

COMPARATIVE THREE-DIMENSIONAL KINEMATICS OF THE HINDLIMB FOR HIGH-SPEED BIPEDAL AND QUADRUPEDAL LOCOMOTION OF LIZARDS

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Summary

Although lizards have been model organisms for testing locomotor performance and in ecomorphological studies, the limb movements of lizards during high-speed locomotion are poorly understood. Thus, we quantified the three-dimensional kinematics of the hindlimb, body and tail for five morphologically distinct species of lizard during steady-speed locomotion near maximum sprinting speed (2–5 m s⁻¹). The kinematics of different species had little multivariate overlap. More than half of the strides of all species had digitigrade foot posture, but the frequency of using digitigrade foot posture varied among species. The combination of digitigrade foot posture and large foot size of the lizards contributed substantially to the high values

of hip height. For each species, different suites of kinematic variables distinguished bipedal from quadrupedal strides. Interspecific morphological variation did not correspond globally to variation in kinematics, although lizard species with elongated hindlimbs took longer strides than species with shorter hindlimbs. The Froude numbers and relative stride lengths of all lizards running near maximal speeds were large compared with those reported previously for other vertebrates.

Key words: locomotion, kinematics, lizard, bipedal, Froude number, comparative phylogeny.

Introduction

Studying the locomotor capabilities of organisms provides an excellent opportunity for determining whether morphology, performance and kinematics have co-evolved. Lizards exhibit tremendous variation in morphology and behavior with respect to locomotor function and, hence, have served as a model system for testing maximal sprinting performance, which may be important for many activities such as escape from predators and feeding (Garland and Losos, 1994). Although many studies have quantified the maximal speeds of lizards (for a review, see Garland and Losos, 1994), few have quantified the relevant kinematics. Further, the majority of kinematics for the locomotion of lizards are for relatively slow speeds that are substantially less than 50% of their maximal sprinting speeds (e.g. Fieler and Jayne, 1998; Jayne and Irschick, 1999; Reilly and Delancey, 1997a,b). Fieler and Jayne (1998) and Jayne and Irschick (1999) found that speed of locomotion had many highly significant effects on the kinematics of the hindlimb in the lizard *Dipsosaurus dorsalis*. Thus, any inference from the relationships between movement and morphology at low speeds may be misleading with regard to how the limbs function near maximal sprinting speeds. For example, the locomotion of lizards is often characterized as having a sprawling limb posture, a plantigrade foot posture and laterally oriented feet (Brinkman, 1981; Reilly and Delancey, 1997a,b), but this characterization is based primarily on research on lizards moving at relatively slow speeds.

Of particular interest to many biologists is how the whole-limb dimensions of lizards and other animals relate to maximal speed (Bauwens et al., 1995; Losos, 1990; Macrini and Irschick, 1998; Miles, 1994). Interspecific differences in limb dimensions would be sufficient to explain differences in linear kinematic quantities if different species of lizard had identical joint angles during maximal-speed running. Authors frequently suggest that long hindlimbs enable lizards to take longer strides, and hence achieve faster speeds, than species with shorter hindlimbs (for a review, see Garland and Losos, 1994). In addition, significant positive correlations between total hindlimb length and speed have been found among different lizard species (Bauwens et al., 1995; Losos, 1990; Miles, 1994). However, lizards with short hindlimbs theoretically could run as fast as species with longer hindlimbs if they attained a sufficiently high stride frequency. Further, elongation of distal elements in mammals and other vertebrates is generally considered a specialization for running quickly (Coombs, 1978; Garland and Janis, 1993; Hildebrand, 1985). However, the function of distal limb elements is poorly known for lizards even though many lizards have extraordinarily long feet and toes compared with other vertebrates (Fig. 1).

Lizards are also an interesting group for examining bipedal locomotion, in part because bipedal running is widespread among phylogenetically diverse taxa (Glasheen and McMahon, 1996; Irschick and Jayne, 1998; Snyder, 1949,

1952, 1962). The widespread occurrence of bipedality in lizards could result from some combination of retaining an ancestral trait and convergent evolution. If lizard species use different joint angles during bipedal running, this would suggest that bipedal running resulted from independent specialization rather than the retention of an ancestral trait. Bipedal locomotion of lizards is commonly presumed to maximize speed and stride length (Snyder, 1962), and stride length is one of many kinematic variables that increase with the speed of quadrupedal locomotion (Fieler and Jayne, 1998; Jayne and Irschick, 1999; Urban, 1965). Thus, the kinematics of bipedal locomotion could represent one end of a continuum of variation that is associated with increased speed, rather than being a particularly distinct mode of locomotion. However, other than the study of Urban (1965), few quantitative data are available to determine whether the kinematics of bipedal and quadrupedal running differ. Snyder (1962) suggested that certain morphological characteristics of lizards such as long limbs and tails are specializations for bipedality, but few studies have examined bipedal locomotion in morphologically diverse species.

We quantified the morphology, hindlimb kinematics and body posture of five lizard species during both quadrupedal and bipedal locomotion near their maximal speeds to provide insights into interspecific variation in sprinting performance and to test the following null hypotheses. (1) Different species run at maximum speeds with similar joint angles within the limbs, but linear kinematic quantities differ as a result of limb dimensions. (2) Among similarly sized species, those with the longest limbs have the greatest stride lengths and run the fastest. (3) Within a single species, the kinematics of bipedal locomotion represents one end of a continuum of variation that is associated with increased speed, rather than being a distinct mode of locomotion.

Materials and methods

Experimental subjects

The lizard species examined were the desert iguana (*Dipsosaurus dorsalis* Baird and Gicard), the zebra-tailed lizard (*Callisaurus draconoides* Blainville), the Mojave fringe-toed lizard (*Uma scoparia* Baird), the desert horned lizard (*Phrynosoma platyrhinos* Wiegmann) and the western whiptail (*Cnemidophorus tigris tigris* Wagler). We chose these five species because they span a wide range of different terrestrial lizard phenotypes (Fig. 1) and their phylogenetic relationships are well understood (Fig. 2). These five species have differing degrees of specialization for bipedality and maximal sprinting performance. At one extreme, *Ca. draconoides* runs very fast, frequently uses bipedal locomotion in nature and has many of the morphological features of a bipedal specialist (Irschick and Jayne, 1998; Snyder, 1962). At the other extreme, *P. platyrhinos* does not run very quickly, has never been observed to run bipedally and appears morphologically adapted for a cryptic existence (Fig. 1). Another advantage of using these species is that individuals of very similar size can be obtained (Fig. 1).

Estes et al. (1988), Frost and Etheridge (1989) and Reeder and Wiens (1996) have elucidated the phylogenetic relationships of the species in this study (Fig. 2). The five species belong to three families: Phrynosomatidae (*Ca. draconoides*, *U. scoparia* and *P. platyrhinos*), Iguanidae (*D. dorsalis*) and Teiidae (*Cn. tigris*). However, *Ca. draconoides*, *U. scoparia* and *P. platyrhinos* are all part of a very closely related clade consisting of only five genera (Reeder and Wiens, 1996). The Phrynosomatidae and Iguanidae belong to the iguanian group, which has more than 40 genera and is distantly related to the Teiidae (Etheridge and de Queiroz, 1988). Therefore, our study compares both closely related and distantly related lizard species.

We collected all lizards near the Kelso dune system in San Bernardino County, California, USA (permit number 802030-01) and transported them back to the University of Cincinnati for experiments. Lizards were caged individually or in pairs and maintained on a diet of either lettuce, broccoli and a powdered mixture of Purina puppy chow and Kellogg Special K cereal (*D. dorsalis*) or crickets which had been fed a dietary 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, which also approximated the body temperatures during experiments. We video-taped all lizards within 3 weeks of capture. After video-taping several individuals of each species, we analyzed data only from the four individuals from each species (only three *P. platyrhinos* were available) that had the fastest running speeds as well as a combination of bipedal and quadrupedal running. We were not able to obtain any bipedal running for *P. platyrhinos*.

Morphological variables

To elucidate morphological differences among the five species, we measured snout-vent length (SVL), mass and 11 linear dimensions (Table 1) using calipers (± 0.1 mm) to measure distances on life-size ventral-view radiographs of anesthetized specimens for which kinematics were examined. Hindfoot length was from the heel to the distal end of the fourth metatarsal (here called tarsals and metatarsals). The length of the forefoot was measured 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 width of the body midway between the two girdles; the trunk length was equal to the longitudinal distance between the shoulder and hip joints.

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 placed the lizards in containers underneath incandescent lamps which allowed them to attain a body temperature of approximately 40 °C. Immediately before and after the lizards ran on the treadmill, we used a thermocouple and a Tegam model 871A digital thermometer to confirm that cloacal temperatures were between 35 and

40 °C. We varied the speed of the treadmill to elicit the fastest possible speed for each lizard, which ranged from approximately 2.0 m s^{-1} (*P. platyrhinos*) to 5.3 m s^{-1} (*Ca. draconoides*). From these video tapes, we selected 2–4 of the fastest quadrupedal and 1–4 of the fastest bipedal strides for each individual. Prior to video-taping, we painted landmarks on the pelvis and hindlimb of each lizard to facilitate digitization of the video images.

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 the digitized coordinates using macros for Microsoft Excel version 7.0 (written by G. Updegraff and B. Jayne). The x axis was the horizontal dimension parallel to the forward direction of travel of the lizards 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.

We digitized the three-dimensional coordinates of the following landmarks on the right side of the lizard: the pelvis, 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. Finally, we digitized four two-dimensional coordinates from a dorsal perspective and five two-dimensional coordinates from a lateral perspective. From the dorsal perspective, we measured the coordinates of the right and left ankles, and the right and left pelvic landmark. From the lateral perspective, we measured the coordinates of the mid-dorsal line nearest the shoulder, the right pelvic landmark, the right shoulder joint, the most ventral portion of the right forelimb and the tail. The x and y coordinates of the tail were measured approximately one trunk length from its base on the dorsal surface. For each species, we transformed the coordinates of the painted pelvic landmarks to approximate the coordinates of the hip (as in Jayne and Irschick, 1999).

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

Three linear quantities described the height of the hip relative to the treadmill. First, we measured hip height at the time of footfall, $Y_{\text{hip}}(\text{ff})$. Second, hip height at footfall minus minimum hip height during stance was 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 two- (x , y) and three-dimensional effective limb lengths (eff2D, eff3D) 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 was the difference between the y 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 right hindfoot was on the ground. Average forward velocity of each stride was stride length (cm) divided by stride duration (s).

We determined the three-dimensional angles of the knee, the ankle and the fourth toe and metatarsal at footfall, at maximum flexion within the stance phase and at the end of stance. Smaller values of the knee angle indicate greater flexion of the joint. The ankle angle was the angle between the tibia and the dorsal side of the metatarsals so that smaller values between 0° and 180° indicate greater dorsiflexion of the foot. The toe joint angle was the angle between the fourth metatarsal and a straight line extending from the base to the tip of the fourth toe, so that larger values greater than 180° indicate greater plantarflexion of the toe. For the knee, ankle and toe joints, we determined the amount of flexion that occurred in the initial yield phase of stance by subtracting the minimum value during stance from the value at footfall. The amount of joint extension during stance was the value at the end of stance minus the minimum value during stance.

To determine the angle of the trunk and the tail, we calculated the two-dimensional angle between the tread surface and a straight line connecting the x – y coordinates on the mid-dorsal line nearest the shoulder and hip (trunk angle) and near the hip and on the tail (tail angle). Positive values of the trunk and tail angles indicate that the chest and distal tail are elevated. For statistical analyses, we used the mean value of all trunk and tail angles for all images within each stride cycle.

From a dorsal perspective, we also measured two additional angles indicating the orientation of the toe and pelvis. The two-dimensional angle between the x axis and the fourth toe was measured at footfall; values of 0° and 90° indicate that the toe is oriented forward and laterally, respectively. The difference between maximum and minimum values of the angles between the x axis and a line connecting the left and right hips indicated the amount of rotation of the pelvis (projected onto a horizontal plane). As discussed by Jayne and Irschick (1999), we could

not directly measure the amount of pelvic roll about the longitudinal axis of the lizard, but pelvic roll seems unlikely to confound the interpretation of our other kinematic variables.

