0.684	0.137	0.122	–	–	–
Relative step length	–0.130	0.167	–0.005	–	–	–
Relative stride length	–0.589	0.086	–0.112	–	–	–
Relative $Y_{\text{hip,footfall}}$	–0.261	0.183	0.119	–	–	–
Relative $X_{\text{toetip,footfall}}$	–0.243	0.350	–0.067	–	–	–
Relative $X_{\text{toetip,endstance}}$	0.016	0.208	–0.286	–	–	–
Knee angle (ff)	–0.321	0.100	–0.095	–0.480	–0.457	–0.337
Knee angle (es)	0.052	–0.507	–0.237	0.447	–0.549	0.162
Ankle angle (ff)	–0.295	0.051	–0.219	–0.410	–0.498	–0.160
Ankle angle (es)	–0.151	0.014	0.026	–0.196	–0.250	–0.264
Toe angle (ff)	0.024	0.212	–0.201	–0.208	0.126	0.224
Toe angle (es)	0.061	–0.127	0.296	0.256	0.125	–0.172
Toe orientation (ff)	0.151	–0.129	0.072	0.347	0.203	0.204
Pelvic rotation	0.056	0.242	0.018	–0.145	0.328	0.102
Minimum femur retraction	0.114	–0.100	–0.135	0.199	0.021	0.266
Maximum femur retraction	0.078	–0.414	–0.049	0.411	–0.316	0.026
Minimum femur depression	0.051	–0.045	0.093	0.084	0.070	–0.069
Maximum femur depression	–0.079	0.091	0.170	–0.170	0.019	–0.295
Minimum femur rotation	0.184	–0.107	0.208	0.324	0.273	0.011
Maximum femur rotation	0.015	–0.289	0.273	0.290	–0.160	–0.334

Substantial loadings (≥ 0.250) are marked in bold type.

DF, discriminant function.

Abbreviations are as in Table 4.

