

Sprawling locomotion in the lizard *Sceloporus clarkii*: the effects of speed on gait, hindlimb kinematics, and axial bending during walking

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(With 4 figures in the text)

Although the hindlimb is widely considered to provide the propulsive force in lizard locomotion, no study to date has analysed kinematic patterns of hindlimb movements for more than one stride for a single individual and no study has considered limb and axial kinematics together. In this study, kinematic data from several individuals of the *Sceloporus clarkii* are used to describe the movement patterns of the axial skeleton and hindlimb at different speeds, to analyse how kinematics change with speed, and to compare and contrast these findings with the inferred effects of speed cited in the literature. Angular limb movements and axial bending patterns (standing wave with nodes on the girdles) did not change with speed. Only the relative speed of retracting the femur and flexing the knee during limb retraction changes with speed. Based on these data and similar results from a recent study of salamanders, it appears that, over a range of speeds involving a walking trot, sprawling vertebrates increase speed by simply retracting the femur relatively faster, thus this simple functional adjustment may be a general mechanism to increase speed in tetrapods. The demonstration that femoral retraction alone is the major speed effector in *Sceloporus clarkii* lends strong functional support to ecomorphological implications of limb length (and especially femur length and caudifemoralis size) in locomotory ecology and performance in phrynosomatid lizards. It also lends support to inferences about the caudifemoralis muscle as a preadaptation to terrestrial locomotion and as a key innovation in the evolution of bipedalism.

Introduction

A large body of literature on the ecological morphology of lizard locomotion has focused on the physiological basis and energetics of locomotion and has emphasized the ecological and evolutionary significance of locomotor performance (reviewed in: Huey, Pianka & Schoener, 1983; Pianka, 1986; Bennett, 1989; Bennett & Huey, 1990; Miles, 1994; Garland & Losos, 1994). A unifying thread in this research is that locomotory performance depends on the integration of organismal systems that combines a certain energetic capacity, that drives a certain morphological system, with a particular muscle physiology, to move the limbs to propel the lizard at speeds that ensure that it will survive, reproduce and pass on its genes in a particular environment or niche. In lizards, each component (energetics, morphology, muscle physiology, ecology) of this integrated organism has seen considerable study except on how the lizard moves the limbs to propel itself at different speeds. Most studies of limb movements in lizards have focused on stride and gait characteristics (Snyder, 1952; Urban, 1965; Daan & Belterman, 1968; Sukhanov, 1974; Rewcastle, 1981, 1983; Brinkman, 1981; Peterson, 1984; Avery *et al.*, 1987; White & Anderson, 1994), and on inferences of limb movements from anatomical studies (Schaeffer, 1941; Snyder, 1952; Brinkman, 1980; Rewcastle, 1980, 1983), but few studies have presented information on kinematic movements of axial or limb segments (Snyder, 1952; Urban, 1965; Landsmeer, 1984; Peterson, 1984; Bels *et al.*, 1992; Ritter, 1992). Only two studies have described

motor and kinematic patterns during lizard locomotion; one on the forelimb during walking in *Varanus* (Jenkins & Goslow, 1983) and one for the hindlimb during walking in *Sceloporus clarkii* (Reilly, 1995). From these studies, a basic understanding of lizard gaits and a gross description of limb movements have emerged but they are largely based on anecdotal and qualitative descriptions of individual strides of lizards that are usually accelerating or decelerating as they run past a stationary camera. Although the hindlimb is widely considered to provide the propulsive force in lizard locomotion (Snyder, 1952; Gray, 1968; Sukhanov, 1974), no study to date has analysed kinematic patterns of hindlimb movements for more than one stride for a single individual, and no study has considered limb and axial kinematics together. The goals of this paper are to use kinematic data from several individuals of the same species to describe the movement patterns of the axial skeleton and hindlimb at different speeds, to analyse how kinematics change with speed, and to compare and contrast these findings with the inferred effects of speed cited in the literature. Details of the kinematics of limb movements compared to those of other tetrapods are presented in Reilly & DeLancey (1997).

Materials and methods

Kinematic recordings were obtained from *Sceloporus clarkii* collected in Molino Basin, Santa Catalina Mountains, 10 miles N. of Tucson, Arizona. Lizards were housed in 10 gallon aquaria in a temperature controlled room (25 °C) and fed water and crickets *ad libitum* for the duration of the experiments. Kinematic data for 3 lizards moving at 3 speeds were analysed for speed effects. *Sceloporus clarkii* was used because it is believed to use generalized sprawling locomotion (Sukhanov, 1974), and because this species is morphologically generalized, possessing the primitive morphology of the family Phrynosomatidae (Miles, 1994). Detailed descriptions of the motor patterns (Reilly, 1995) and kinematics for one speed (Reilly & DeLancey, 1997) are presented elsewhere. This analysis is the first study of lizard locomotion which analyses the kinematics of multiple strides at several known speeds.

Kinematic analysis

The lizards were filmed under strobe lights at 200 fields per second using a NAC HSV-400 high-speed video system. Elapsed time in milliseconds was recorded on each video frame during filming. Lateral and dorsal views of the lizards running were filmed (using mirrors) on a 70 cm long canvas treadmill with a background marked with lines every 10 cm. A series of quadrupedal running bouts was elicited by pinching the tail when the lizard moved out of the video field. The body temperature of the lizards during the runs was 27–30 °C. Reflective landmarks were painted on the lizards (Fig. 1) to mark the vertebral column and the sacrum, pelvis, acetabulum, knee, ankle and tip of the longest (fourth) toe. The limb landmarks were visible in both the lateral and dorsal views. The vertebral column was marked using the following landmark points (based on obvious points, paint dots, or intersections of chevron markings along the back): the tip of the snout, the occiput (midline posterior of skull), the pectoral girdle (midline between the arms), 4 equally spaced trunk segments, the penultimate trunk vertebra (directly dorsal to the pubic symphysis), the sacral vertebra, the first caudal vertebra (directly between the posterior tips of the ilia), and several caudal segments.