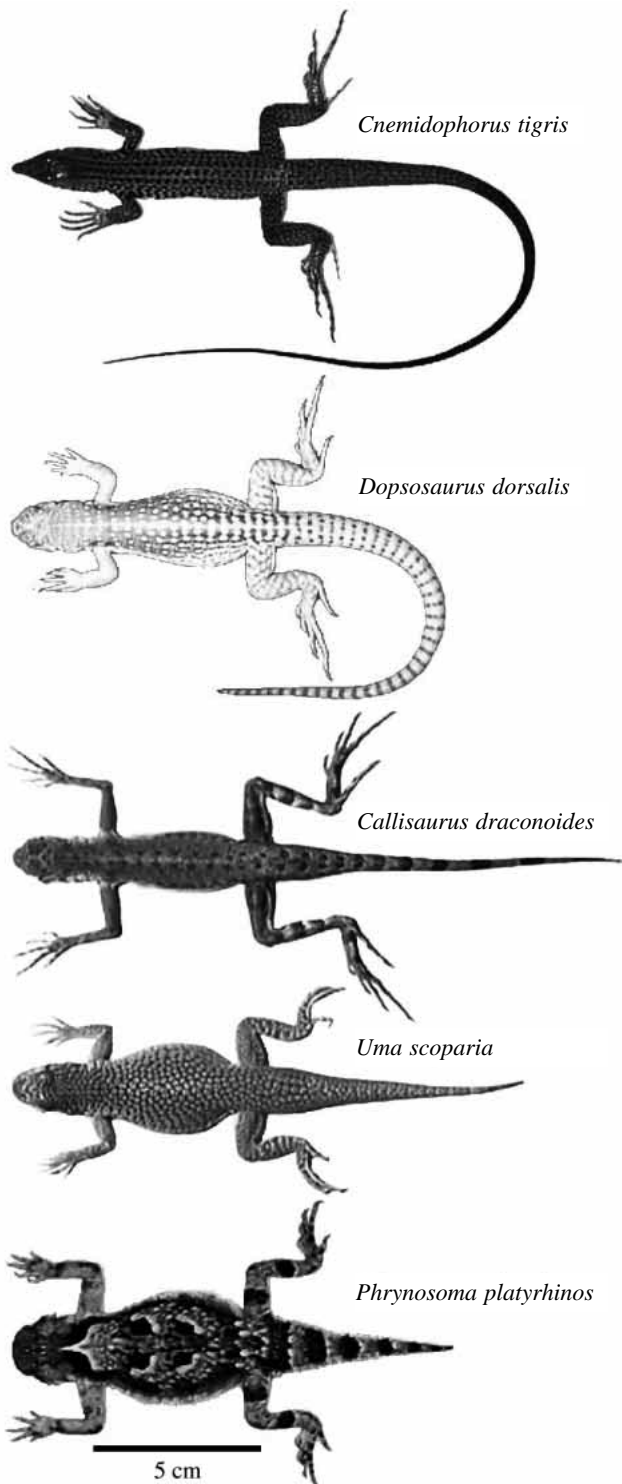


Fig. 1. Dorsal views of anesthetized specimens of the five lizard species for which kinematics were analyzed. Note the similarity in overall body size, but the considerable differences in stoutness, limb dimensions and tail length. All specimens are shown at the same magnification.

For each of the four 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 that 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 distal femur was below or above the horizontal reference plane, respectively.

Phylogenetic analyses

Patterns of ancestry among species can confound interspecific comparisons (Felsenstein, 1985; Garland et al., 1992; Martins and Garland, 1991), and this problem is most acute when closely related species are most similar. The three species in the closely related sand lizard clade (*P. platyrhinos*, *Ca. draconoides* and *U. scoparia*) appeared quite dissimilar morphologically (Figs 1, 2), but we performed an autocorrelation analysis (Cheverud et al., 1985) to determine whether phylogeny was a confounding factor (software created by T. Dow and J. Cheverud, and modified by D. Miles and A. Dunham). If no phylogenetic effect exists, then statistical methods incorporating phylogeny are unnecessary (Gittleman and Luh, 1992). We calculated autocorrelation coefficients between the mean scores for the first three discriminant functions for each species from a multivariate analysis of morphology and a matrix using the number of nodes separating each species as a measure of phylogenetic distance. All three discriminant functions of morphology had large negative autocorrelation coefficients (-0.66 , -0.59 and -0.86), indicating that closely related species actually tended to be morphologically dissimilar. Phylogenetic relationships were thus not a strong confounding factor for morphology. For select, simple correlation analyses among species we also verified that the results using standard statistical tests were similar to those generated using the independent-contrasts approach (Felsenstein, 1985). For the independent-contrasts analysis, we set all branch lengths to one.

Statistical analyses

For all analyses, we used SYSTAT 5.0 (Wilkinson, 1992), and $P < 0.05$ was the primary criterion for statistical significance. In the text, we provide relevant details such as F -values and degrees of freedom (d.f., indicated as subscripts of F) to clarify the magnitude of statistical differences and the potential effects of multiple comparisons. The five species

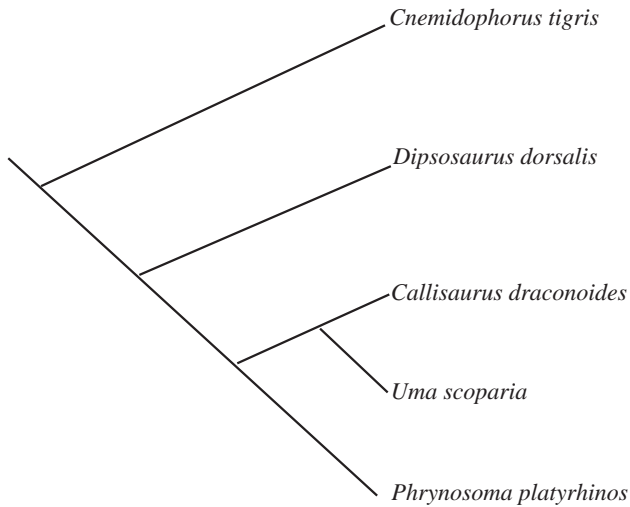


Fig. 2. A phylogeny of the five lizard species examined in this study from analyses by Estes et al. (1988), Frost and Etheridge (1989) and Reeder and Wiens (1996). For graphical clarity, several additional lizard taxa are not shown; hence, none of the groups of species shown in the phylogeny is monophyletic.

examined had similar overall body size (Fig. 1), and SVL had low correlation coefficients with all morphological variables among all individuals (Pearson r values generally less than 0.40). Thus, we did not remove the effects of body size from any morphological or kinematic variable. To examine morphological differences among species, we performed a discriminant function analysis (DFA) on all the morphological variables, except mass and SVL, using species as the classification criterion.

To provide a global test for interspecific differences in

kinematics, we performed DFAs using species ($N=5$) as the classification criterion for two subsets (see Results) of kinematic variables for all quadrupedal and bipedal strides. Theoretically, two species could have identical joint angles, but if the dimensions of their limbs are different, then linear kinematic quantities would differ. Thus, to clarify the extent to which variation in limb dimensions affected conclusions regarding overall kinematic similarity, we performed one DFA using only angular kinematic variables ($N=16$) and another DFA that included linear and timing variables in addition to the angular variables ($N=23$). For all kinematic variables, we performed two-way analyses of variance (ANOVAs) for the quadrupedal data using species as a fixed factor and individual (nested within species) as a random factor. The absence of a balanced experimental design precluded using bipedality as a third factor in the ANOVAs that involved all five species.

For the two species (*Ca. draconoides* and *D. dorsalis*) in which all individuals ran both bipedally and quadrupedally, we tested for global differences in kinematics ($N=23$ variables) between bipedal and quadrupedal strides using a DFA in which each combination of species and bipedal/quadrupedal locomotion was the classification criterion ($N=4$ categories). To test for kinematic differences between bipedal and quadrupedal strides within each species, we performed separate two-way ANOVAs for each kinematic variable using stride type (bipedal or quadrupedal, fixed) and individual (random) as crossed factors.

To assess the extent to which morphological and kinematic differences among species were correlated, we calculated mean Mahalanobis distances (D) from both DFAs that used the pooled bipedal/quadrupedal data from all five species. The values of D were from each individual stride to the centroid of each species. We used a program written by J. Cheverud to determine whether

Table 1. Values for 13 morphological traits for five species of lizard

Variable	<i>Ca. draconoides</i>	<i>U. scoparia</i>	<i>P. platyrhinos</i>	<i>D. dorsalis</i>	<i>Cn. tigris</i>
SVL (cm)	7.6±0.45 ^a	8.0±0.63 ^a	7.9±0.52 ^a	8.7±0.40 ^a	8.5±0.09 ^a
Mass (g)	9.5±1.50 ^a	16.0±4.22 ^{a,c}	25.7±2.67 ^{b,c}	24.0±1.65 ^{b,c}	17.3±1.0 ^{a,c}
Tail length (cm)	10.1±1.13 ^b	6.3±0.58 ^{a,b}	4.1±0.45 ^a	14.4±0.55 ^{b,c}	18.8±2.26 ^c
Femur length (cm)	1.9±0.09 ^a	1.7±0.18 ^a	1.7±0.09 ^a	1.6±0.04 ^a	1.6±0.03 ^a
Tibia length (cm)	2.1±0.06	1.7±0.10 ^a	1.6±0.10 ^a	1.8±0.05 ^a	1.5±0.04 ^a
Tarsals and metatarsals length (cm)	1.3±0.05 ^b	1.1±0.08 ^{a,b}	0.9±0.05 ^a	1.2±0.06 ^{a,b}	1.1±0.01 ^{a,b}
Fourth toe length (cm)	1.9±0.10 ^a	1.3±0.12 ^b	1.1±0.03 ^b	1.8±0.13 ^a	2.0±0.03 ^a
Humerus length (cm)	1.6±0.07 ^b	1.4±0.13 ^{a,b}	1.7±0.07 ^b	1.2±0.05 ^a	1.0±0.05 ^a
Ulna length (cm)	1.2±0.06 ^{a,b}	1.1±0.13 ^{a,b}	1.4±0.05 ^b	0.9±0.04 ^a	1.0±0.05 ^a
Forefoot length (cm)	1.5±0.07 ^a	1.3±0.12 ^a	1.3±0.04 ^a	1.2±0.09 ^a	1.2±0.03 ^a
Pelvic width (cm)	0.9±0.05 ^a	1.0±0.08 ^a	1.3±0.05	0.9±0.04 ^a	0.8±0.01 ^a
Body width (cm)	1.6±0.11 ^{a,b}	2.4±0.30 ^a	4.0±0.22	2.4±0.06 ^a	1.4±0.07 ^b
Trunk length (cm)	4.4±0.22 ^a	4.7±0.43 ^a	5.4±0.34 ^a	5.4±0.30 ^a	4.6±0.07 ^a

Values are means ± S.E.M.

$N=4$ individuals sampled per species (except for *P. platyrhinos*, for which $N=3$).

SVL, snout–vent length.

Identical letters indicate the species within a row that did not differ significantly from each other (one-way ANOVA, Tukey HSD multiple-range test).

pairwise (e.g. *C. draconoides*/*U. scoparia*) morphological distances were correlated with pairwise kinematic values of *D* using a Mantel test. The Mantel test creates a set of randomized data sets (we used 1000 randomizations) and compares how many of the randomized data sets have correlation coefficients greater than that for the actual data. For the morphological data set, mean values of *D* were for individuals, whereas for the kinematic data set, they were for individual strides.

Results

Morphology

The five species of lizards were similar in overall size, but they differed significantly in their stoutness, tail length and limb dimensions (Fig. 1; Table 1). One-way ANOVAs revealed that the species did not differ significantly in two linear measures of overall size (SVL: $F_{4,14}=0.95$, $P>0.25$; trunk length: $F_{4,14}=2.4$, $P>0.10$), but they did differ significantly in mass ($F_{4,14}=6.6$, $P<0.005$) and many limb dimensions (Table 1).

The DFA of morphological traits (Table 2) was highly significant overall (Wilks' $\lambda<0.001$, $F_{44,17}=21.7$, $P<0.001$), indicating that the five species were morphologically distinct with respect to the linear measurements of shape (Fig. 3A). All four discriminant functions were significant (test of residual roots, all *P* values <0.015). The length of the tibia had the greatest loading with DF1 (Table 2). The lengths of the tail, fourth toe, humerus and ulna and pelvic and body width all had relatively high loadings with DF2 (Table 2). The first DF clearly differentiated all three of the phrynostomatids, with *P. platyrhinos* and *D. dorsalis* having the highest negative values and *Ca. draconoides* having the highest positive values (Fig. 3A, horizontal spacing between clusters). The second DF neatly separated the species *D. dorsalis* and *Cn. tigris* with short forelimb elements from all of the Phrynostomatids (Fig. 3A, vertical spacing between clusters).

Table 2. Loadings from a discriminant function analysis of 11 morphological variables for 19 individual lizards representing five lizard species

Variable	DF1	DF2
Tail length	-0.053	-0.162
Femur length	0.044	0.011
Tibia length	0.088	-0.016
Tarsals and metatarsals length	0.046	-0.055
Fourth toe length	0.023	-0.141
Humerus length	0.065	0.094
Ulna length	0.034	0.074
Forefoot length	0.047	0.005
Pelvic width	-0.010	0.138
Body width	-0.061	0.191
Trunk length	-0.037	0.019

DF1 and DF2 refer to discriminant functions 1 and 2, respectively.