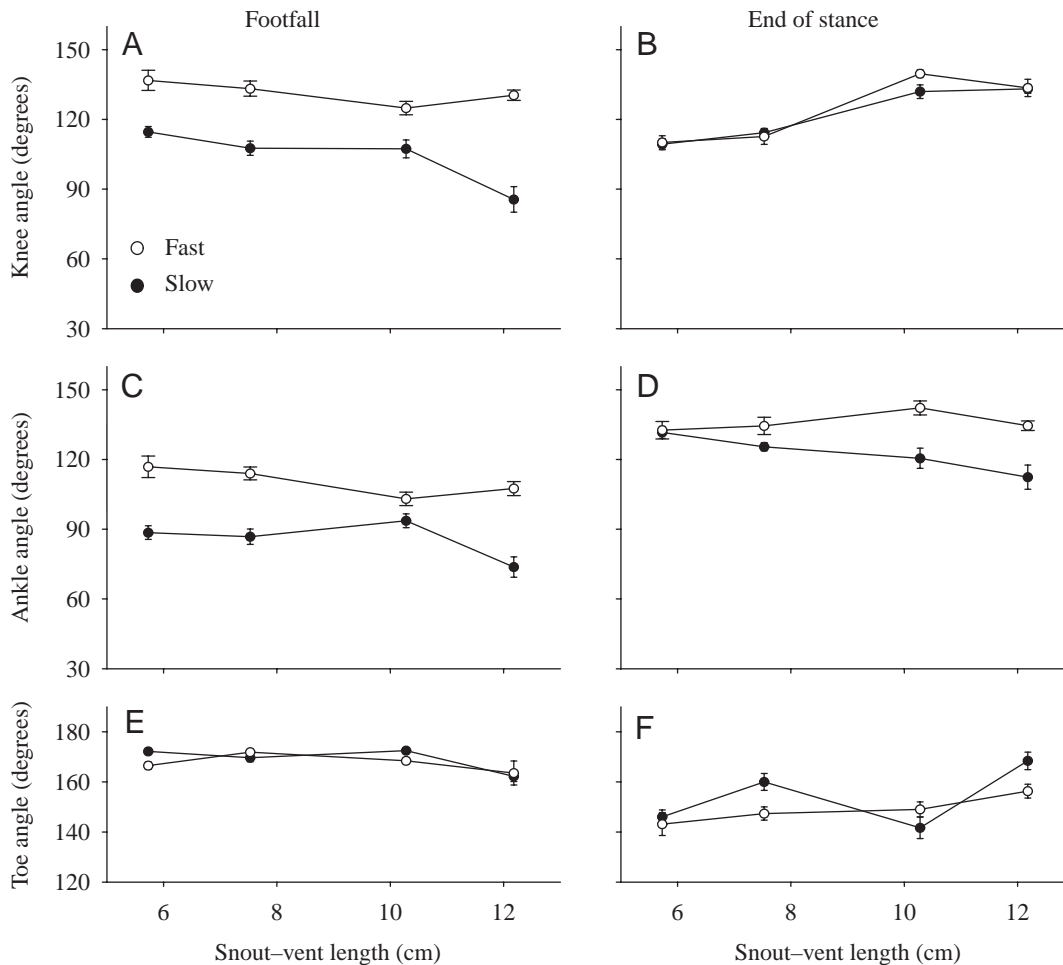


Fig. 6. Mean values of joint angles for the knee (A,B), ankle (C,D) and toe (E,F) at footfall (A,C,E) and at the end of stance (B,D,F). Values are means \pm S.E.M. Table 4 summarizes significant differences among size classes and speeds. Some of the standard errors are smaller than the symbols. Open and filled symbols represent fast (250 cm s⁻¹) and slow (50% duty factor) locomotion, respectively.

rotation. Fast locomotion had low duty factors and high values of relative stride length, relative hip height at footfall, and knee and ankle angles at footfall (Table 6).

The DFA with only angular variables was highly significant overall (Wilks' $\lambda=0.014$, $F_{98,647}=6.4$, $P<0.001$), and the first four discriminant functions were significant (canonical correlations 0.88, 0.81, 0.79 and 0.57, respectively) and explained 95% of the variance. The slow locomotion of the larger lizards (subadults and adults) was particularly distinctive (Fig. 10C,D). The first, second and third DFs primarily segregated the slow locomotion of adults, speeds and the slow locomotion of subadults, respectively (Fig. 10C,D). Of the total number of strides, 82% were correctly classified. The major (substantial loadings, Table 6) attributes of the locomotion of larger lizards were small knee and ankle angles at footfall, a large knee angle at the end of stance and high values of maximum femur retraction.

Discussion

Size had pervasive effects on the kinematics of *D. dorsalis*:

14 out of 33 kinematic variables had significant size effects, and 15 variables had significant size by speed interactive effects. However, decreases in relative (divided by SVL) linear kinematic variables with increased size could reflect the disproportionately short limbs of larger *D. dorsalis* (Table 1; Fig. 1; Marsh, 1988). Three relative (SVL) linear kinematic variables did decrease significantly with increased size, and reanalysis of these variables as proportions of total hindlimb length revealed no significant main size effects. However, the predictions from the negative allometry of the hindlimb were contradicted by three other relative (SVL) linear kinematic variables which increased significantly with increased size. We also used angles as a size-independent method of quantifying movement, but many angular variables changed significantly with size. Therefore, the negative allometry of the hindlimbs was not sufficient to explain the widespread kinematic differences associated with size.

Equivalent speeds

Lizards do not have conspicuous changes in their footfall patterns (trot *versus* gallop) or discontinuities in kinematics as