Lizards were run repeatedly at each of 3 preset speeds encompassing a 3-fold increase in speed from about 1 to 3 km/h (exact speeds below). A total of 22 strides of the right leg during which the lizards exactly matched the treadmill speed was used in the analysis: 2 strides from one individual (SVL = 90 mm) at 0.270 m s⁻¹ (0.972 km/h); 5 strides each for 2 additional individuals (SVLs = 92, 91 mm) at both 0.476 (1.71 km/h) and 0.833 m s⁻¹ (3 km/h). For each video field for each stride, the co-ordinates of each landmark were digitized using Measurement TV (Updegraff, 1990). The co-ordinate data were then used to calculate 2 dimensional angles for each video field indicating movements of the pelvis, hip joint and knee joint (in dorsal view) and movements of the foot relative to



FIG. 1. Kinematic landmarks and angles used to describe limb movements in *Sceloporus clarkii*. The landmarks are: (L) lumbar dot, over the penultimate trunk vertebra (dorsal to the pubic symphysis); (S) sacral dot, over the sacrum; (C) caudal dot, over the first caudal vertebra (directly between the posterior tips of the ilia); (H) hip dot, over the acetabulum; (K) knee dot; (A) ankle dot; and (T) toe dot, on the tip of the 4th toe. The following angles were calculated: pelvic angle, the angle between line CL and the direction of travel (indicating pelvic rotation); hip angle, the angle between line HK and CL (indicating femoral retraction/protraction); knee angle, angle HKA (indicating knee flexion and extension); and ankle angle, angle KAT (indicating foot flexion and extension). Axial landmarks are described in the text.

the crus (in lateral view) through the stride as illustrated in Fig. 1. Because the limb moves almost entirely in the horizontal plane (Snyder, 1954; Table 5) and the crus never passes under the knee, 2-dimensional angles were used to provide an accurate measure of the minima and maxima and excursions of joint movements during locomotion.

To illustrate kinematic limb patterns for each speed, mean kinematic profiles were generated by plotting the mean angles (\pm S.E.) for each frame for one individual at the slow speed ($n = 2$) and another individual at the medium and high speeds ($n = 5$ each). Strides were aligned by treating the time of right foot down as time zero for each of the individual strides averaged within speeds. Axial bending patterns were illustrated by superimposing stick figures of head to tail landmark values for each frame for all of the frames for a complete stride. To compare gaits at different speeds, the timing of footfalls was measured for each foot for each stride (for a complete cycle for

each of the 4 feet) and mean gait diagrams for each speed were plotted using mean footfall values for all 4 feet for each speed.

Kinematic variables

Limb and pelvic movements

To assess the effects of speed on hindlimb kinematics quantitatively, a series of angular and timing variables were taken from each stride to describe pelvic and limb movements. The variables were chosen to capture the angles and timing of minimum and maximum positions of the pelvis and each of the 3 major joints of the hindlimb, the hip (H), knee (K), and ankle (A), as described in Fig. 1. Angular variables were as follows. The angles of each joint (H, K, A) were taken at the time of right foot down (DN) and right foot up (UP). These angles indicate the positions of the 3 joints at the beginning (DN) and end (UP) of the *stance phase* (ST: from foot down to foot up), and conversely, the *swing phase* (SW: from foot up to the next foot down). Movement of the limb as a whole in terms of the direction of movement of the foot is termed *protraction* and *retraction* when the foot is being moved anteriorly and posteriorly, respectively (which are sometimes termed *recovery* and *transport* phases, respectively). Because protraction and retraction of the limb do not often correspond to the stance and swing phases (maximum protraction occurs 0–20 ms before foot down: see THMAXPROT vs. STRIDEDUR in Table II), we also measured the angle of the hip at maximum limb protraction (HMAXPROT), the angle of the hip at maximum limb retraction (HMAXRET), and the angle of excursion (EXC) of the hip during retraction of the limb (HRETEXC). The knee is flexed to a minimum (MIN) and then extended to a maximum (MAX) during both the stance and swing phases, thus angles were taken to quantify the minimum, maximum and excursion of the knee joint during both phases (KMINST, KMAXST, KEXCST, KMINSW, KMAXSW, KEXCSW). The ankle is maximally extended (EXT) just prior to foot down and this angle was measured (AMAXEXT). The ankle is then flexed to a minimum during the stance phase and then extended to a maximum just after foot up and this period delineates the power stroke (PS) of the retraction phase. Thus, we measured the minimum, maximum and excursion of the ankle during the power stroke (AMINPS, AMAXPS, AEXCPS). The last angular variable is the maximum of rotation of the pelvis relative to the direction of travel (PELVMAX).

Timing variables were taken to describe aspects of the stride and the timing of joint movements. The durations (DUR) of the stance phase, swing phase, and entire stride were measured (STANCEDUR, SWINGDUR, STRIDEDUR, respectively). The rest of the timing variables are either times to (T) various joint angles (from time 0 at right foot down), or the durations (DUR) of angular excursions described above. These are: the time to hip maximum retraction (THMAXRET), protraction (at the end of the stride, THMAXPROT), and hip protraction duration (THRETDUR); the time to minimum and maximum knee positions during the stance (TKMINST, TKMAXST) and swing (TKMINSW, TKMAXSW) phases and their durations (KDURST, KDURSW); the time of maximal angle extension prior to foot down (TAMAXEXT) and the time to the minimum and maximum ankle angle during the power stroke (TAMINPS, TAMAXPS) and this excursion (ADURPS); and the time to the maximum pelvic rotation (TPELVMAX). Detailed descriptions of each variable are listed in **Appendix I**.

Limb adduction

The knee and toe displacement loops (from co-ordinate data) were examined and their lateral widths were measured to examine the amount of adduction of the limb with speed. Displacement loops circumscribe the movements of the landmark in one plane for a single stride. For example, in dorsal view a narrow displacement loop indicates that the landmark is moving in a more or less longitudinal plane with the stance and swing trajectories of the landmark staying in the same longitudinal plane. A wider loop indicates that the landmark moves more medially during the stance phase than the swing phase, indicating greater adduction of the limb. A change in the width of the knee or toe displacement loops with speed indicates that the amount of limb adduction changes with speed and, thus, that the animal is shifting from a more sprawling posture to a more erect one.

Changes in limb adduction with speed were quantified using the lateral width of the knee, and toe displacement loops (from dorsal view), as well as the vertical depth of the knee loop from lateral view.

Axial bending

Axial kinematics were quantified using 8 variables describing the maximum amplitudes and longitudinal positions of landmarks along the vertebral column. Because roughly consistent standing waves with 2 nodes were found at all speeds, minima and maxima of wave peaks and nodes were measured from each stride. The maximum amplitude of lateral movements of the snout, the trunk region, and the tail were measured. The minimum amplitude in the pectoral region (the pectoral node) and the pelvic region (the pelvic node) were taken and the positions of these nodes along the relative to the vertebral landmarks was taken as well. Axial data were digitized for one individual at each speed (individual 3 at 0.270 m s^{-1} ($n = 2$) and individual 1 at the other 2 speeds ($n = 5$ each).

Statistical analyses

To identify kinematic variables that varied significantly with speed, values for each variable were averaged for each individual and the individual means were regressed against speed. Significant regressions of angular variables will indicate joint movements that vary with speed. Timing variables were regressed against speed in both real time and with timing variables for each stride scaled to the stride duration for that stride. Timing variables are expected to change with speed in real time, however, significant regressions of timing variables scaled to stride duration will indicate how the relative timing of joint movements varies with speed. Variables that differ with speed will then be used to describe how lizards modulate limb use to increase their velocity.