Loadings ≥ 0.07 are marked in bold type.

Canonical correlations for DF1 and DF2 were each 0.99.

Kinematics

We were able to obtain very fast locomotion for the kinematic analysis. Out of a total of 112 strides analyzed, 71 had values of speed greater than 3.5 m s^{-1} , and the mean speeds per species were within 10% of previously reported maximal sprinting speeds for all species (Table 3). All mean values of duty factors for each species were less than or equal to 35%, and three species had mean duty factors less than or equal to 25% (Table 4).

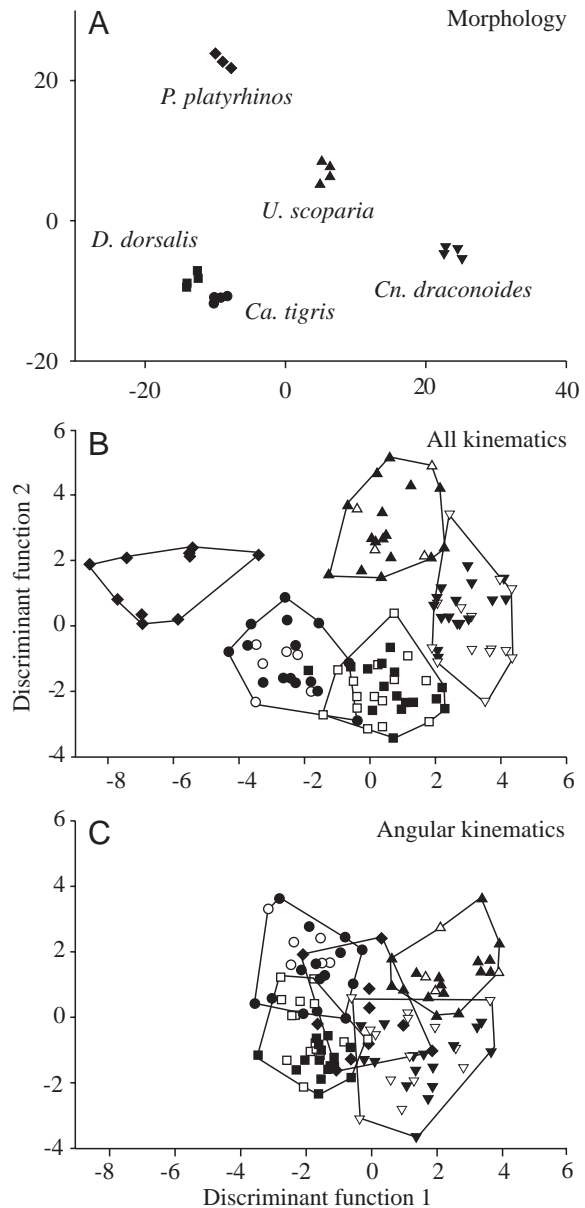


Fig. 3. Discriminant function 1 versus discriminant function 2 from three separate analyses of (A) 11 morphological variables, (B) 23 angular, timing and linear kinematic variables, and (C) 16 angular variables. Each species ($N=5$) was used as a category in the analysis. Each point is either an individual lizard (A) or a stride (B,C). Different symbol shapes represent different lizard species. For B and C, filled symbols are quadrupedal strides, and open symbols are bipedal strides. Tables 2 and 6 provide variable loadings for the morphological and kinematic analyses, respectively.

Table 3. Values for all strides (quadrupedal and bipedal strides were pooled) within a species for speed and stride length from the present study and maximal values from other studies on these species

Species	This study			Previous studies			Reference
	<i>N</i> *	Speed (m s ⁻¹)	Stride length (cm)	<i>N</i> ‡	Maximum speed (m s ⁻¹)	Maximum stride length (cm)	
<i>Ca. draconoides</i>	14, 16	4.2±0.1 (3.6–5.3)	32.3±1.0 (24.0–46.6)	30	4.4±0.2 (2.6–6.4)	35.8±1.4 (21.0–52.0)	Irschick and Jayne (1999)
<i>U. scoparia</i>	4, 16	3.9±0.1 (3.2–4.3)	26.3±0.7 (20.3–30.9)	28	4.0±0.2 (2.4–5.1)	31.0±11.7 (18.5–40.0)	Jayne and Ellis (1998)§
<i>P. platyrhinos</i>	10	2.1±0.1 (1.6–2.5)	18.3±0.7 (16.0–21.0)	8	2.4±0.2 (1.5–3.0)	21.1±1.6 (13.5–26.5)	B. Jayne (unpublished data)§
<i>D. dorsalis</i>	15, 16	3.7±0.1 (3.0–4.2)	31.8±0.7 (23.6–40.5)	8	3.6±0.3¶ (2.8–5.0)	29.0±1.7 (23.8–35.0)	Marsh (1988)
<i>Cn. tigris</i>	6, 15	3.2±0.05 (2.8–3.7)	28.0±1.0 (19.0–36.8)	19	2.8 ¹	Not available	Cullum (1997)

Values are means ± S.E.M. with range in parentheses.

*N**: number of bipedal and quadrupedal strides, respectively; *N*, number of individuals.

For kinematics, *N*=4 individuals per species, except *P. platyrhinos* (*N*=3).

§Analyzed footprints of escape locomotion in the field.

¶Data only for small (18–28 g lizards).

¹Data for a different subspecies (*Cn. t. gracilis*) from that in the current study (*Cn. t. tigris*).

General description of limb movements

Five features of the foot characterized high-speed locomotion of the lizards in this study. First, the posture of the foot was commonly digitigrade both at footfall and throughout the stance phase (Figs 4, 5). For all species, 55 % of the total number of quadrupedal and bipedal strides had digitigrade foot posture at footfall. *Ca. draconoides* and *U. scoparia* had digitigrade foot posture most frequently, whereas *P. platyrhinos* always had plantigrade foot posture (Table 4). Second, the fifth toe had a markedly different orientation from all other toes, creating a conspicuous gap between the fifth toe and the fourth metatarsal; the claw of the fifth toe contacted the ground substantially lateral and posterior to the other claws (Figs 4, 5). Third, plantarflexion of the ankle and fourth toe continued even after the end of stance; hence, rather than passively rolling over the foot during high-speed running, lizards appear to plantarflex these structures actively at the end of stance. Fourth, maximum ankle (Fig. 6) and toe joint angles both occurred during the early swing phase, and they approached values of 180° and 220°, respectively. Finally, near the end of stance, the joints within the fourth toe were commonly still flexed dorsally (Figs 4, 5), even though the collective structures of the foot were in the process of being plantarflexed.

The hips of the lizards were quite high throughout the stride cycle (Figs 4, 5). For example, hip heights commonly exceeded the length of the tibia at footfall and throughout the entire stance phase (Figs 4, 5). Substantial depression of the femur during stance (commonly 30°) contributed to the large values of hip height (Table 5). At footfall, both the knee and ankle angles commonly exceeded 120° (Table 5; Figs 4, 5).

The knee was often extended sufficiently so that the ankle was anterior to the knee rather than beneath it at footfall (Figs 4, 5). Extension of the knee beyond 90° can also contribute to increased hip height when the femur is depressed.

The timing of maximal flexion and extension of the knee and ankle were similar for all species (Fig. 6). The knee and ankle generally had minimum and maximum angles near midstance and just after the end of stance, respectively. Femur rotation and retraction were nearly in phase, and the timing of maximal femur rotation and maximal knee extension was also nearly synchronous for all species (Fig. 6).

Interspecific differences

The multivariate analyses revealed that the five species were kinematically quite distinct (Fig. 3B,C). The DFAs were highly significant (all variables: Wilks' λ =0.004, $F_{92,338}$ =10.9, P <0.001; angular variables only: Wilks' λ =0.033, $F_{64,362}$ =7.9, P <0.001). All four discriminant functions were highly significant (test of residual roots, all P values <0.001) for both analyses. The canonical correlations for the analysis of all variables (0.94, 0.87, 0.83 and 0.70) were slightly greater than those for angular variables only (0.871, 0.77, 0.73 and 0.56). We focus on the first two discriminant functions of each analysis because of their very high canonical correlations. The DFAs of all kinematic variables (Fig. 3B) and of angular variables only (Fig. 3C) correctly classified 108 and 101 strides, respectively, out of a total of 112 strides according to species.

For the DFA of all kinematic variables (Fig. 3B), the most important variables for separating species were stride and step length, stride duration, duty factor, hip height at footfall,

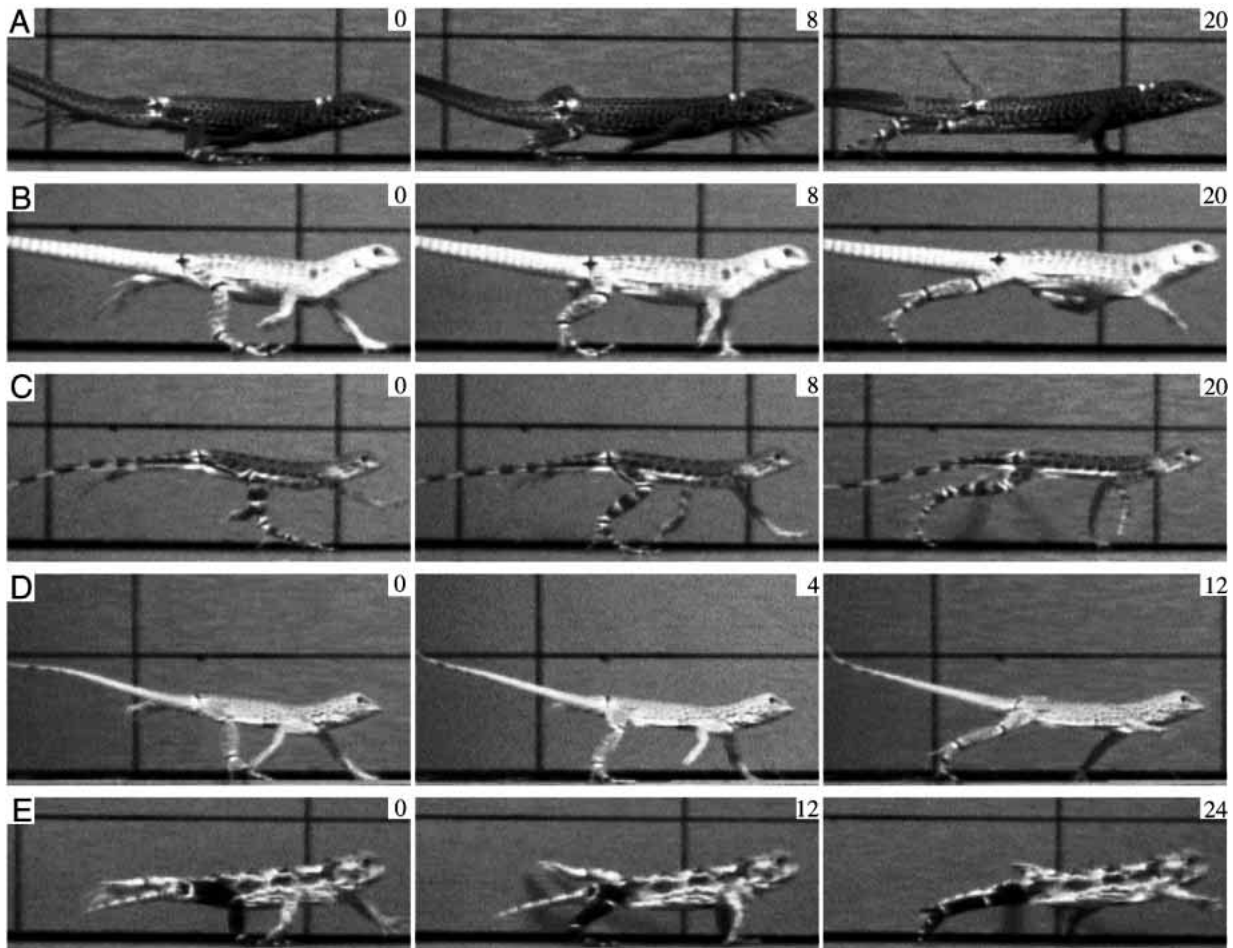


Fig. 4. Right lateral views of quadrupedal strides at footfall (left), near midstance (middle) and at the end of the stance phase (right) for *Cnemidophorus tigris* (A), *Dipsosaurus dorsalis* (B), *Callisaurus draconoides* (C), *Uma scoparia* (D) and *Phrynosoma platyrhinos* (E). For A–E, the forward speeds were 3.1, 3.5, 4.0, 3.7 and 2.4 m s^{-1} , respectively. All images are shown to the same scale, and the vertical lines in the background are 10 cm apart. Within each row of images, the position of the grid in the background varies for those individuals that were not matching tread speed. Numbers at the upper right-hand corner of each image indicate elapsed time after footfall in milliseconds. The right hindlimbs were painted to facilitate the digitization of coordinates. Video clips of lizard locomotion can be viewed on the world-wide web at www.biology.uc.edu/faculty/jayne/videos.htm.