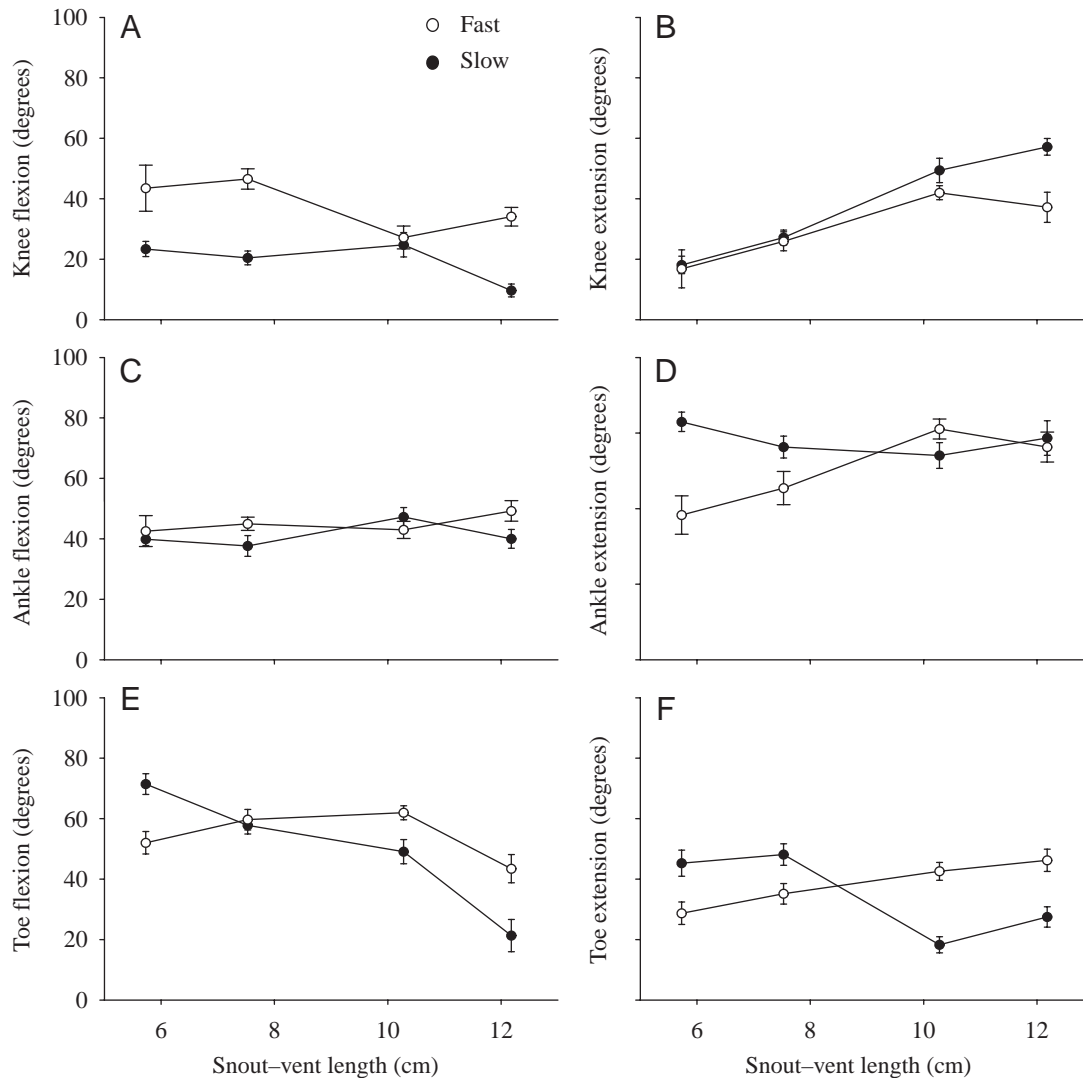


Fig. 7. Mean values of flexion (A,C,E), and extension (B,D,F) for the knee (A,B), ankle (C,D) and toe (E,F) during stance. Values are means \pm S.E.M. Table 4 summarizes significant differences among size classes and speeds. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively.

speed increases, both of which often define the equivalent speeds of mammals (Heglund et al., 1974; Heglund and Taylor, 1988). Two additional metrics for defining equivalent speeds are a 50% duty factor and equal Froude numbers (Alexander and Jayes, 1983; Hildebrand, 1985), and we chose slow-speed locomotion of *D. dorsalis* that conformed to both these criteria. However, different sizes of *D. dorsalis* moved at equivalent speeds without having equivalent kinematics.