Results

Limb movements

Mean angular data for limb positions and excursions for each of the three individuals are presented in Table I. Mean timing data are presented in Table II. Representative kinematic profiles for each joint and the rotation of the pelvis are presented scaled to stride duration in Fig. 2. Regression statistics for the effects of speed on angular data (Table III) revealed that none of the angular measures varied with speed at the alpha level ($P = 0.01$).

Regression statistics for the timing variables scaled to stride duration are presented in Table IV. In real time, 13 of the 17 timing variables varied significantly with speed ($P_s \leq 0.036$) with all involving faster movements as speed increases (Table II). When the timing of kinematic movements are scaled to stride length, only three variables vary significantly with speed at the alpha level of 0.02 (Table IV). The hip retraction time (HRETDUR), time from foot down to maximum hip retraction (THMAX-RET), and the time to minimum knee angle during the stance phase (TKMINST) decrease as the lizard moves faster.

Mean widths of displacement loops for the knee and toe are presented in Table V. Comparisons of the means and standard deviations shows that the displacement loops for the knee (in both lateral and dorsal view) and the toe in dorsal view are very consistent between speeds, indicating that the degree of adduction of the femur and the entire limb does not change with speed.

Axial movements

Axial kinematic data are presented in Fig. 3 and Table VI. *Sceloporus clarkii* walks using a rough

TABLE I

Kinematic movement data (means \pm standard errors for angles and excursions) for the right hindlimb of three *Sceloporus clarkii* running at three speeds. Variables are described in the text

ANGLE (in degrees)	0.270 m s ⁻¹	0.476 m s ⁻¹		0.833 m s ⁻¹	
	Individual 3	Individual 1	Individual 2	Individual 1	Individual 2
HDN	62 \pm 5	56 \pm 4	55 \pm 1	63 \pm 3	47 \pm 3
HUP	82 \pm 1	76 \pm 3	90 \pm 2	91 \pm 2	89 \pm 2
HMAXPROT	59 \pm 1	50 \pm 1	57 \pm 1	58 \pm 1	43 \pm 2
HMAXRET	88 \pm 3	81 \pm 2	91 \pm 1	105 \pm 1	76 \pm 4
HRETEXC	29 \pm 3	30 \pm 2	35 \pm 2	47 \pm 2	32 \pm 6
KDN	104 \pm 3	70 \pm 1	90 \pm 2	82 \pm 2	80 \pm 4
KUP	83 \pm 7	78 \pm 4	77 \pm 6	73 \pm 5	83 \pm 3
KMINST	69 \pm 1	61.8 \pm 2	64 \pm 6	56 \pm 2	65 \pm 4
KMAXST	96 \pm 6	92 \pm 3	86 \pm 4	91 \pm 2	97 \pm 1
KEXCST	27 \pm 5	31 \pm 3	22 \pm 5	35 \pm 4	31 \pm 4
KMINSW	66 \pm 2	62 \pm 3	62 \pm 2	50 \pm 1	58 \pm 6
KMAXSW	105 \pm 4	86 \pm 2	80 \pm 7	83 \pm 4	85 \pm 7
KEXCSW	39 \pm 2	24 \pm 4	24 \pm 1	32 \pm 4	27 \pm 7
ADN	70 \pm 11	57 \pm 2	53 \pm 6	58 \pm 4	67 \pm 7
AUP	155 \pm 11	148 \pm 17	167 \pm 5	146 \pm 7	142 \pm 8
AMINPS	36 \pm 2	29 \pm 1	25 \pm 2	21 \pm 2	42 \pm 4
AMAXPS	162 \pm 4	189 \pm 8	166 \pm 5	189 \pm 6	156 \pm 6
AEXCPS	136 \pm 6	134 \pm 12	141 \pm 5	168 \pm 4	114 \pm 3
AMAXEXT	61 \pm 13	64 \pm 4	54 \pm 6	57 \pm 2	79 \pm 12
PELVMAX	16 \pm 7	25 \pm 3	21 \pm 2	21 \pm 2	19 \pm 2

standing wave of axial movement that has two nodes. One node is centred on the pectoral girdle (axial landmark 3) and the other is centred at axial landmark 8 on the penultimate trunk vertebra that is just dorsal to the pubic symphysis (Fig. 3). Although lateral displacements of the tail tended to increase and the displacement of the pectoral node tended to decrease, these were not significantly different when regressed against speed ($P_s > 0.067$). The displacement of the snout, however, decreased significantly with speed (Table VI).

Stride and gait characteristics

In going from 0.270 to 0.833 m s⁻¹, the stride, stance and swing durations decreased by about 40% in real time (Table II). Mean stride frequency increased significantly ($P = 0.002$) from 3.4 to 5.8 strides per second and stride length increased significantly ($P = 0.002$) from 80 mm to 143 mm per stride.

Gait diagrams for the three speeds are presented in Fig. 3. At all three speeds, *Sceloporus clarkii* maintained tight coupling of opposite fore- and hindfeet with the overlap of the couplets tending to decrease with speed. Based on the footfall data for all four feet, the stance phase (means scaled to stride duration) for both the hindfeet (63.9 to 56.9 to 52.4%) and forefeet (60.7 to 55.9 to 47.9%) tended to decrease with increasing speed and at each speed the hindfeet were on the ground slightly longer than the forefeet. The same trend was evident in the data for the right hindlimb (Table II), but the relative duration of the stance phase did not decrease significantly with speed based on the regression (Table IV: STANCEDUR). Therefore, over this range of speeds, *Sceloporus clarkii* goes from a 'moderate walk' to a 'fast walk' (*sensu* Hildebrand, 1976).