$X_{\text{toetip}}(\text{ff})$, toe orientation at footfall, minimum femur retraction, maximum femur depression, minimum femur rotation and tail angle (Table 6). Fig. 3B shows how DF1 separated species such as *P. platyrhinos* (with short stride lengths, high duty factors and low hip heights) from species such as *Ca. draconoides* and *U. scoparia* (with long stride lengths, low duty factors and high hip heights). Compared with the other species, *D. dorsalis* had the lowest values of DF2 (Fig. 3B), which resulted in part from large values of step length and $X_{\text{toetip}}(\text{ff})$ (Table 4) and low values of minimum femur rotation (Table 5).

For the DFA of angular variables only (Fig. 3C), the most important variables for separating species were knee angle at the end of stance, toe orientation at footfall, minimum and maximum femur retraction, minimum femur depression, minimum femur rotation and mean tail angle (Table 6). The first discriminant function of the DFA on angular variables clearly separated *Ca. draconoides* and *U. scoparia* from *Cn. tigris* and *D. dorsalis* (Fig. 3C), partly as a result of low values of minimum femur rotation

for the latter two species (Table 5). The patterns of overlap among different species in the kinematic space of the two DFAs differed. *P. platyrhinos* was less distinct in the DFA of angular variables (Fig. 3C), which suggests that its relatively short limbs contributed considerably to its uniqueness in the DFA that included linear measurements (Fig. 3B).

Of the total of 13 whole-stride and linear variables for quadrupedal locomotion summarized in Table 4, 10 differed significantly among species. Speed, stride length, hip height at footfall and the two measures of effective limb length all differed significantly among species, with *Ca. draconoides* and *P. platyrhinos* having the highest and lowest mean values, respectively (Table 4). The mean speed of *P. platyrhinos* (2.1 m s^{-1}) was only approximately half that of *Ca. draconoides*. *Ca. draconoides* also had the single longest quadrupedal (41.9 cm) and bipedal (46.6 cm) strides observed in this study. A *U. scoparia* had the quadrupedal stride with the shortest duration (52 ms) and, with the exception of *P.*

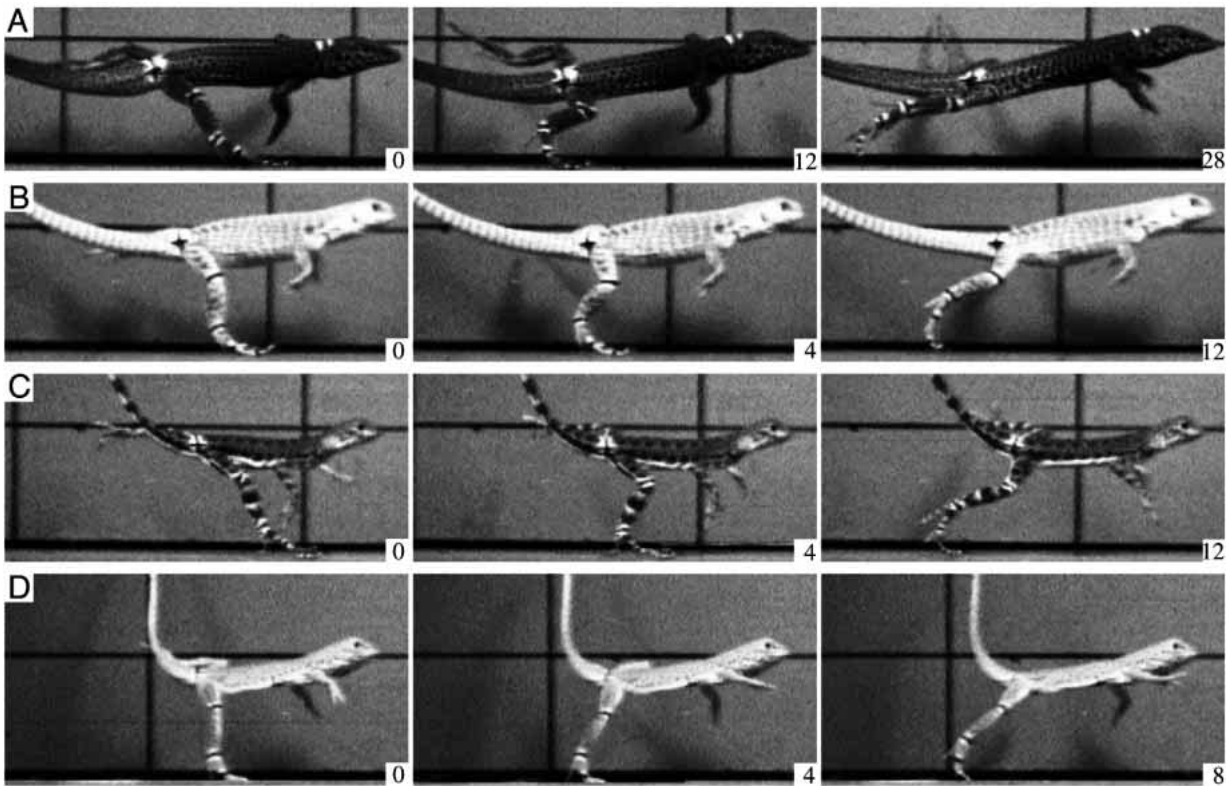


Fig. 5. Right lateral views of bipedal strides at footfall (left), near midstance (middle) and at the end of the stance phase (right) for *Cnemidophorus tigris* (A), *Dipsosaurus dorsalis* (B), *Callisaurus draconoides* (C) and *Uma scoparia* (D). For A–D, the forward speeds were 3.1, 4.1, 5.3 and 3.9 m s⁻¹, respectively. A–D are of the same individuals as shown in Fig. 4A–D, and the labeling, scale and alignment of images are the same as in Fig. 4.

platyrhinus, all species had several strides with a duration of less than 80 ms. Hence, stride frequencies were commonly greater than 12 Hz. *D. dorsalis* had the highest mean value for X_{toetip} at footfall, whereas *P. platyrhinus* had the highest mean value of X_{toetip} at the end of stance (Table 4). Both the excursion in the x direction and the minimum y value of the ankle differed significantly among species (ΔX : $F_{4,14}=5.8$, $P<0.01$; Y_{min} : $F_{4,14}=5.1$, $P<0.01$), and these interspecific differences are also apparent in the shape of the loops shown in Fig. 7. *Ca. draconoides* had the largest magnitudes of both $Y_{\text{min,ankle}}$ (mean -2.6 cm) and ΔX_{ankle} (mean 5.9 cm); whereas *P. platyrhinus* had the smallest mean magnitude $Y_{\text{min,ankle}}$ (-1.5 cm) and the second smallest mean value of ΔX_{ankle} (4.8 cm).

Of a total of 16 angular variables for quadrupedal locomotion summarized in Table 5, nine differed significantly among species. Compared with other species, the knee of *P. platyrhinus* was more flexed at footfall and more extended at the end of stance, and the toe was more extended at the end of stance (Table 5). Of all the species, the fourth toe of *D. dorsalis* was most nearly pointed straight forward at footfall, whereas the fourth toe of *U. scoparia* was pointed laterally by nearly 20° (Table 5). On average, the femur of *Cn. tigris* was retracted more than that of any of the other species, whereas the femur of *Ca. draconoides* was retracted least (Table 5). *D. dorsalis* and *Cn. tigris* had the lowest mean values of minimum femur rotation, which approached zero, indicating that the

plane through the femur and tibia was nearly perpendicular to the ground (usually at the end of swing, Fig. 6). *P. platyrhinus* was also unusual because its trunk was consistently elevated relative to the tread surface (Fig. 4E; Table 5) and, because the tail of *P. platyrhinus* was held nearly straight relative to the body, it pointed down more than in any other species (Table 5). In contrast, the tail of *U. scoparia* was elevated to a remarkably high extent compared with all other species (Table 5).

Bipedal versus quadrupedal

The DFA is most useful for revealing whether a particular set of variables can differentiate bipedal and quadrupedal locomotion regardless of the species. The univariate comparisons within each species provide further insights by revealing whether *Ca. draconoides* and *D. dorsalis* run bipedally in different ways.

For *Ca. draconoides* and *D. dorsalis*, bipedal and quadrupedal strides were kinematically distinct (Fig. 8), as indicated by a DFA that was highly significant overall (Wilks' $\lambda=0.0101$, $F_{69,105}=5.5$, $P<0.001$). The first DF separated the two species. The second DF separated bipedal and quadrupedal strides, and only two were misclassified. The two variables that loaded highest were minimum femur rotation (DF1) and trunk angle (DF2) (Table 6).

Of the 29 kinematic variables summarized in Tables 4 and 5, bipedal strides differed significantly from quadrupedal

Table 4. Values of linear and timing variables for quadrupedal strides of five species of lizard and F-values testing for differences among species in two-way ANOVAs performed separately for each kinematic variable

Variable	<i>Cd</i> N=16	<i>Us</i> N=16	<i>Pp</i> N=10	<i>Dd</i> N=16	<i>Ct</i> N=15	<i>F</i> _{4,14}
Speed (m s ⁻¹)	4.0±0.1 (0.5)	3.9±0.1 (-0.1)	2.1±0.1	3.6±0.1 (0.1)	3.1±0.1 (0.1)	34.5**
% Strides digitigrade	75	75	0	19	47	–
Stride length (cm)	31.9±1.1 (-0.1)	26.4±0.7 (0.5)	18.3±0.7	32.5±0.9 (-1.5)	26.8±1.2 (4.3)	14.3**
Step length (cm)	7.4±0.2 (0.7)	4.5±0.3 (-0.3)	6.4±0.1	8.0±0.3 (-0.2)	7.6±0.2 (0.5)	20.5**
Stride width (cm)	5.1±0.4 (-0.8)	4.7±0.4 (0.1)	4.2±0.4	4.1±0.3 (-0.3)	3.6±0.2 (-0.2)	1.0
Stride duration (ms)	80±3 (-6)	69±2 (-1)	89±3	91±3 (-8*)	86±4 (11)	3.6*
Duty factor (%)	24±1 (1)	17±1.1 (-1)	35±2.4	25±0.7 (1)	29±1.4 (-3)	11.3**
<i>X</i> _{toetip(ff)} (cm)	4.1±0.2 (0.1)	2.7±0.2 (-0.2)	2.9±0.1	4.2±0.1 (0)	3.9±0.1 (0.3)	7.3*
<i>X</i> _{toetip(es)} (cm)	-3.7±0.3 (0.1)	-2.3±0.3 (0.4)	-4.0±0.2	-3.4±0.1 (-0.1)	-3.8±0.2 (0.2)	3.8*
<i>Y</i> _{hip(ff)} (cm)	2.8±0.1 (0.2)	2.6±0.2 (0.3)	1.5±0.1	2.7±0.1 (0.1)	2.1±0.2 (0.4)	6.2*
ΔY _{hip,stance} (cm)	0.3±0.1 (0.1)	0.2±0.1 (0)	0.3±0.1	0.2±0.1 (0)	0.3±0.1 (0.2)	1.1
ΔY _{hip,total} (cm)	0.7±0.1 (0.1)	0.5±0.1 (0.7)	0.5±0.1	0.5±0.1 (0.2)	0.6±0.1 (0.2)	1.6
eff2D(ff) (cm)	4.3±0.3 (0.5)	3.3±0.2 (0)	1.8±0.3	3.2±0.2 (0.6)	3.0±0.3 (0.6)	6.7*
eff3D(ff) (cm)	5.1±0.3 (0.8)	4.2±0.2 (0.5)	2.6±0.3	3.5±0.2 (0.6)	3.5±0.3 (0.5)	10.4*

Values are means ± 1 S.E.M. for quadrupedal locomotion; *X*_{toetip(ff)}, *X*_{toetip(es)}, horizontal positions of the toetip at footfall and at the end of stance, respectively; *Y*_{hip(ff)}, distance of the hip above the treadmill at footfall; *Y*_{hip,stance}, hip height at footfall minus minimum hip height during stance; *Y*_{hip,total}, maximum hip height minus minimum hip height; eff2D(ff), eff3D(ff), two- and three-dimensional effective limb length at footfall, respectively.