We relied primarily on the walk–run transition to compare the kinematics of different-sized *D. dorsalis*, just as this and other gait transitions have facilitated comparisons among species of different sizes, but how similar is the walk–run transition of lizards to that of other vertebrates? For both mammals (Heglund and Taylor, 1988) and birds (Gatesy and Biewener, 1991), stride frequency during a walk increases more rapidly with increased speed compared with running, and Heglund and Taylor (1988) and others have fitted different

linear regressions of stride frequency *versus* speed for different gaits. For adult *D. dorsalis* ($50\text{--}350 \text{ cm s}^{-1}$), the slope of stride frequency *versus* speed decreased with increased speed, and Fielers and Jayne (1998) fitted a quadratic function to these data. If stride frequency increases discontinuously with speed, then separate linear regressions are appropriate, whereas continuous data with decreasing slope are better modeled with a quadratic function. Thus, all the available data show a diminished slope with increased speed, but no simple statistical solution can resolve whether the best description of such data is two straight lines or a single quadratic function. Subjectively, the stride frequency data for lizards and birds (Gatesy and Biewener, 1991) appear more continuous than those of mammals.

As size increases both within (Drucker and Jensen, 1996a,b) and among (Garland, 1983; Heglund et al., 1974) species, both the absolute speed at which a gait transition occurs and the maximum speed of locomotion generally increase. In *D.*