The percentage of the stride that the forefeet followed the ipsilateral hindfeet remained fairly

TABLE II

Kinematic timing data for right hindlimb movements of *Sceloporus clarkii* running at three speeds. Means \pm standard errors are presented with means scaled to the stride duration (below in parentheses). Variables are described in the text

VARIABLE (in ms)	0.270 ms ⁻¹	0.476 ms ⁻¹		0.833 ms ⁻¹	
	Individual 3	Individual 1	Individual 2	Individual 1	Individual 2
SWINGDUR	117 \pm 12 (0.40)	98 \pm 10 (0.44)	90 \pm 7 (0.42)	83 \pm 5 (0.46)	70 \pm 2 (0.43)
STANCEDUR	178 \pm 3 (0.60)	126 \pm 13 (0.56)	126 \pm 11 (0.58)	97 \pm 3 (0.54)	93 \pm 4 (0.57)
STRIDEDUR	295 \pm 10 (1.00)	224 \pm 13 (1.00)	216 \pm 5 (1.00)	180 \pm 4 (1.00)	163 \pm 5 (1.00)
THMAXPROT	285 \pm 1 (0.97)	207 \pm 11 (0.92)	215 \pm 5 (1.00)	174 \pm 5 (0.97)	146 \pm 4 (0.90)
THMAXRET	179 \pm 5 (0.61)	111 \pm 7 (0.50)	116 \pm 5 (0.54)	66 \pm 6 (0.37)	58 \pm 6 (0.36)
HRETDUR	189 \pm 5 (0.64)	128 \pm 6 (0.57)	117 \pm 1 (0.54)	72 \pm 6 (0.40)	75 \pm 6 (0.46)
TKMINST	93 \pm 38 (0.32)	55 \pm 5 (0.25)	42 \pm 5 (0.20)	19 \pm 2 (0.11)	24 \pm 3 (0.15)
TKMAXST	148 \pm 18 (0.50)	95 \pm 11 (0.42)	105 \pm 5 (0.49)	71 \pm 5 (0.39)	81 \pm 4 (0.50)
KDURST	55 \pm 20 (0.19)	79 \pm 7 (0.35)	81 \pm 4 (0.38)	52 \pm 4 (0.29)	57 \pm 5 (0.35)
TKMINSW	218 \pm 18 (0.74)	163 \pm 10 (0.73)	183 \pm 11 (0.85)	139 \pm 4 (0.77)	112 \pm 6 (0.69)
TKMAXSW	283 \pm 3 (0.96)	207 \pm 8 (0.92)	219 \pm 4 (1.01)	176 \pm 4 (0.98)	155 \pm 4 (0.95)
KDURSW	65 \pm 20 (0.22)	44 \pm 5 (0.20)	36 \pm 10 (0.17)	37 \pm 3 (0.21)	43 \pm 5 (0.26)
TAMINPS	58 \pm 13 (0.20)	44 \pm 3 (0.20)	55 \pm 10 (0.25)	36 \pm 3 (0.20)	26 \pm 4 (0.16)
TAMAXPS	185 \pm 5 (0.63)	138 \pm 5 (0.59)	129 \pm 11 (0.60)	117 \pm 4 (0.57)	98 \pm 4 (0.60)
ADURPS	128 \pm 17 (0.43)	88 \pm 11 (0.39)	74 \pm 1 (0.34)	67 \pm 3 (0.37)	72 \pm 6 (0.44)
TAMAXEXT	240 \pm 15 (0.81)	213 \pm 11 (0.95)	216 \pm 5 (1.00)	163 \pm 5 (0.91)	147 \pm 4 (0.90)
TPELVMAX	150 \pm 23 (0.51)	105 \pm 7 (0.47)	95 \pm 3 (0.44)	85 \pm 5 (0.46)	78 \pm 5 (0.48)

constant (57.4 to 51.2 to 51.5), indicating that the lizards were maintaining a 'trot' (*sensu* Hildebrand, 1985). Thus, according to the Hildebrand (1976) gait model, the lizards were using a moderate to fast walking trot over the three-fold increase in speed employed in this study.

Discussion

Speed and gaits

Sukhanov (1974) and Hildebrand (1976) concluded that, as lizards move faster quadrupedally, they progress from a lateral sequence walk through a transitional phase to the walking trot which becomes a running trot at higher speed. The gait data of White & Anderson (1994), however, clearly show that at high speeds lizards may also pass through another transitory phase into a diagonal sequence run. In

TABLE III

Regression statistics for the effects of speed on angular movements of the hindlimb in *Sceloporus clarkii* based on means of three individuals moving at three speeds (0.270, 0.476, and 0.833 m s⁻¹)

Variable	R ²	F _{df = 1,4}	P
HDN	0.115	0.391	0.576
HUP	0.373	1.787	0.274
HMAXPROT	0.230	0.898	0.413
HMAXRET	0.023	0.069	0.810
HRETEXC	0.428	2.240	0.231
KDN	0.218	1.220	0.350
KUP	0.089	0.293	0.626
KMINST	0.374	1.795	0.273
KMAXST	0.006	0.018	0.903
KEXCST	0.323	1.434	0.317
KMINSW	0.814	13.104	0.036
KMAXSW	0.441	2.366	0.222
KEXCSW	0.005	0.014	0.914
ADN	0.009	0.027	0.880
AUP	0.397	1.972	0.255
AMINPS	0.001	0.003	0.957
AMAXPS	0.640	5.327	0.104
AEXCPS	0.598	4.462	0.125
AMAXEXT	0.180	0.660	0.476
PELVMAX	0.085	0.278	0.635

terms of discrete gaits, their data demonstrate that lizards use a lateral sequence walk at very low speeds, a trot at medium to fast speeds, and a diagonal sequence run at high speeds. The gaits of *Sceloporus clarkii* in this study went from a moderate walking trot at 0.270 m s⁻¹ to a fast walking trot at the higher two speeds and their gait was just on the cusp of being considered a "run" (duty factor < 0.5) at 0.833 m s⁻¹. Therefore, this study focuses on the most common gait used by lizards, describing how kinematics change as a trot is speeded up from a moderate walk to a run.

Sceloporus clarkii employs a consistent trot over the three-fold increase in speed because the diagonal feet maintain about the same phase relationship (Table IV) and the percentage of the stride that forefeet followed ipsilateral hindfeet remained basically constant (Fig. 4). This corresponds well with gait patterns from a single sequence of strides of similar-sized *Teratoscincus scincus* illustrated by Sukhanov (1974: Fig. 6). This sequence was the only one from numerous sequences, from this and other species, in which Sukhanov was able to get a consistent gait pattern. The *Teratoscincus* lizard accelerated from 0.30 to 0.86 m s⁻¹ over seven strides and exhibited essentially the same gait patterns shown in Fig. 4. Thus, both *Teratoscincus* and *Sceloporus* maintain a consistent trot at speeds as low as 0.27 m s⁻¹, with no indication of shifting into a transitional gait. Nearly identical gait patterns (trots) are found in walking at between 0.07 and 0.254 m s⁻¹ salamanders (Edwards, 1977; Ashley-Ross, 1994a, b), except that salamanders begin to transition into a lateral-sequence diagonal-couplets walk at the lower end of this speed range.