Cd, *C. draconoides*; *Us*, *U. scoparia*; *Pp*, *P. platyrhinos*; *Dd*, *D. dorsalis*; *Ct*, *C. tigris*.

Values in parentheses are the difference between the quadrupedal and bipedal means (values >0 indicate that the bipedal mean was greater).

An asterisk beside the difference between quadrupedal and bipedal means indicates a significant difference between bipedal and quadrupedal strides (two-way ANOVAs; **P*<0.05; ***P*<0.01).

strides for two variables for *Ca. draconoides* and for five variables for *D. dorsalis*. For all of the following tests for differences between bipedal and quadrupedal strides within each of these species [two-way ANOVA, factors: bipedal versus quadrupedal (d.f.=1) and individuals (d.f.=3)] values of

F-tests of 10.1 and 167 have *P*-values of 0.05 and 0.001, respectively. Trunk angle increased significantly and maximum femur rotation decreased significantly during the bipedal running of both *Ca. draconoides* (*F*=18.3, 15.5, respectively) and *D. dorsalis* (*F*=264, 67.9, respectively);

Table 5. Values of angular kinematic variables for quadrupedal strides of five species of lizard and F-values indicating differences among species in two-way ANOVAs performed separately for each kinematic variable

Variable	<i>Cd</i> N=16	<i>Us</i> N=16	<i>Pp</i> N=10	<i>Dd</i> N=16	<i>Ct</i> N=15	<i>F</i> _{4,14}
Knee angle (ff) (degrees)	116±4 (8)	125±4 (5)	107±5	129±3 (1)	132±4 (11)	4.7*
Knee angle (es) (degrees)	117±3 (5)	123±5 (16)	135±4	113±3 (1)	135±5 (-10)	3.9*
Ankle angle (ff) (degrees)	118±4 (10)	137±5 (6)	118±8	131±3 (12)	132±4 (18)	2.2
Ankle angle (es) (degrees)	131±3 (8)	141±5 (8)	158±6	150±4 (5)	154±6 (-7)	2.8
Toe angle (ff) (degrees)	10±2 (8)	162±3 (-1)	164±3	166±2 (-3)	170±2 (-4)	1.1
Toe angle (es) (degrees)	144±6 (-1)	150±4 (-16)	160±4	131±4 (4)	149±6 (-10)	3.2*
Toe orientation (ff) (degrees)	10±2 (8)	19±3 (10)	9±3	3±2 (5)	10±4 (-3)	4.1*
Pelvic rotation (degrees)	52±3 (4)	50±3 (-9)	54±6	45±2 (8**)	55±3 (15)	0.6
Minimum femur retraction (degrees)	-55±2 (-1)	-49±2 (6)	-46±3	-58±2 (1)	-51±3 (-3)	3.1
Maximum femur retraction (degrees)	26±3 (-5)	36±2 (-7)	36±5	35±3 (2)	48±4 (6)	3.6*
Minimum femur depression (degrees)	-10±2 (-3)	-26±3 (-4)	-13±1	-9±2 (-13**)	-16±4 (-10)	4.1*
Maximum femur depression (degrees)	31±2 (2)	27±1 (7)	20±3	38±2 (0)	34±3 (8)	2.0
Maximum femur rotation (degrees)	104±2 (-4*)	100±3 (-8)	98±4	101±3 (-11*)	95±3 (3)	0.8
Minimum femur rotation (degrees)	28±2 (-10)	13±2 (0)	21±2	5±2 (-8)	4±3 (-10)	11.4**
Trunk angle (degrees)	1±1 (7*)	6±1 (9)	11±1	2±1 (9**)	6±1 (9)	5.8*
Tail angle (degrees)	14±5 (-2)	29±5 (9)	-10±2	-4±1 (5)	3±2 (3)	7.0*

P*<0.05; *P*<0.01.

Abbreviations and values in parentheses are as in Table 4.

Table 5). *U. scoparia* and *Cn. tigris* also had trends indicating that the trunk was more elevated during bipedal running (Table 5; Figs 4, 5). Compared with quadrupedal strides, the bipedal strides of *D. dorsalis* (Tables 4, 5) also had significantly ($F=13.0$) lower values of stride duration, greater pelvic rotation ($F=13.8$) and lower values of minimum femur depression ($F=10.9$). For *D. dorsalis*, Fig. 7 also illustrates how, as result of lower minimum values of femur depression, the knee moves well above the hip during the swing portion of bipedal strides. Speed did not differ significantly between bipedal and quadrupedal strides, even though, for *Ca. draconoides*, the mean speed for all bipedal strides was 13% greater than for quadrupedal strides (Table 4).

To clarify what movements create forelimb clearance during bipedal locomotion, we calculated two correlations within both *D. dorsalis* and *Ca. draconoides*. The minimum height of the fourth toe of the forelimb relative to the treadmill surface

(clearance) had a significant positive correlation with the sine of the trunk angle for *D. dorsalis* (Pearson $r=0.79$, 13 d.f., $P<0.001$), but not for *Ca. draconoides* ($r=-0.16$, 12 d.f., $P>0.25$). The maximum shoulder-toe distance, for which smaller values indicate that the forelimb was more tucked in, had a significant negative correlation with clearance for *Ca. draconoides* ($r=-0.63$, 12 d.f., $P<0.005$) but not for *D. dorsalis* ($r=-0.46$, 13 d.f., $P>0.05$).

Although definitive statistical tests for differences between bipedal and quadrupedal locomotion were not possible within either *Cn. tigris* or *U. scoparia*, some additional trends were apparent. For example, for bipedal locomotion of *Cn. tigris*, maximum femur depression was commonly greater (Table 5; Fig. 7, note the position of the knee loop relative to the hip), the knee and ankle were often more extended at footfall (Figs 4, 5; Table 5) and the pelvis often rotated more (Table 5).

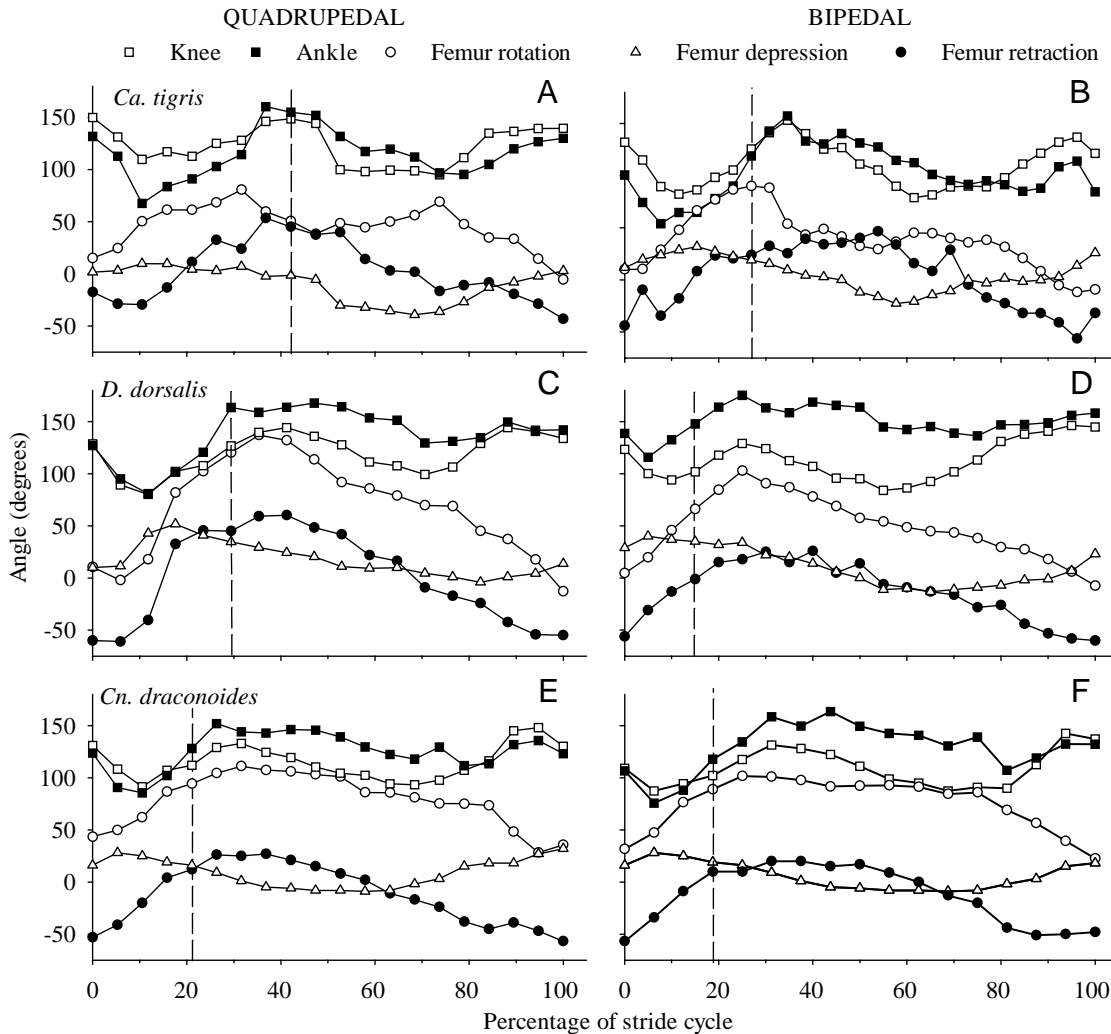


Fig. 6. Values of the angles of femur retraction, femur rotation and femur depression and of the knee and ankle joints versus time (% of stride cycle) for a quadrupedal (left) and bipedal (right) stride of *Cnemidophorus tigris* (A,B), *Dipsosaurus dorsalis*, (C,D) and *Callisaurus draconoides*. (E,F). For A–F, the forward speeds were 3.1, 3.0, 4.2, 4.1, 4.8 and 5.0 m s⁻¹, respectively. For each species, the quadrupedal and bipedal data are from the same individual. The dashed line indicates the end of the stance phase, and footfall occurs at 0% of the stride cycle.

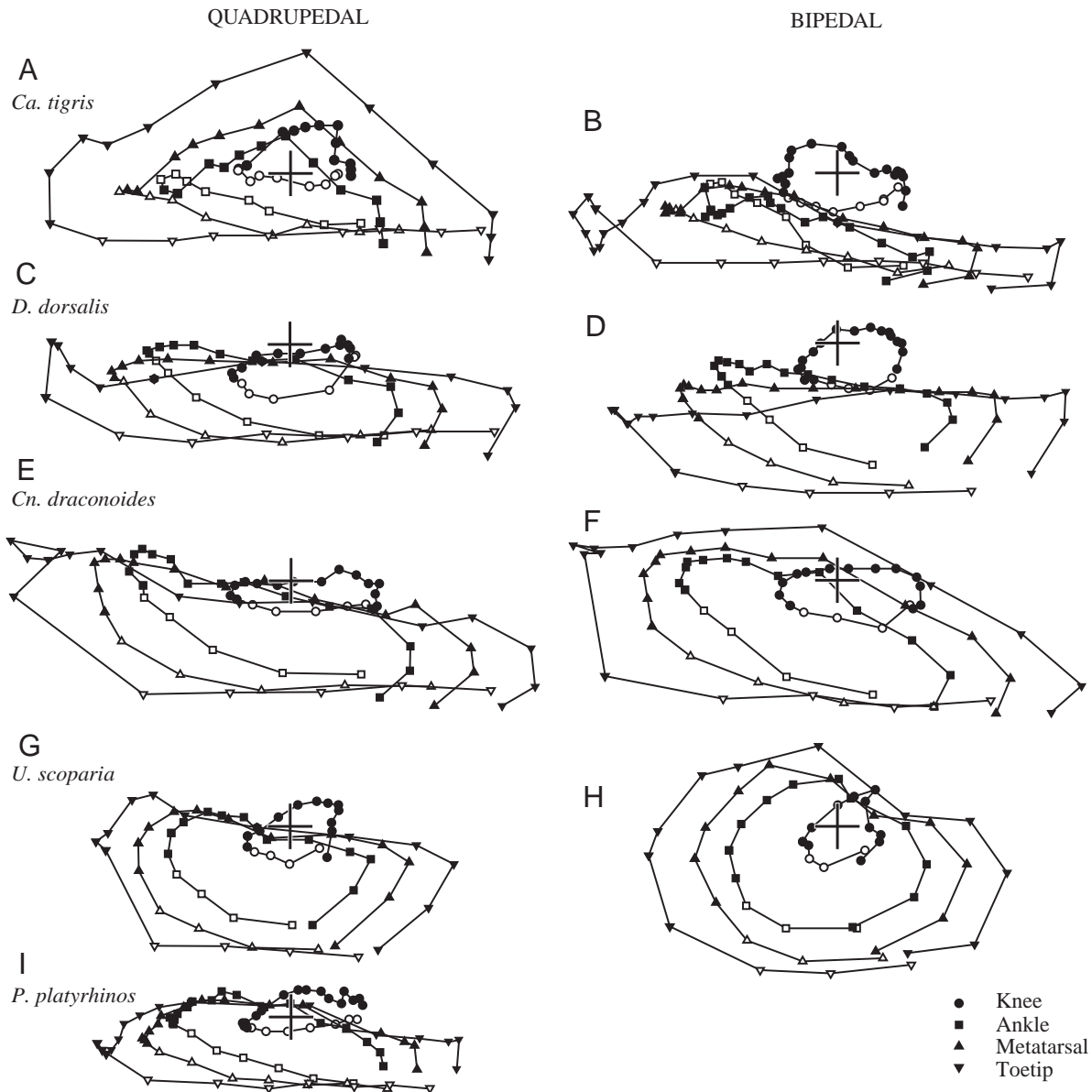


Fig. 7. Lateral views of paths (y versus x) made by the right knee, ankle, metatarsal and toetip landmarks during quadrupedal (left) and bipedal (right) locomotion for *Cnemidophorus tigris* (A,B), *Dipsosaurus dorsalis* (C,D), *Callisaurus draconoides* (E,F), *Uma scoparia* (G,H) and *Phrynosoma platyrhinos* (I). For A–I, the forward speeds per stride were 3.1, 3.0, 4.2, 4.1, 4.8, 5.0, 3.6, 3.9 and 2.4 m s^{-1} , respectively. The hip is located at point 0, 0, marked by a cross, and positive values of x and y indicate a position forward and dorsal to the hip. The open and filled symbols represent the stance and swing portions of the stride, respectively. The direction of overall movement in the loops is clockwise. The time between successive points is 4 ms. For each species, the quadrupedal and bipedal data are from the same individual.