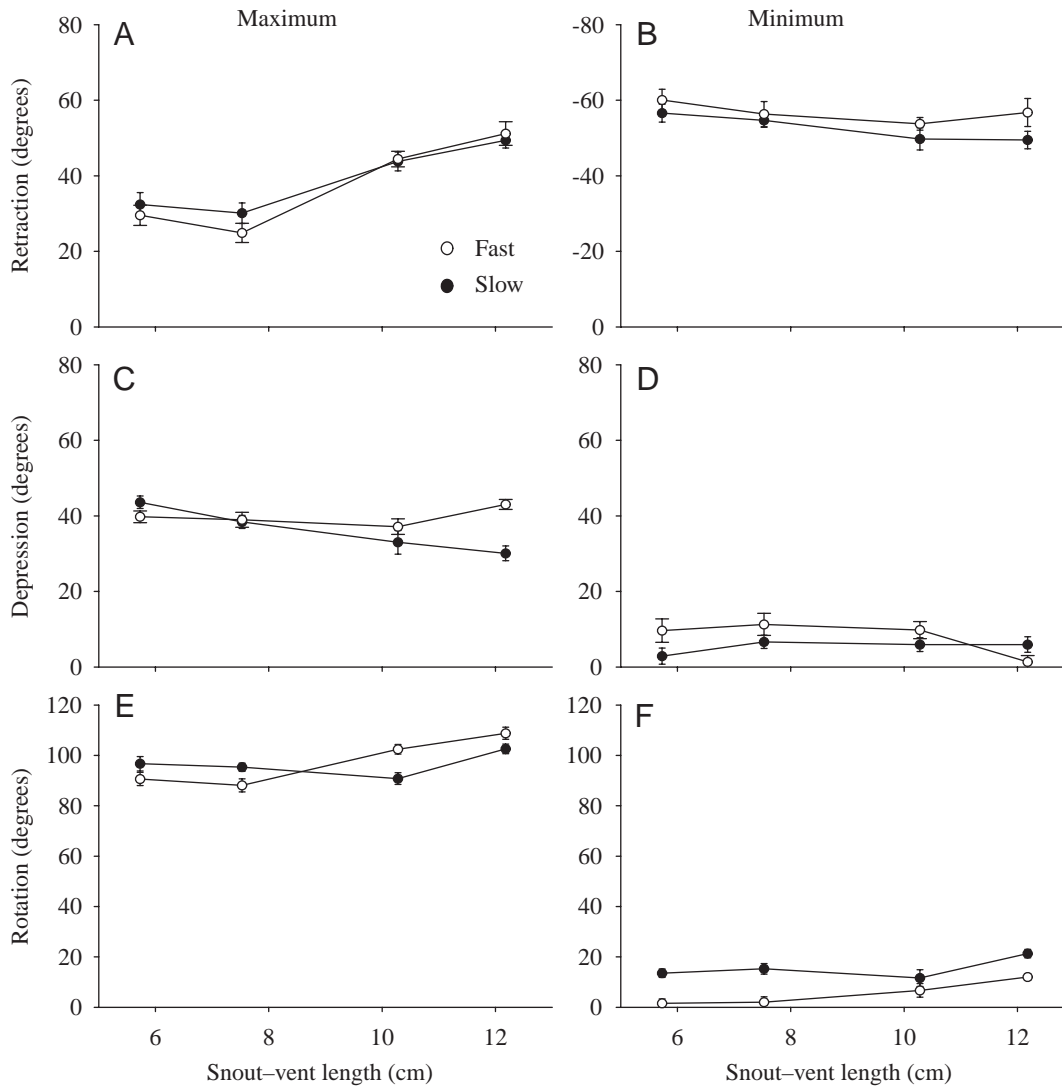


Fig. 8. Mean maximum (A,C,E) and minimum (B,D,F) values of retraction (A,B), depression (C,D) and rotation (E,F) of the femur. Values are means \pm S.E.M. Table 5 summarizes significant differences among size classes and speeds. Some of the standard errors are smaller than the symbols. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively.

dorsalis, the predicted maximum speeds increase significantly with size (324 cm s^{-1} and 402 cm s^{-1} for juveniles and adults) (at 40°C , Marsh, 1988). The mean speeds at the walk-run transition tended to increase with size as values of juvenile and adult *D. dorsalis* ranged from 99 to 119 cm s^{-1} , but this variation among size classes was not quite statistically significant. Interestingly, when expressed as a percentage of maximum speed (31% and 30% , respectively), the speeds at the walk-run transition differed even less among sizes than for absolute speeds. Thus, besides using a constant percentage of a gait-transition speed (discussed in Drucker and Jensen, 1996a), comparing animals of different sizes may also be facilitated by using a constant percentage of maximal speed.

Intraspecific versus interspecific size effects

Previous intraspecific studies of the effects of size on the limb joint angles during vertebrate locomotion are limited

mainly to chickens and humans. During the first 2 weeks post-hatching, younger chicks have smaller knee and ankle angles at footfall than older chicks during walking, and the ontogenetic kinematic differences were generally greater for walking than for running (Muir et al., 1996). Compared with adult humans, infants generally have a hyperflexed knee joint during the whole step cycle and greater ankle extension contributes to a more digitigrade foot posture (Forssberg, 1985). Juvenile lizards had more extended knee and ankle joints and a more digitigrade foot posture than adults, particularly at the slow speed. Thus, the available ontogenetic data for vertebrates show few clear generalities for limb kinematics, but these interspecific comparisons may be confounded by substantial differences in the precocity of lizards, chickens and humans.

Two of the most thorough ontogenetic studies of scaling in kinematics are for the feeding of fishes (Richard and

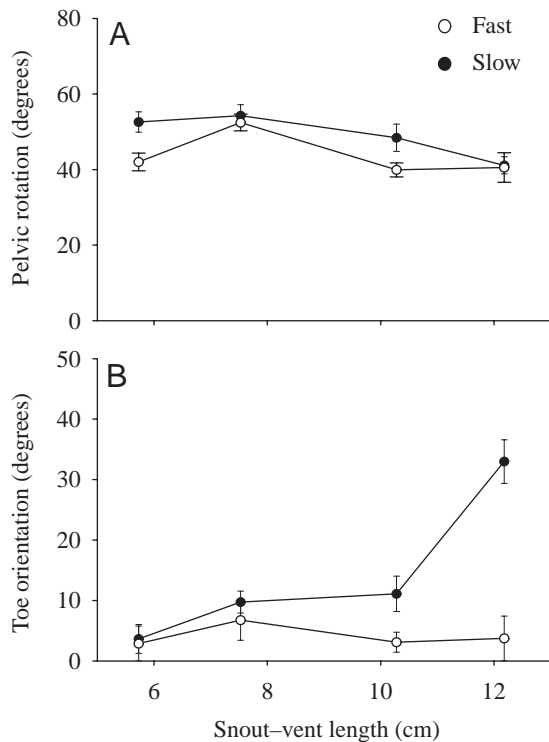


Fig. 9. Mean values of pelvic rotation (A) and the angle of toe orientation (B). Values are means \pm S.E.M. Table 5 summarizes significant differences among size classes and speeds. Open and filled symbols represent fast (250 cm s⁻¹) and slow (50% duty factor) locomotion, respectively.