Speed and kinematics

To run faster with the same gait, stride duration must decrease, and stride frequency and/or length must increase, hence, most aspects of the limb movements must occur faster in real time (Sukhanov,

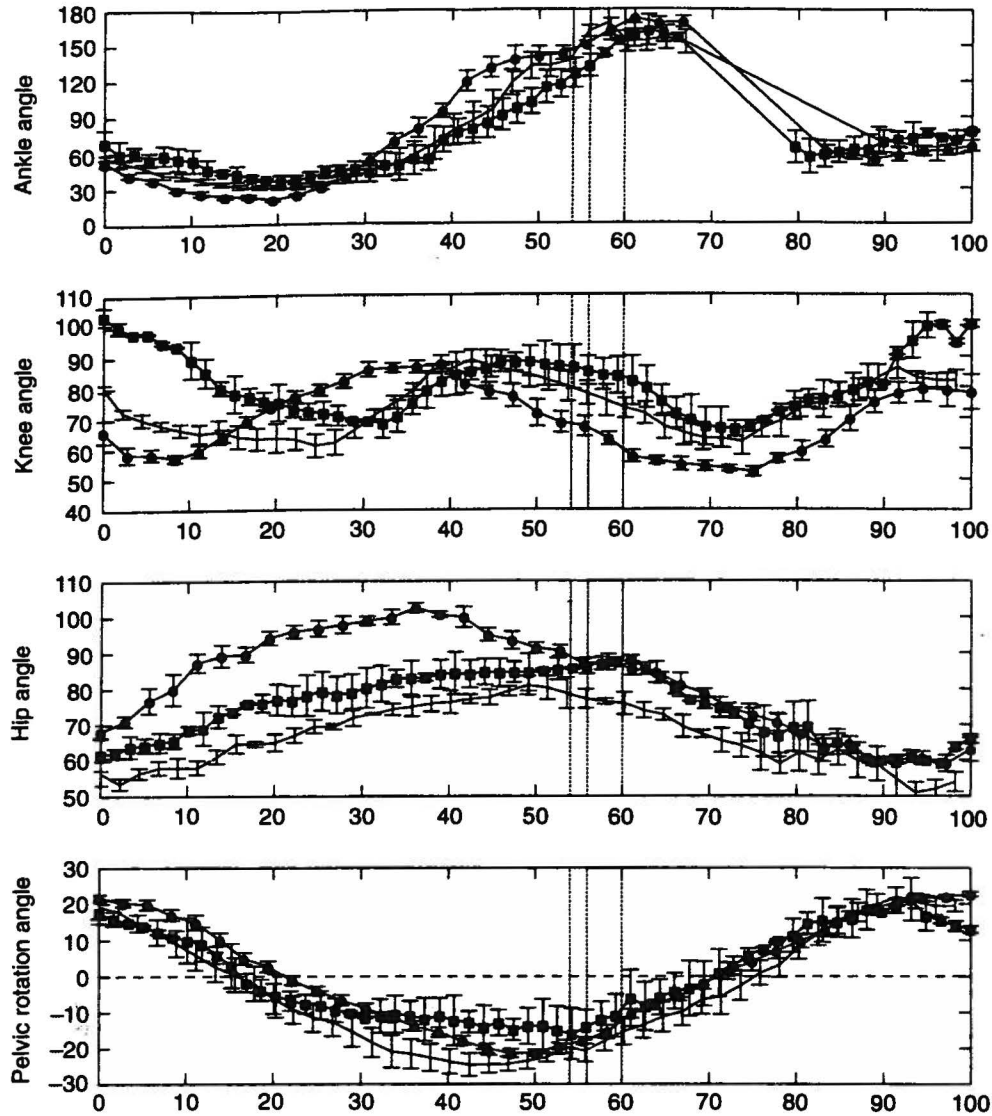


FIG. 2. Mean profiles for right hindlimb joint kinematics in *Sceloporus clarkii* trotting at three speeds adjusted to stride duration. Means \pm standard errors are shown for one individual moving at 0.270 m s^{-1} (\blacksquare : $n=2$) and second individual moving at 0.476 m s^{-1} (\blacktriangle : $n=5$) and 0.833 m s^{-1} (\bullet : $n=5$). The x-axis indicates time in percentage of stride duration from right foot down (0%) to the next foot down (100%). The ankle angle is in lateral view and data are omitted during the time the limb is swung toward the camera during the swing phase. The other angles are in dorsal view. The pelvic angle swings from the left (+ve values) to the right (-ve values). The hip is protracted (low values) and retracted (higher values). The knee is flexed (low values) and extended (higher values). The ankle is flexed (low values) and extended (high values). The vertical lines on each plot indicate the mean time for the end of the stance phase (foot up) for the fast, medium and slow speeds, respectively, from right to left.

TABLE IV

Regression statistics for the effects of speed on the relative timing of hindlimb movements in *Sceloporus clarkii* based on means scaled to stride duration for three individuals moving at three speeds (0.270, 0.476, and 0.833 m s⁻¹). Note that significant speed effects are observed in only three variables: two variables describing the timing of hip retraction and one describing flexion of the knee during limb retraction

Variable	R ²	F _{d.f. = 1,4}	P
SWINGDUR	0.604	4.575	0.122
STRIDEDUR	—	—	—
STANCEDUR	0.604	4.575	0.122
THMAXPROT	0.195	0.726	0.457
THMAXRET	0.981	155.921	0.001*
HRETDUR	0.934	42.645	0.007*
TKMINST	0.890	24.224	0.016*
TKMAXST	0.061	0.196	0.688
KDURST	0.214	0.816	0.433
TKMINSW	0.001	0.001	0.979
TKMAXSW	0.043	0.136	0.737
KDURSW	0.010	0.030	0.873
TAMINPS	0.018	0.657	0.477
TAMAXPS	0.425	2.216	0.233
ADURPS	0.001	0.0001	0.984
TAMAXEXT	0.035	0.110	0.762
TPELVMAX	0.300	1.288	0.339

* = significant

1974; Hildebrand, 1976; Ashley-Ross, 1994a). Thus, it is not surprising that 13 of the 17 timing variables decreased with speed in real time as would be generally expected. However, based on the regressions of kinematic variables on speed, there is a surprisingly constant pattern of limb movements. Across a three-fold increase in speed, the extent and ranges of angular movements of the limb joints did not change (Table III).