Discussion

Comparisons between morphology and kinematics

Biologists have long been interested in determining whether variation in movement corresponds with variation in morphology (Dullemeijer, 1974; Lauder, 1995, 1996; Lauder and Reilly, 1996; Rudwick, 1964). Although lizards have been a model system for correlating whole-organism performance to morphology (Bauwens et al., 1995; Garland, 1985; Losos, 1990; Miles, 1994; Sinervo, 1990; Tsuji et al., 1989), no previous study of lizards has investigated whether locomotor kinematics correspond with morphology.

We first address whether variation in kinematics globally corresponded to variation in morphology among the five species in this study. All five species of lizard were morphologically and kinematically distinct (Fig. 3), but a Mantel test detected no significant global correspondence between the morphological data (Fig. 3A) and either of the kinematic (Fig. 3B,C) data sets ($P > 0.9$). Using different methods to analyze the cranial morphology and feeding of four salamander species, Lauder and Reilly (1996) also found no global correspondence between morphology and kinematics. Using such multivariate methods to test for

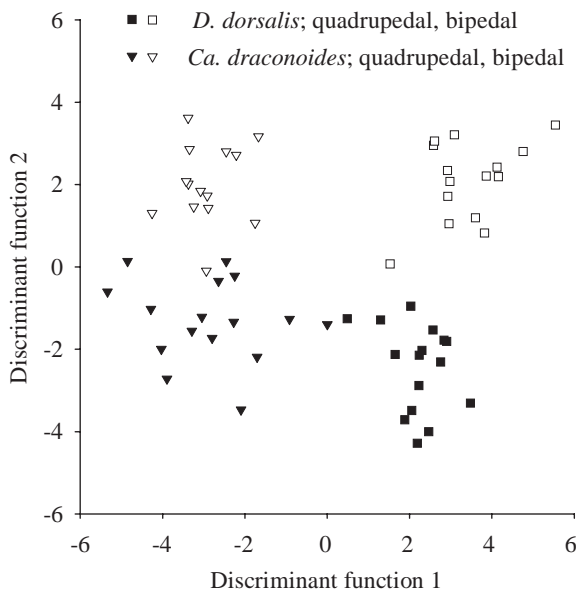


Fig. 8. Discriminant function 1 versus discriminant function 2 for an analysis of 23 angular, timing and linear kinematic variables for the two species (*Dipsosaurus dorsalis* and *Callisaurus draconoides*) in which all individuals performed both quadrupedal and bipedal running. Each combination of species and bipedal or quadrupedal locomotion was used as a category ($N=4$) in the analysis. Symbols are as in Fig. 3. Table 6 provides variable loadings for the analysis.

global patterns is a useful first step for relating morphology to kinematics because the functional relationships between the morphology and kinematics of lizard limbs are so poorly understood.

We only used linear measurements to describe morphology, and the kinematics of all species were most distinct when linear kinematic quantities were included in the multivariate analyses. For example, *P. platyrhinos* was both a morphological (Fig. 3A) and kinematic (Fig. 3B) outlier when linear quantities were used, but when linear kinematic measures were excluded, *P. platyrhinos* was kinematically intermediate (Fig. 3C). Using only angular variables had little effect on the extent of overlap in kinematics among the remaining species, although these species also differed in their limb dimensions. These multivariate relationships between morphology and kinematics might be obscured because linear measurements of morphology will not usually have any necessary causal relationship with joint angles. However, joint angles are necessary to predict the effects of linear morphological measurements on linear kinematic variables. For example, if femur depression is 0° , then the length of the femur is irrelevant to hip height, but a necessary consequence of a constant positive value of femur depression is increased hip height. Thus, generating *a priori* expectations for linear kinematic quantities on the basis of linear morphological dimensions is more straightforward than for angular kinematic quantities, but generating such hypotheses requires information on joint angles.

Therefore, clarifying the relationships between specific

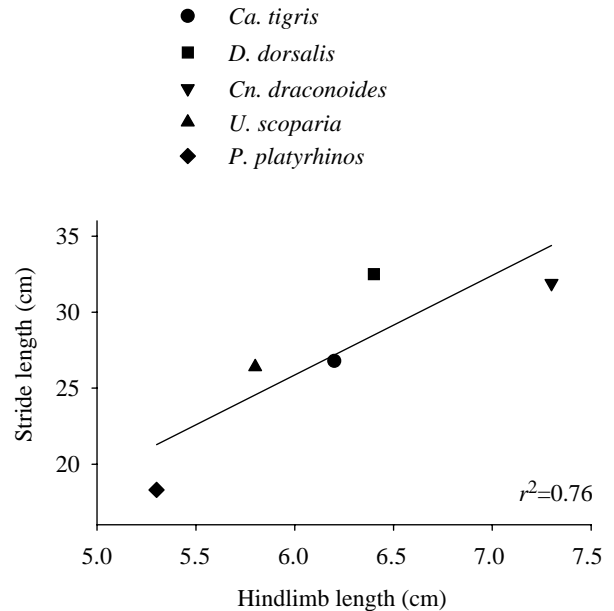


Fig. 9. Mean values of stride length versus hindlimb length for each of the five species of lizard. The simple Pearson product-moment correlation coefficient ($r=0.87$) among quadrupedal species means was significant ($P<0.05$, 3 d.f.), and an alternative analysis using phylogenetically independent contrasts was also significant.

linear morphological and linear kinematic variables can provide insights that are not obvious from the multivariate methods. Table 7 summarizes simple correlations among the species means between morphology and select kinematic variables; calculating correlations using phylogenetically independent contrasts did not affect which of the correlations was statistically significant. Increased longitudinal displacements could potentially enhance step length and, hence, the distance that the limb has available to transmit forces while it contacts the ground which, in turn, might increase stride length. Only the length of the fourth toe was significantly correlated with X_{toetip} at footfall (Table 7), indicating that species with long fourth toes achieve greater forward extension.

The length of the fourth toe had the highest correlation with step length (Table 7), but it was not statistically significant. The difference between X_{toetip} at footfall and at the end of stance approximates step length. The rank order of the correlation coefficients of X_{toetip} at footfall for each of the limb dimensions was the same as that for step length, whereas this was not the case for X_{toetip} at the end of stance (Table 7). Hence, the interspecific differences in the forward extension of the toetip contribute the most to the interspecific variation in step length. Unexpectedly, the limb dimensions that correlated best with stride length differed from those that correlated best with step length (Table 7).

The distance traveled during each stride when neither of the hindfeet touches the ground (suspended phase = 100% minus $2 \times$ duty factor) is impressive (e.g. 52% of the stride length

Table 6. Loadings from the three discriminant function analyses of kinematics

Variable	All species All kinematics		All species Angular kinematics		<i>D. dorsalis</i> and <i>Ca. draconoides</i> All kinematics	
	DF1	DF2	DF1	DF2	DF1	DF2
Stride length	0.306	-0.302	–	–	-0.027	-0.020
Step length	0.052	-0.578	–	–	0.022	0.025
Stride duration	-0.142	-0.311	–	–	0.151	-0.201
Duty factor	-0.232	-0.242	–	–	0.026	0.049
$Y_{\text{hip}}(\text{ff})$	0.330	-0.057	–	–	-0.077	0.094
$X_{\text{toetip}}(\text{ff})$	0.121	-0.434	–	–	0.009	0.007
$X_{\text{toetip}}(\text{es})$	0.048	0.211	–	–	0.076	-0.035
Knee angle (ff)	0.018	-0.147	-0.154	0.184	0.113	0.040
Knee angle (es)	-0.135	0.129	0.023	0.334	-0.068	0.055
Ankle angle (ff)	-0.010	-0.051	-0.089	0.198	0.163	0.141
Ankle angle (es)	-0.058	-0.089	-0.123	-0.041	0.129	0.111
Toe angle (ff)	-0.010	-0.084	-0.071	-0.001	-0.059	-0.052
Toe angle (es)	-0.089	0.158	0.094	0.169	-0.094	0.044
Toe orientation (ff)	0.062	0.285	0.294	0.177	-0.161	0.201
Pelvic rotation	-0.045	-0.047	-0.061	0.078	-0.073	0.178
Minimum femur retraction	-0.099	0.240	0.144	0.310	-0.070	-0.022
Maximum femur retraction	-0.189	-0.130	-0.287	0.474	0.187	-0.048
Minimum femur depression	-0.030	-0.151	-0.078	-0.338	-0.090	-0.214
Maximum femur depression	0.083	-0.285	-0.220	-0.082	0.134	-0.006
Minimum femur rotation	0.113	0.354	0.468	-0.312	-0.414	-0.146
Maximum femur rotation	0.054	0.064	0.109	-0.074	-0.128	-0.160
Trunk angle	-0.139	0.036	-0.076	0.233	0.158	0.525
Tail angle	0.202	0.451	0.519	0.306	-0.213	0.075

Loadings ≥ 0.24 are marked in bold type.

Missing values indicate data not included in analysis.

Abbreviations and values are as in Tables 2, 4 and 5.

based on mean values of quadrupedal locomotion for a *Ca. draconoides*). This suggests that the speeds and forces propelling the animal up and forward prior to the suspended phase would better predict the distance traveled per stride cycle than some of the displacements of the limbs that we quantified for the stance phase. Furthermore, although the length of the tarsals and metatarsals is modest compared with the rest of the limb, increasing the length of this lever arm may have more profound effects on the speed of movement and on force production than on displacement during stance.

The species of lizards that we studied generally had less

variation in stride durations (69–91 ms) than in stride length (18.3–32.5 cm). Those species with greater total limb lengths (hip to toetip) took significantly longer strides (Fig. 9) and, hence tended to be faster than the species with shorter hindlimbs. Frequently, interspecific studies of relationships between total hindlimb length and speed are not accompanied by data on both stride length and the dimensions of individual elements of the hindlimb (Bauwens et al., 1995; Losos, 1990; Miles, 1994). Our study of lizards emphasizes the variable importance of different portions of the hindlimb, particularly the distal portions, for running at maximal speeds (Table 7).

Table 7. Simple Pearson product-moment correlation coefficients (r) between species means of kinematics and morphology

Limb dimension	Kinematic variable					
	Speed	Stride length	Step length	$X_{\text{toetip}}(\text{ff})$	$X_{\text{toetip}}(\text{es})$	$Y_{\text{hip}}(\text{ff})$
Total length	0.73	0.87*	0.53	0.80	-0.11	0.77
Femur length	0.34	0.16	0.12	0.03	-0.06	0.30
Tibia length	0.65	0.64	0.19	0.43	0.05	0.71
Tarsals and metatarsals length	0.88*	0.96*	0.39	0.73	0.16	0.92*
Fourth toe length	0.49	0.77	0.73	0.91*	-0.26	0.53

* $P < 0.05$; all correlation coefficients have 3 degrees of freedom.

Abbreviations are as in Table 4.

Miles (1994) and Van Damme et al. (1997) provide additional support for the functional importance of the distal limb.