Wainwright, 1995; Wainwright and Shaw, 1999). The jaw dimensions and relevant lever arms of largemouth bass (*Micropterus salmoides*) scaled isometrically, as did maximal linear and angular displacements of the jaw during prey capture (Richard and Wainwright, 1995), whereas neither the limb dimensions nor the locomotor kinematics of *D. dorsalis* scaled in such a simple fashion. Further, Wainwright and Shaw (1999) found that the scaling of the duration of opening and closing of the mouth could largely be predicted from the scaling of the lever arms from three fish species. Richard and Wainwright (1995) and Wainwright and Shaw (1999) chose feeding behaviors that approximated physiological maximum performance, whereas both speeds that we used for *D. dorsalis* were substantially below the maximum speed for this species (Irschick and Jayne, 1999; Marsh, 1988). In the light of the speed-dependence of size effects within *D. dorsalis*, it remains unclear whether the kinematics of different-sized *D. dorsalis* would converge at maximal speeds.

Small *D. dorsalis* have disproportionately long hindlimbs, similar to the ontogenetic allometries of most other lizard species (Garland and Losos, 1994). The relatively long hindlimb length of small *D. dorsalis* resulted primarily from their relatively long distal limb elements. The adults of particularly fast species of lizard (e.g. *Callisaurus draconoides*) also have relatively long distal limb elements (Irschick and Jayne, 1999).

The negative allometry of the hindlimb length relative to the snout-vent length of *D. dorsalis* closely resembles the negative allometry between stride length and snout-vent length for both speeds in our study. Similarly, for the maximal-speed running of *D. dorsalis*, stride length has negative allometry (Marsh, 1988). Our slow-speed data (50% duty factor) and those of Marsh (1988) both seem likely to represent different types of equivalent speeds, but some of our scaling relationships for the (submaximal) high-speed data should be viewed with caution because they may not represent an equivalent speed among lizards of different sizes. At the slow speed, the scaling of step length is similar to that of hindlimb length. In contrast to step length, step duration at slow speed has such a strong negative allometry that the scaling coefficient is significantly less than 1 even when it is scaled to hindlimb length. Step duration (contact time) also has negative allometry with limb length for other vertebrate taxa (Hoyt et al., 2000).

The contractile properties of muscles vary ontogenetically in *D. dorsalis* and in many other vertebrates. For example, from hatchlings to adult *D. dorsalis*, the time to peak tension for isometric twitches increases from approximately 7 to 12 ms (Marsh, 1988). The normalized power output does not change significantly with size, but the frequency at which maximal power occurs decreases with increased size (Johnson et al., 1993). *In vivo* data on the strain of limb muscles in *D. dorsalis* are lacking but the similarity of scaling of stride length and hindlimb length led Johnson et al. (1993) to assume that limb movements and muscle strain were similar in small and large *D. dorsalis* at maximal speed. A different joint angle implies a different strain for a muscle that spans that joint. Thus, in the light of the widespread ontogenetic differences in joint angles that we found for *D. dorsalis*, muscle strain is also likely to vary with size, although we lack kinematic data for maximal speeds.

Comparisons among different-sized species within birds (Gatesy and Biewener, 1991) and within mammals (Biewener, 1983) have shown that smaller species tend to have 'crouched' limbs compared with larger species. Two key attributes of a more crouched limb posture are greater flexion of the joints within the limb (Gatesy and Biewener, 1991) and greater angles of the limb elements relative to a vertical reference line (Biewener, 1983). Limb sweep angles (θ) are the angular excursions of a line extending from the hip to the tip of the toe from footfall to the end of stance. Gatesy and Biewener (1991) constructed a vertical reference to subdivide θ into protraction (α) and retraction (β) components and greater values of any of these angles have been used to indicate a more crouched limb posture. With decreased size among different species of bird, values of θ and β increased, whereas α remained constant (Gatesy and Biewener, 1991). With decreased size from horses to mice, θ generally increased (McMahon, 1975), and all but one (femur) of four longbones had greater angles relative to a vertical reference at midstance (Biewener, 1983).