Three of the timing variables varied with speed (Table IV). The hip retraction time (from maximal protraction (HRETDUR) or foot down (THMAXRET)) decreased from about 64 to 36% of stride duration, thus the femur was retracted about 44% faster. In addition, the time to maximal knee flexion

TABLE V

Mean widths (\pm standard deviations) of displacement loops indicating the degree of lateral (for the knee and fourth toe landmarks in dorsal view) and vertical (for the knee landmark in lateral view) displacement (mm) of the limb during running at three speeds. Data are from individual 3 ($n = 2$) at the slow speed and individual 1 at the higher two speeds ($n = 5$ each). Note that none of the displacements varies with speed

Speed (m s ⁻¹)	Maximum displacements (mm)		
	Knee (dorsal view)	Toe (lateral view)	Knee (lateral view)
0.270	13.5 \pm 1.5	13.5 \pm 2.0	10.5 \pm 1.1
0.476	17.4 \pm 3.5	14.8 \pm 2.3	14.3 \pm 2.7
0.833	15.9 \pm 3.3	11.1 \pm 2.0	10.1 \pm 2.2

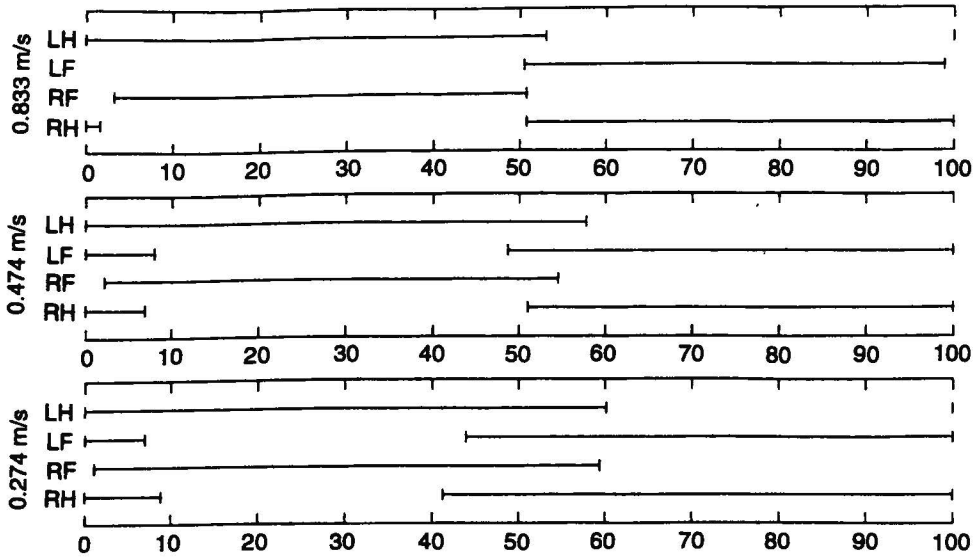


FIG. 3. Mean gait patterns for *Sceloporus clarkii* walking at three speeds. Lines indicate stance phases for all four feet based on mean foot fall times (vertical lines) for a different individual at each speed ($N=2$ for the slow speed and 5 for the faster speeds). Note that a trot is maintained across this range of speeds.

(TKMINST) decreased from about 32 to 13% of stride duration for about a 60% increase in knee flexion time. Biomechanically, faster retraction of the femur would be expected to increase the speed of flexion of the knee joint as well because the caudifemoralis muscle (the primary femur retractor) has an accessory tendon extending to the tibia (Snyder, 1954), and stimulation experiments (Snyder, 1952) have shown that the caudifemoralis muscle also flexes the knee. Because none of the angular minima, maxima, or excursions for the hip or knee changed significantly during limb retraction (Table III), and there is no evidence for greater adduction of the femur with speed (Table V), it appears that the femur

TABLE VI

Mean axial kinematic data for *Sceloporus clarkii* walking at three speeds. Lateral displacements of peaks (for the snout, trunk, and tail) and nodes of standing wave are given in mm. The pectoral node occurred on the pectoral girdle (axial landmark 3) and the pelvic node occurred just anterior to the pelvis (axial landmark 8). Data are from individual 3 ($N=2$) at the slow speed and individual 1 at the higher two speeds ($N=5$ each). Note that only the snout displacement varied with speed

Lateral displacement	Displacements (mean \pm S.D.)		
	0.270 m s ⁻¹	0.476 m s ⁻¹	0.833 m s ⁻¹
Snout (max.)*	20.8 \pm 2.4	15.2 \pm 3.1	11.0 \pm 2.6
Pectoral node (min.)	10.5 \pm 6.4	9.5 \pm 2.3	5.5 \pm 2.0
Trunk (max.)	18.0 \pm 2.0	17.6 \pm 1.2	13.4 \pm 2.2
Pelvic node (min.)	10.0 \pm 0.10	9.7 \pm 2.0	9.7 \pm 1.7
Caudal (max.)	18.0 \pm 4.2	21.2 \pm 4.9	24.2 \pm 5.8

* $P=0.028$

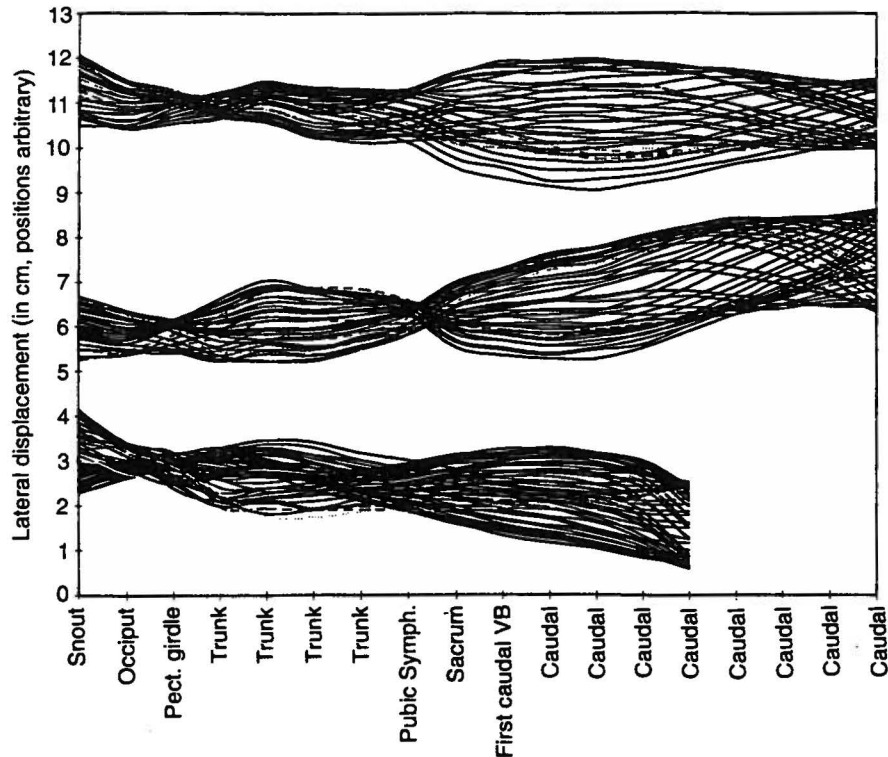


FIG. 4. Axial bending patterns over a three-fold increase in speed in *Sceloporus clarkii*. One representative stride from 0.270 m s^{-1} (bottom), 0.476 m s^{-1} (middle) and 0.833 m s^{-1} (top) are shown with superimposed stick figures of the axial landmarks for each frame during the stride. y -axis values indicate y -co-ordinates from video images in cm measured for each of the landmarks indicated along the x -axis (positions of each speed are arbitrary).

and knee move through the same range of angles during retraction but they are simply retracted faster to increase locomotor speed.