Lizards running at high speeds frequently have digitigrade foot posture at footfall and throughout stance (Figs 3, 4); therefore, elongated distal limb elements can increase the effective limb length. Furthermore, lizards also have extremely long fourth toes (Fig. 1), but their function has rarely been considered. Of the dimensions we measured within the hindlimb, those of the distal elements of the hindlimb, such as the fourth toe on the hindfoot, were the best morphological correlates of stride length and of the amount of forward extension (Table 7). Both the ankle (Fig. 6) and the fourth toe continued to plantarflex substantially after the end of stance, and the speed of movement of the tip of the fourth toe was fastest during early swing (Fig. 7). Thus, the foot and fourth toe probably generate propulsive forces rather than being passive structures that the lizard 'rolls over', as Brinkman (1981) suggested for the low-speed locomotion of an iguana.

Comparisons with general models of locomotion of limbed vertebrates

We obtained speeds that are probably near the physiological maximum for each of the five species of lizard (Table 3), and although the speeds varied substantially among the different species, we studied specimens with very similar body size (Fig. 1). Hence, for data from our study, size is unlikely to confound the interpretation of the results, but size can potentially complicate comparisons of our data with those for other species of animal.

Froude numbers are dimensionless quantities that are commonly used to facilitate comparisons among diverse species of different sizes, such as mice and horses (Farley et al., 1993). We calculated Froude numbers as $ug^{-1/2}L^{-1/2}$ (where u is speed of locomotion, L is a characteristic length and g is the gravitational constant), similar to Farley et al. (1993). Using mean values of speed and $Y_{\text{hip}}(\text{ff})$ for quadrupedal running (Table 4), the Froude numbers ranged from 5.4 (*P. platyrhinos*) to 8.0 (*D. dorsalis*), values that are greater than that of world-class human sprinters ($ug^{-1/2}L^{-1/2}=3.2$, $u=10\text{ m s}^{-1}$). The highest Froude number reported for dogs by Alexander and Jayes (1983) in a survey of mammalian locomotion was approximately 5. For the single fastest stride of each individual in the present study, Froude numbers differed significantly among species (one-way ANOVA, $F_{4,14}=6.2$, $P<0.005$), only because *P. platyrhinos* had lower values than the other four species (Tukey HSD, multiple-range test). Among the four species of lizard with similar Froude numbers, several angular kinematic quantities differed significantly and cannot be attributed simply to differences in their limb dimensions. Using the criterion of maximal attainable speed, all five species in our study moved at physiologically 'equivalent' speeds (Table 3). However, on the basis of the Froude numbers, only four species were similar, and on the basis of detailed kinematics, all species were distinct (Fig. 3). Consequently, Froude numbers may be of limited

utility for predicting kinematic similarity within closely related animals with similar body size.

Relative stride length (stride length divided by hip height) is another dimensionless quantity used for making interspecific comparisons of limbed locomotion. From our mean values for quadrupedal locomotion (Table 4), and using $Y_{\text{hip}}(\text{ff})$, relative stride lengths ranged from 10.2 (*U. scoparia*) to 12.8 (*Cn. tigris*) and were greater than those predicted from the scaling equations of Alexander and Jayes (1983) both for non-cursorial mammals and for faster gaits of cursorial mammals.

Recent models of limbed locomotion have emphasized the commonality of mechanics and certain kinematic quantities despite considerable variation in speed and limb morphology (Alexander and Jayes, 1983; Farley et al., 1993; McMahon and Cheng, 1990). The mass/spring model (Farley et al., 1993; McMahon and Cheng, 1990) of limbed locomotion relates the mechanical stiffness to (1) changes (ΔL) in the length of the limb from footfall (L_0) to midstance, (2) half the angle θ swept by the leg from footfall to a vertical reference line, and (3) changes in the height of the center of mass during the stance phase (Δy). Using mean values of quadrupedal locomotion (Table 4), values of $\Delta L/L_0=100[\text{eff}2\text{D}(\text{ff})-Y_{\text{hip,stance}}]/\text{eff}2\text{D}(\text{ff})$ ranged from 22% (*D. dorsalis*) to 41% (*Cn. tigris*), and the mean value of $\Delta L/L_0$ for the quadrupedal data of all species of lizards in this study approximated 33%. We also used three-dimensional data to calculate $\Delta L/L_0=100[\text{eff}3\text{D}(\text{ff})-\text{eff}3\text{D}$ at minimum hip height] and this quantity averaged approximately 16% for the quadrupedal data of all species of lizard. Thus, the lateral orientation of the limb of lizards causes a substantial overestimation of actual limb compression when values are calculated from two-dimensional data (x, y). Farley et al. (1993) found that values of $\Delta L/L_0$ approximated 25% for several species of mammal of different sizes running with Froude numbers between 1 and 2.

Dynamic similarity predicts that quantities such as θ should be constant if animals have equal Froude numbers (Alexander, 1989; Alexander and Jayes, 1983; Farley et al., 1993), but methods for calculating θ are not standardized. For our quadrupedal data, we calculated θ as 90° minus $\arcsin[Y_{\text{hip}}(\text{ff})/(\text{effective limb length})]$, and we used three methods for determining two-dimensional effective limb lengths as the distance from the hip to (1) the most posterior point of footfall (eff2D), (2) the tip of the fourth toe at footfall, and (3) the tip of the fourth toe at the end of stance. For method 1, θ did not differ significantly among species (two-way ANOVA, $F_{4,14}=3.0$, $P>0.05$), and the mean value across all species was 39° . For methods 2 and 3, the mean values across all species were 55° and 52° , respectively, and both these quantities differed significantly among species ($F_{4,14}=4.0$, $P<0.05$; $F_{4,14}=6.0$, $P<0.01$, respectively) such that *P. platyrhinos* and *Cn. tigris* had the highest values (e.g. at footfall, mean $\theta = 63^\circ$ and 58° , respectively). Thus, the species with the slowest speed and lowest Froude number (*P. platyrhinos*) had the highest values of θ (based on methods 2 and 3).

For adult *D. dorsalis* moving at speeds of 50, 100, 150, 200

and 250 cm s^{-1} (Jayne and Irschick, 1999), mean values of θ using method 1 were 16° , 22° , 23° , 24° and 27° , respectively, whereas using method 2 the mean values of θ were 52° , 59° , 55° , 56° and 59° , respectively. For the quadrupedal locomotion of *D. dorsalis* in this study, mean values of θ using methods 2 and 3 were similar (56° and 50°), whereas the mean value using method 1 was 34° . Farley et al. (1993) found that values of θ increased by an average of 31% as the speed of locomotion increased within each species, and the values at the fastest speeds observed were 40° (dog), 28° (goat), 29° (horse) and 55° (kangaroo). The feet of lizards are relatively long compared with those of most mammals, and the extent of the plantar surface that contacts the ground varies with speed to a greater extent in lizards than for most mammals. Consequently, if the effective limb length of lizards is measured using the toetip when the entire plantar surface contacts the ground, then θ will overestimate the extent to which the femur and tibia sweep a particular arc length.

Compared with the normal running of humans during 'Groucho running', the vertical oscillation of the hip (Δy) and the angle of the thigh relative to the horizontal surface decreases, step length increases and vertical forces are dampened, resulting in a 'smoother ride' (McMahon et al., 1987). For the rapid locomotion of lizards, the angle of femur depression at footfall was very low (commonly less than 20° ; Fig. 6), and the values of the ratio of step length to leg length (femur + tibia) for the quadrupedal locomotion of lizards were uniformly high, with mean values ranging from 1.3 (*U. scoparia*) to 2.5 (*Cn. tigris*). Therefore, some aspects of lizard locomotion resemble 'Groucho running', but we are unable to determine whether the values of either Δy or of the vertical forces of lizards are unusually low.

Bipedal and quadrupedal locomotion

The transition between bipedal and quadrupedal locomotion of lizards is particularly noteworthy because lizards lack many of the other obvious gait transitions that occur in mammals, such as the trot–gallop transition (Hildebrand, 1985). For example, three criteria used to distinguish walking from running are that for walking (1) the duty factor exceeds 50%, (2) the height of the hip increases from the beginning to the middle of stance, and (3) the maximal gravitational potential energy occurs at the time of minimal vertical kinematic energy (Cavagna et al., 1977; Hildebrand, 1985). Fieler and Jayne (1998) and Jayne and Irschick (1999) studied a wide range of speeds of quadrupedal locomotion (50 – 250 cm s^{-1}) of adult *D. dorsalis* for which duty factors ranged from 38 to 68%, but the height of the hip, which is near the center of mass, always declined from the beginning to the middle of stance. The only force data for the walking and running of lizards have phase relationships of energy that are characteristic of both walking and running (Farley and Ko, 1997). Thus, despite changes in the mechanics of quadrupedal locomotion in lizards with speed, kinematic correlates are conspicuously absent.

Does the difference between bipedal and quadrupedal locomotion merely parallel the continuum of kinematic

variation observed within different speeds of quadrupedal locomotion? Of the five kinematic variables that distinguished the quadrupedal and bipedal locomotion of *D. dorsalis*, only stride duration changed similarly (significant decrease) both with increased quadrupedal speed (Jayne and Irschick, 1999) and during bipedal running. Minimum femur rotation changed in a different manner for bipedal locomotion compared with increased speed of quadrupedal locomotion. However, elevating the trunk (and pelvis) could decrease our values of femur rotation because they were measured relative to a vertical plane. The values in Table 5 suggest that the positive bipedal trunk angles of *D. dorsalis* largely account for the apparent change in femur rotation. None of the remaining differences in variables for bipedal running and different speeds of *D. dorsalis* was confounded by the changes in trunk angle. Therefore, the bipedal locomotion of *D. dorsalis* does not appear to be at one end of a continuum of variation associated with increased speed. However, for all the species that ran bipedally, we observed but did not analyze, several strides for which only one forelimb touched the ground; analyzing these transitional strides could blur the distinction between bipedal and quadrupedal locomotion.

Similarly, does variation in kinematics among species of lizards occur in the same variables that vary with speed within a single species? The present study included 24 of the kinematic variables (Tables 4, 5 excluding speed, $X_{\text{toetip}}(\text{ff})$, $X_{\text{toetip}}(\text{es})$ and trunk and tail angles) analyzed by Jayne and Irschick (1999), for which 13 differed significantly among species in the present study and 16 varied significantly with speed (Jayne and Irschick, 1999). Further, 10 of the 24 variables in common differed significantly both with speed (Jayne and Irschick, 1999) and among species. Hence, many features of the kinematics that vary significantly with speed within a generalized species of iguanian lizard also vary significantly among different speeds of lizards that were running near maximal speed.

The propensity of lizards to run bipedally varies considerably (Irschick and Jayne, 1998, 1999; Jayne and Ellis, 1998), but bipedal locomotion is widespread among species of lizard (Snyder, 1962; Urban, 1965). The modest sampling of species in the present study detected interspecific differences in bipedal locomotion, even between very close relatives (*Ca. draconoides* and *U. scoparia*). If the widespread occurrence of bipedal locomotion in lizards reflects an ancestral trait that was widely retained, then we might expect kinematic similarity of bipedal locomotion among different species. If bipedality within lizards is ancestral, then our data suggest either that considerable evolutionary divergence has occurred from the ancestral mode of bipedality or that bipedality has arisen several times.

Bipedalism has definitely evolved several times within vertebrates: lizards, birds and humans all use alternate movements of the limbs during bipedal locomotion (bipedal striding), in contrast to the hopping of many groups of saltatory mammals. The advantages of bipedal locomotion are still not well understood either for lizards or for other groups of

vertebrates (Djawdan and Garland, 1988; Gatesy and Biewener, 1991; Glasheen and McMahon, 1996; Irschick and Jayne, 1998, 1999; Snyder, 1949, 1952, 1962). Snyder (1962) suggested that bipedal locomotion of lizards was faster than quadrupedal locomotion, and bipedality in other clades of vertebrate is often presumed to evolve by enhancing speed (Djawdan and Garland, 1988). Additional key attributes of bipedal locomotion in lizards described by Snyder (1962) include trunk elevation and using the tail as a counterbalance.

Two recent studies have clarified how bipedal and quadrupedal locomotion differ in two closely related species of lizard. During the first five strides of accelerating from a standstill on a 3 m long sand-covered racetrack, the speeds of bipedal and quadrupedal strides did not differ significantly within either *Ca. draconoides* or *U. scoparia* (Irschick and Jayne, 1998). In contrast, during the escape locomotion of *Ca. draconoides* in the field, which averaged 10 m in length, the length of bipedal strides averaged 1.18 times the length of quadrupedal strides (Irschick and Jayne, 1999), similar to the 1.12 ratio of bipedal and quadrupedal speeds for this species in the present study (Table 4). For the other species that ran bipedally in the present study, mean values of speed for bipedal and quadrupedal strides were almost indistinguishable (Table 4). Consequently, the bipedal running of lizards does not necessarily provide a performance advantage for speed.