In contrast to the interspecific data for birds and mammals, smaller *D. dorsalis* were less crouched at the slow speed as a result of more extended knee and ankle joints at footfall, and

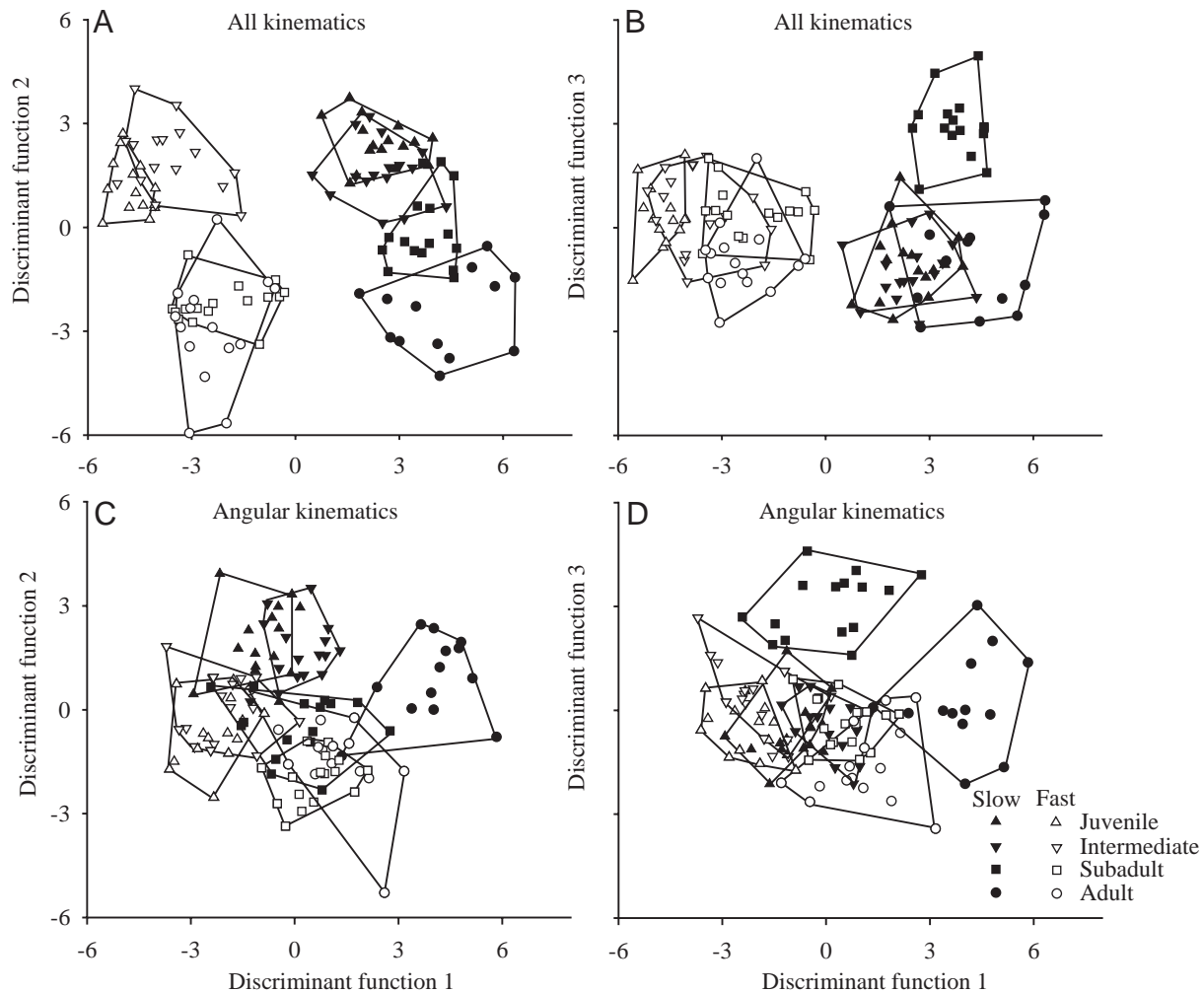


Fig. 10. Discriminant functions 2 and 3 versus discriminant function 1 from two separate analyses of a total of 20 relative linear, timing and angular variables (A,B) and a total of 14 angular variables (C,D). Circles, squares, upside-down triangles and right-side-up triangles represent individual strides of adult, subadult, intermediate and juvenile *Dipsosaurus dorsalis*, respectively. Table 6 provides loadings for both discriminant function analyses. Open and filled symbols represent fast (250 cm s^{-1}) and slow (50% duty factor) locomotion, respectively.