One of the most surprising findings of this study is a lack of kinematic change in the distal elements of the limb with speed. Although flexion of the knee occurs faster with speed, the timing and angular excursions of knee extension during the propulsive stroke (Tables I–IV: K- and TK- variables) did not change with speed. Plantar flexion of the ankle is a major component generating propulsion during locomotion, yet the timing and angular excursions of ankle flexion (TAMINPS, AMINPS), ankle extension (AMAXPS, AEXCPS, TAMAXPS), and the duration of plantar flexion (ADURPS) did not change significantly with speed (Tables I–IV). In addition, the lateral displacements of the fourth toe and the lateral and vertical displacements of the knee did not change with speed (Table V), indicating that the positional relationship between the knee and the toe remained the same. Thus, the kinematics of knee extension and plantar flexion during the propulsive stroke remained the same over this range of speeds. The apparent insignificance of plantar flexion in contributing to speed is in contrast to anatomical predictions that the distal limb elements are the major component generating propulsive force (Brinkman, 1980, 1981; Rewcastle, 1981, 1983).

In terms of limb adduction in *Sceloporus clarkii*, the knee and toe displacement loops did not change with speed, demonstrating that this lizard is not only using a sprawling posture, but it is maintaining

this basic posture as speed increases. There is no transition to a more erect posture as had been observed with increased speed and gait change in the alligator (Gatesy, 1991), which is commonly inferred to be a key reason for the evolutionary transition to erect postures and faster locomotion in mammals and archosaurs (Hildebrand, 1976, 1985; Gatesy, 1990).

Pelvic and axial movements remained constant as well. Maximum pelvic rotation from the direction of travel was highly conserved (Table IV, Fig. 2) ranging only from 16 to 25 degrees over all individuals and speeds (Table I) which matches the ranges of values for the alligator (Gatesy, 1991), a salamander (Ashley-Ross, 1994a, b) and several other lizard species (Ritter, 1992). The time of peak pelvic rotation occurred at from 44 to 51% of stride duration (Table IV), consistently just before foot up (54 to 60% of stride duration) and thus, maximum pelvic rotation occurs at from 81–85% of the stance phase. A similar pattern for peak pelvic rotation is seen in the trotting salamander, *Dicamptodon* (Ashley-Ross, 1994b).

As speed increases, the lizards maintain a loose standing wave of axial bending with nodes on the pectoral girdle and the anterior end of the pelvis (Fig. 3). This verifies other observations of standing waves in lizards (Ritter, 1992) and Reilly's (1995) prediction of a standing wave based on the fact that *Sceloporus clarkii* exhibits simultaneous unilateral onset of axial muscles during locomotion at the high speed. The positions of the nodes did not shift with locomotor speed and the node (minimum) and peak (maximum) amplitudes did not change (except for the snout). This matches Daan & Belterman's (1968) report that lizards tended to show little or no change in lateral bending with speed. Lateral displacement of the tip of snout decreased with speed (Table VI). This tendency to focus the head more forward as speed increases has been shown in other lizards (Ritter, 1992) and a marsupial using lateral undulation (Pridmore, 1992). A standing wave pattern with nodes near the girdles is the same as seen in walking salamanders (Ashley-Ross, 1994b) and axial patterns of several lizards shown by Ritter (1992).

The functional basis of increasing speed

Previous descriptions of the sprawling limb cycle differ on which components of the limb generate the majority of propulsive force. Some hypothesize that the proximal elements are more important in generating propulsive force (Snyder, 1952; Sukhanov, 1974; Hildebrand, 1985; Ashley-Ross, 1994b) than the distal elements (Rewcastle, 1981, 1983). It seems obvious that axial bending, femoral retraction, knee extension, and plantar flexion of the foot have important synergistic contributions to generating propulsion during the limb cycle, but which aspects change with speed? Although force and kinematic data are needed to pinpoint key components producing propulsive force, our kinematic results suggest that, for this species, there may be a fairly simple functional explanation of how speed is increased.

Over the range of speeds we studied virtually all of the axial, pelvic, and limb kinematics remained the same; with only a few timing variables changing. This finding corresponds with studies of a salamander (Ashley-Ross, 1994b) and mammals (Goslow, *et al.*, 1973, 1981; Grillner, 1975; Halbertsma, 1983) which report little to no change in angular excursions of the limbs with speed, but some timing changes. Speed in *Sceloporus clarkii* was increased by simply retracting the femur and flexing the knee faster relative to stride length while everything else remains the same. Although the limb is retracted in a fundamentally different way (Reilly & DeLancey, 1997), a similar pattern occurs in the similarly-sized salamander *Dicamptodon tenebrosus* (Ashley-Ross, 1994a). Quantitative analysis of kinematic speed effects in this salamander showed that no angular variables changed and that only one swing phase limb timing variable was significantly different across speeds (time to

minimum pelvic-femur angle during the swing phase). This variable can be subtracted from the duty factor (Ashley-Ross, 1994b: Table I) to show that relative femoral retraction time decreases significantly with speed as well. The observation that femoral retraction increases with speed in the first two sprawling vertebrates to be studied quantitatively, suggests that simply increasing femoral retraction rate may be a general mechanism by which speed is increased at walking speeds. This idea is supported by functional inferences made by Rewcastle (1983) and Snyder (1952). Rewcastle argues that the velocity of limb retraction and hence the velocity of the animal is related to femur length because femur length is proportionately the greatest in species showing the greatest celerity. Snyder (1952) argued convincingly (based on stimulation experiments) that the caudifemoralis muscle is the major retractor of the entire limb through its action in retracting the femur and flexing the knee. Furthermore, he showed that, in six species of lizards, the caudifemoralis muscle (which is relatively large in *Sceloporus clarkii*) comprises up to 36% of the hindlimb muscle mass and up to 56% of the mass of the muscles spanning the hip joint (Snyder, 1954), pointing to a major influence of this muscle and therefore femoral retraction as the primary component producing propulsive force in lizards. Gatesy (1990) has expanded these arguments to make inferences about the evolution of locomotion in theropods; and a similar basis for increasing speed has been shown in the vervet monkey (Vilensky & Gankiewicz, 1990). In addition, Reilly & DeLancey (1997) relate the novel caudifemoralis morphology of lizards to functional differences in limb retraction compared to the amphibians and mammals and hypothesize that these correlated traits may be the functional basis for a fundamental dichotomy in the functional morphology of erect locomotion in mammals vs. saurians.