During bipedal locomotion, the clearance of the forelimb relative to the locomotor surface can be enhanced by (1) increasing hip height, (2) increasing the trunk angle and (3) lifting the forelimbs, and all these quantities increased for bipedal locomotion compared with quadrupedal locomotion. For bipedal locomotion, *D. dorsalis* and *Ca. draconoides* had similar hip heights. *Ca. draconoides* had lower trunk angles and 30% longer forelimbs than *D. dorsalis*, but *Ca. draconoides* had greater clearance between their forelimbs and the treadmill (13 mm *versus* 8 mm, respectively), primarily as a result of tucking in the forelimbs closer to the body. By contrast, *D. dorsalis*, which has a longer and heavier tail than *Ca. draconoides*, was more reliant on increased trunk angle to increase forelimb clearance. Thus, besides interspecific differences in hindlimb kinematics, these two species achieved forelimb clearance using different mechanisms.

Three factors may explain why lizards run without using their forelimbs. First, running at high speeds with the forelimbs above the ground may prevent the forelimbs from interfering with the hindlimbs. The longitudinal positions of the ipsilateral feet of lizards commonly overlap during high-speed running (Fig. 4, see also Sukhanov, 1974; Urban, 1965), and we have observed lizards stumbling over their forelimbs in the present study. Second, attaining velocities similar to those for the hindlimb may be difficult for the relatively short forelimbs of lizards (Table 1). Third, increased trunk angles and, hence, increased forelimb clearance may provide no advantage and could occur simply as a result of high torques about the hip joint. For the first bipedal stride of *Ca. draconoides* accelerating from a standstill, trunk angles averaged

approximately 20° and speed approximated only 1 ms⁻¹ (Irschick and Jayne, 1998), whereas for steady high-speed bipedal running (4.5 ms⁻¹), trunk angles averaged only 8°. Many previous values of trunk angles for the bipedal locomotion of lizards are high (for a review, see Urban, 1965), but they lack accompanying information on whether the lizards were accelerating or running at steady speeds.

The trunk angle of running lizards can be affected by the tail since its weight can help to balance the weight of the trunk during bipedal locomotion, but the extent to which balance is maintained by this passive mechanism rather than by some active muscular mechanism is unclear. The passively generated torque of the tail about the hip joint would be maximized if the tail were held horizontally, since this would position the center of mass of the tail as far as possible from the center of the hip. For each species in this study, mean tail angles increased during bipedal running (Table 5), but these increases were not statistically significant. *U. scoparia* had the highest tail angle (mean 29°), but most of its locomotion was quadrupedal. Thus, high tail angles do not correlate in a simple fashion with bipedal running. Furthermore, high angles of the tail would decrease its effectiveness as a counterbalance by shifting the tail's center of mass anteriorly. However, lizards might elevate the tail to keep it from interfering with the hindlimb. Furthermore, dorsiflexion of the tail should stretch the caudofemoralis muscle, which is an extremely large muscle that helps to propel lizards by retracting the hindlimb during the stance phase (Reilly, 1995). Thus, lifting the tail could enhance the force generated by this important propulsive-phase muscle, and this enhancement is likely to be most important for running at high speeds such as those observed in this study.

For lizards, long tails are frequently associated with bipedality (Snyder, 1962), and tail length correlates positively with sprinting speed among phylogenetically diverse species (Zani, 1996). Furthermore, species of lizard with long tails frequently have the largest caudofemoralis muscles (Zani, 1996). In the sand lizard clade (*Ca. draconoides*, *U. scoparia* and *P. platyrhinos*), the probability of bipedal running decreased with decreased tail length. However, *Cn. tigris* had the longest tail, but ran bipedally only infrequently. Thus, the lack of bipedal running in *P. platyrhinos* might result either from an insufficient tail to serve as an effective counterbalance or from a relatively small mechanical output due to a small caudofemoralis muscle.

Conclusions

The different species of lizard ran at maximum speeds with different joint angles. Furthermore, conspicuous differences in limb dimensions of certain species predictably enhanced interspecific differences in kinematics when both linear and angular kinematic variables were analyzed. For these similarly sized species, those with the longest limbs had both the greatest stride lengths and the greatest speed. Elongated distal limb elements appeared to be particularly important for enhancing both stride length and speed. Previous data (Fieler and Jayne, 1998; Jayne and Irschick, 1999) and our data for *D. dorsalis*

suggest that bipedal locomotion is kinematically distinct rather than representing one end of a continuum of variation associated with speed. We also found that bipedal locomotion was kinematically distinct among different species, suggesting unique evolutionary specialization.

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References

- Alexander, R. McN.** (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.
- Alexander, R. McN. and Jayes, A. S.** (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool., Lond.* **201**, 135–152.
- Bauwens, D., Garland, T. J., Castilla, A. M. and Van Damme, R.** (1995). Evolution of sprint speed in lacertid lizards, morphological, physiological and behavioral covariation. *Evolution* **49**, 848–863.
- Brinkman, D.** (1981). The hind limb step cycle of *Iguana* and primitive reptiles. *J. Zool., Lond.* **181**, 91–103.
- Cavagna, G. A., Heglund, N. C. and Taylor, R. C.** (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Cheverud, J. M., Dow, M. M. and Leutenegger, W.** (1985). The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. *Evolution* **39**, 1335–1351.
- Coombs, W. P. J.** (1978). Theoretical aspects of cursorial adaptations in dinosaurs. *Q. Rev. Biol.* **53**, 393–418.
- Cullum, A. J.** (1997). Comparisons of physiological performance in sexual and asexual whiptail lizards (Genus *Cnemidophorus*): implications for the role of heterozygosity. *Am. Nat.* **150**, 24–47.
- Djawdan, M. and Garland, T. J.** (1988). Maximal running speeds of bipedal and quadrupedal rodents. *J. Mammal.* **69**, 765–772.
- Dullemeijer, P.** (1974). *Concepts and Approaches in Animal Morphology*. Van Gorcum: Van Gorcum Press.
- Estes, R., de Queiroz, K. and Gauthier, J.** (1988). Phylogenetic relationships within Squamata. In *Phylogenetic Relationships of the Lizard Families* (ed. R. Estes and G. Pregill), pp. 119–282. Stanford: Stanford University Press.
- Etheridge, R. and de Queiroz, K.** (1988). Phylogeny of Iguanidae. In *Phylogenetic Relationships of the Lizard Families* (ed. R. Estes and G. Pregill), pp. 283–367. Stanford: Stanford University Press.
- Farley, C. T., Glasheen, J. and McMahon, T. A.** (1993). Running spring: speed and animal size. *J. Exp. Biol.* **185**, 71–86.
- Farley, C. T. and Ko, T. C.** (1997). Mechanics of locomotion in lizards. *J. Exp. Biol.* **200**, 2177–2188.
- Felsenstein, J.** (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Fidler, C. L. and Jayne, B. C.** (1998). Effects of speed on the hindlimb kinematics of the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **201**, 609–622.
- Frost, D. R. and Etheridge, R.** (1989). A phylogenetic analysis and taxonomy of iguanian lizards. *Misc. Publ. Univ. Kansas* **81**, 1–65.
- Garland, T., Jr** (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond. A* **207**, 425–439.
- Garland, T., Jr, Harvey, P. H. and Ives, A. R.** (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *System. Biol.* **41**, 18–32.
- Garland, T., Jr and Janis, C. M.** (1993). Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool., Lond.* **229**, 133–151.
- Garland, T., Jr and Losos, J. B.** (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240–302. Chicago: University of Chicago Press.
- Gatesy, S. M. and Biewener, A. A.** (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool., Lond.* **224**, 127–147.
- Gittleman, J. L. and Luh, H. K.** (1992). On comparing comparative methods. *Annu. Rev. Ecol. Syst.* **23**, 383–404.
- Glasheen, J. W. and McMahon, T. A.** (1996). Size-dependence of water-running ability in basilisk lizards (*Basiliscus basiliscus*). *J. Exp. Biol.* **199**, 2611–2618.
- Hildebrand, M.** (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 38–57. Cambridge, MA: Belknap Press of Harvard University Press.
- Irschick, D. J. and Jayne, B. C.** (1998). Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard, *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Biol.* **201**, 273–287.
- Irschick, D. J. and Jayne, B. C.** (1999). A field study of effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. *Physiol. Biochem. Zool.* **72**, 44–56.
- Jayne, B. C. and Ellis, R. V.** (1998). How inclines affect the escape behaviour of a dune dwelling lizard, *Uma scoparia*. *Anim. Behav.* **55**, 1115–1130.
- Jayne, B. C. and Irschick, D. J.** (1999). Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). *J. Exp. Biol.* **202**, 143–159.
- Lauder, G. V.** (1995). On the inference of function from structure. In *Functional Morphology in Vertebrate Paleontology* (ed. J. J. Thomason), pp. 1–18. Cambridge: Cambridge University Press.
- Lauder, G. V.** (1996). The argument from design. In *Adaptation* (ed. M. R. Rose and G. V. Lauder), pp. 55–91. San Diego: Academic Press.
- Lauder, G. V. and Reilly, S. M.** (1996). The mechanistic basis of behavioral evolution: comparative analysis of musculoskeletal function. In *Phylogenies and the Comparative Method in Animal Behavior* (ed. E. Martins), pp. 105–137. Oxford: Oxford University Press.
- Losos, J. B.** (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**, 1189–1203.

- Macrini, T. E. and Irschick, D. J.** (1998). An intraspecific analysis of trade-offs in sprinting performance in a West Indian Lizard (*Anolis lineatopus*). *Biol. J. Linn. Soc.* **63**, 579–591.
- Marsh, R. L.** (1988). Ontogenesis of contractile properties of skeletal muscle and sprint performance in the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **137**, 119–139.
- Martins, E. P. and Garland, T. J.** (1991). Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**, 534–557.
- McMahon, T. A. and Cheng, G. C.** (1990). The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23** Suppl. 1, 65–78.
- McMahon, T. A., Valiant, G. and Frederick, E. C.** (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326–2337.
- Miles, D. B.** (1994). Covariation between morphology and locomotory performance in sceloporine lizards. In *Lizard Ecology: Historical and Experimental Perspectives* (ed. L. J. Vitt and E. R. Pianka), pp. 207–235. Princeton: Princeton University Press.
- Reeder, T. W. and Wiens, J. J.** (1996). Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. *Herpet. Monogr.* **10**, 43–84.
- Reilly, S. M.** (1995). Quantitative electromyography and muscle function of the hind limb during quadrupedal running in the lizard *Sceloporus clarki*. *Zool. Analyt. Complex Syst.* **98**, 263–277.
- Reilly, S. M. and Delancey, M. J.** (1997a). Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. *J. Exp. Biol.* **200**, 753–765.
- Reilly, S. M. and Delancey, M. J.** (1997b). Sprawling locomotion in the lizard *Sceloporus clarkii*: the effects of speed on gait, hindlimb kinematics and axial bending during walking. *J. Zool., Lond.* **243**, 417–433.
- Rudwick, M. J. S.** (1964). The inference of function from structure in fossils. *Br. J. Phil. Sci.* **15**, 27–40.
- Sinervo, B.** (1990). The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**, 279–294.
- Snyder, R. C.** (1949). Bipedal locomotion of the lizard *Basiliscus basiliscus*. *Copeia* **1949**, 129–137.
- Snyder, R. C.** (1952). Quadrupedal and bipedal locomotion of lizards. *Copeia* **1952**, 64–70.
- Snyder, R. C.** (1962). Adaptations for bipedal locomotion of lizards. *Am. Zool.* **2**, 191–203.
- Sukhanov, V. B.** (1974). *General System of Symmetrical Locomotion of Terrestrial Vertebrates and some Features of Movement of Lower Tetrapods*. New Delhi: Amerind Publ. Co. Pvt. Ltd.
- Tsuji, J. S., van Berkum, F. H., Huey, R. B., Garland, T. J. and Shaw, R. G.** (1989). Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphological correlates. *Evol. Ecol.* **3**, 240–252.
- Urban, E. K.** (1965). Quantitative study of locomotion in teiid lizards. *Anim. Behav.* **13**, 513–529.
- Van Damme, R., Aerts, P. and Vanhooydonk, B.** (1997). No trade-off between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.* **60**, 493–503.
- Wilkinson, L.** (1992). SYSTAT for Windows: Statistics, Version 5 Edition. Evanston: SYSTAT Inc.
- Zani, P. A.** (1996). Patterns of caudal-autonomy evolution in lizards. *J. Zool., Lond.* **240**, 201–220.