they also had a more depressed (closer to a vertical) femur (Fig. 8C). Further, smaller *D. dorsalis* retracted their femur less near the end of stance, whereas the angle of femur protraction was unaffected by size. We used hip height and two-dimensional effective limb length at footfall and at the end of stance to calculate θ , α and β for the slow speed: only β changed significantly (increased) with increased size (two-way ANOVA, $F_{3,12}=10.2$, $P<0.01$). Thus, with changing size among bird species and within *D. dorsalis*, movements related to retraction changed significantly, but in opposite directions. In addition, unlike both birds and mammals, θ was unaffected by size in *D. dorsalis* as a result of a non-significant decrease in α that offset the increase in β .

The different conclusions regarding limb posture among different species of mammals versus those for different sizes of *D. dorsalis* might result from the qualitative differences in limb structure between ungulates and rodents, which have dominated previous samples of large and small mammals, respectively (Biewener, 1983; McMahon, 1975). Generalities

regarding limb posture could be strengthened if data were systematically compared within and among higher mammalian taxa. The observed differences in the effects of size on limb posture between birds and *D. dorsalis* are less readily explained by conspicuous variation in limb structure among the bird taxa studied by Gatesy and Biewener (1991). Thus, the lack of congruence between our intraspecific data and previous interspecific data makes it difficult to argue that size alone is the causal factor for trends regarding crouched limbs.

The scaling of differences in bone cross-sectional area among different-sized species of mammal is less than expected for resisting a given amount of deformation, and yet the limb bones of mammals of different sizes have very similar peak stresses and strains (Biewener, 1989, 1990). Consequently, Biewener (1990) suggested that more erect limb posture in larger species of mammals is an important mechanism for reducing bending stresses. Although Blob and Biewener (1999) have measured strain in the limb bones of large iguanas (*Iguana iguana*; $>300 \text{ g}$), ontogenetic scaling data for bone

cross-sectional area are lacking for lizards. If the leg bones of smaller lizards were disproportionately long and thin, then greater extension of limb joints and a more nearly vertical limb during running could help to alleviate bone stress. More erect limbs characterize both small size and increased speed within a particular size of *D. dorsalis* (Jayne and Irschick, 1999). Whether both types of increasing limb erectness in *D. dorsalis* necessarily diminish strain is not obvious, especially since the recent study of Blob and Biewener (1999) showed that bone strain can increase with increased erectness of the limb in alligators (*Alligator mississippiensis*).

Blob and Biewener (1999) also found very high amounts of torsional loading in the iguana limb bones compared with those of mammals, and this was attributed to the relatively sprawled orientation of the iguana limb compared with mammals. *D. dorsalis* displays some kinematic changes with size that could also affect the loads experienced by the limbs. For instance, at the slow speed, the orientation of the fourth (and longest) toe of juvenile *D. dorsalis* was nearly straight forward, whereas that of adults was pointed approximately 33° laterally. Consequently, increased torsional loading of the toe bones appears likely for adults relative to juveniles at the slow speed. A more lateral orientation of the hindfoot and toes could also prevent ipsilateral feet from interfering with each other, but paradoxically a more lateral orientation of the toe is most conspicuous in larger lizards that have disproportionately small hindfoot lengths.

The magnitude of differences in joint angles among different sizes of *D. dorsalis* is large and often similar to many of the interspecific differences found by Irschick and Jayne (1999) in a study of the high-speed running of five similarly sized, yet morphologically distinct, lizard species. Fourteen of the angular kinematic variables quantified in the current study were also examined by Irschick and Jayne (1999), and ten of these variables had either a significant size or size by speed interactive effect. Of these ten variables, seven differed significantly among the species studied by Irschick and Jayne (1999). One such variable was maximum femur retraction, which differed by 22° both between juvenile and adult *D. dorsalis* at the fast speed and between the largest and smallest mean values for different species. The tremendous ontogenetic variation in the kinematics of *D. dorsalis* illustrates how size could impair the detection of interspecific differences in kinematics, as Richard and Wainwright (1995) have also discussed for fish.

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