An additional timing adjustment that appears to be general is that of the onset of limb retraction relative to the timing of foot down. In *Dicamptodon* (Ashley-Ross, 1994a, b), *Sceloporus* (This study; In prep.) and vervet monkeys (Vilensky & Gankiewicz, 1990), the onset of limb retraction begins earlier relative to foot down as speed increases. Thus, the foot hits the substratum after the limb begins to retract, reducing braking impulses and loss of momentum that may occur and speeding up limb retraction.

Ecomorphological implications of hindlimb function in lizards

Mean maximum sprint speed in *Sceloporus clarkii* averages 1.89 m s^{-1} (on racetracks: Miles, 1994) and the average speed over a 2-metre track averages 1.24 m s^{-1} (Miles, unpubl. data). The range of speeds used in this study therefore extends from 21 to 67% of average track speed and 14 to 44% of maximum sprint speed. Thus, this study describes the function of the hindlimb that occurs over a considerable portion of the lizard's locomotory acceleration to average and sprint speeds. That lizards run fast is the keystone of a large foundation of research on the ecological, morphological and physiological bases of locomotor performance (Garland & Losos, 1994). *How* lizards run faster has primarily been the subject of inference. In general, lizards are thought to increase speed by: 1) changing the stride length via changes in the amplitude of standing axial bending waves (Snyder, 1952; Sukhanov, 1974); 2) switching from standing to travelling waves of axial bending (Edwards, 1977; Ritter, 1992); or 3) increasing the force of limb propulsion (Snyder, 1954; Gatesy, 1990). Obviously, our data for *Sceloporus clarkii* support the third hypothesis only, and pinpoint femoral retraction as the primary mechanism to increase speed. However, we have looked at increases in speed over only about the first half of maximal speeds used by these lizards. At higher speeds, lizards may begin to change the amplitude of their standing wave of axial bending or modulate axial bending into a travelling wave starting from the pelvic node. It is also possible that other aspects of the limb propulsion kinematics will change as well. First, the femur may continue to be retracted relatively

faster. This would involve earlier offset times but larger amplitudes of motor activity in the caudifemoralis muscle (simultaneous EMG data for strides used in this study are presently under study to test this hypothesis). Second, lizards could begin to use greater femoral excursions to increase stride length and speed as do birds (Gatesy, 1990). Third, whereas plantar flexion kinematics did not change in our study, any increase in forces produced by this component could easily increase overall propulsive forces at higher speeds. Finally, the limb could be adducted with associated changes in knee and ankle kinetics to create a more erect posture. Only quantitative studies over a wider range of speeds will identify whether axial bending changes as speed is increased further and what aspects of limb movement are changed to propel the lizard up to maximal sprint speed.

A key assumption in lizard ecomorphology is that limb length and its relationship to body length are related to climbing ability, running speed, substratum use, and the use of bipedal locomotion (Sukhanov, 1974; Rewcastle, 1981; Pounds, 1989; Losos & Sinervo, 1989; Sinervo & Losos, 1991; Miles, 1994). The demonstration that femoral retraction alone is the major speed effector over a moderate range of ecologically relevant speeds, lends strong functional support to the ecomorphological implications of limb length (and especially femur length and caudifemoralis size) in locomotory ecology and performance studies in lizards. It also lends support to inferences about the caudifemoralis muscle as a preadaptation to terrestrial locomotion (Peters & Goslow, 1983; Russell & Bauer, 1992) and as a key innovation in the evolution of bipedalism and erect postures (Bakker, 1971; Charig, 1972; Biewener, 1989; Gatesy, 1990). Considerable further study of locomotion in other sprawling vertebrate species is needed to develop a sound functional foundation from which hypotheses and inferences about the evolution of locomotor performance and the evolution of erect and bipedal locomotory postures can be forged and tested. However, based on the few studies to date on sprawling locomotion, it appears that sprawling and erect locomotion may be functionally more similar than has been thought in the past (Gray, 1968; Hildebrand, 1985; Gatesy, 1991).

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Appendix 1

Description of kinematic variables used in the study. Ankle angles are in lateral view and the other angles are in dorsal view. The hip is protracted (low values) and retracted (higher values). The knee is flexed (low values) and extended (higher values). The ankle is flexed (low values) and extended (high values). 'Time-to' timing variables are from time zero (foot down). Excursion durations are the time from the minimum to the maximum of a given angle indicating the timing of the full range of motion of the joint

ADN	Ankle angle at foot down
ADURPS	Power stroke excursion duration of the ankle from its minimum to maximum angle
AEXCPS	Power stroke excursion duration of the ankle from its minimum to maximum angle
AMAXEXT	Minimum ankle angle just prior to foot down
AMAXPS	Maximum ankle angle during the power stroke
AMINPS	Minimum ankle angle during the power stroke
AUP	Ankle angle at foot up
HDN	Hip angle at foot down
HMAXPROT	Hip angle at maximum protraction of the limb
HMAXRET	Hip angle at maximum retraction of the limb
HRETDUR	Excursion duration of the hip from its minimum to maximum angle
HRETEXC	Excursion of the hip from its minimum to maximum angle
HUP	Hip angle at foot up
KDN	Knee angle at foot down
KDURST	Stance phase excursion time of the knee from its minimum to maximum angle
KDURSW	Swing phase excursion duration of the knee from its minimum to maximum angle
KEXCST	Stance phase excursion of the knee from its minimum to maximum angle
KEXCSW	Swing phase excursion of the knee from its minimum to maximum angle
KMAXST	Maximum knee angle during the stance phase
KMAXSW	Maximum knee angle during the swing phase
KMINST	Minimum knee angle during the stance phase
KMINSW	Minimum knee angle during the swing phase
KUP	Knee angle at foot up
PELVMAX	Maximum angle of right pelvic rotation
STANCEDUR	Duration of the stance phase
STRIDEDUR	Duration of the stride
SWINGDUR	Duration of the swing phase
TAMAXEXT	Time to the minimum ankle angle just prior to foot down
TAMAXPS	Time to the maximum ankle angle during the power stroke
TAMINPS	Time to the minimum ankle angle during the power stroke
THMAXPROT	Time to the hip angle at maximum protraction of the limb
THMAXRET	Time to the hip angle at maximum retraction of the limb
TKMAXST	Time to the maximum knee angle during the stance phase
TKMAXSW	Time to the maximum knee angle during the swing phase
TKMINST	Time to the minimum knee angle during the stance phase
TKMINSW	Time to the minimum knee angle during the swing phase
TPELVMAX	Time to the maximum angle of right pelvic rotation
