

SPRAWLING LOCOMOTION IN THE LIZARD *SCELOPORUS CLARKII*: QUANTITATIVE KINEMATICS OF A WALKING TROT

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Accepted 21 November 1996

Summary

Although the hindlimb is widely considered to provide the propulsive force in lizard locomotion, no study to date has investigated the kinematic patterns of the lizard hindlimb during running for more than one stride for a single individual. The quantitative kinematics of the hindlimb, pelvis and backbone are described here for two individuals of the lizard *Sceloporus clarkii* using a fast walking trot on a treadmill moving at a constant speed of 0.833 m s^{-1} . Pelvic rotation, femoral retraction, knee flexion and posterior movement of the foot all begin before the foot hits the substratum and, thus, there is a terminal portion of the swing phase during which the limb is retracting. Pelvic rotation (to the opposite side), femoral protraction and knee flexion all begin before the foot leaves the substratum. The foot, however, continues to move posteriorly into the early swing phase. Thus, limb retraction and protraction movements do not directly correlate with footfall phases. Axial bending involves a

rough standing wave with two nodes, one centered on each limb girdle. In *Sceloporus clarkii*, the foot clearly remains lateral to the knee and, thus, has a more sprawling posture than that of any other vertebrate studied to date. Therefore, the generalization that the 'lacertilian' foot passes under the knee joint is no longer supported. The kinematics of sprawling locomotion in *Sceloporus clarkii* are compared and contrasted with the general understanding of lizard locomotion based on qualitative work to date. Comparisons with other tetrapods reveal a fundamental functional dichotomy in hindlimb retraction mechanics in salamanders and mammals *versus* lizards that may be related to a key morphological difference in the saurian caudifemoralis muscle.

Key words: *Sceloporus clarkii*, kinematics, caudifemoralis, Sauria, sprawling locomotion, functional morphology, lizard.

Introduction

The evolution of terrestrial locomotion is generally understood as a transition from a sprawling posture with the limbs sweeping laterally to the body, as in salamanders and lizards, to an erect posture with the limbs sweeping underneath the body, as seen in mammals and archosaurs (Gregory, 1912; Gray, 1968; Bakker, 1971; Charig, 1972; Rewcastle, 1981). Although inferences about this transition are often made (Bakker, 1971; Dodson, 1974; Parrish, 1987; Rewcastle, 1981; Peters and Goslow, 1983; Gatesy, 1991) and no aspect of terrestrial locomotion has seen more functional study than erect locomotion (Hildebrand, 1976, 1985, 1989), surprisingly limited functional data are available on tetrapods using sprawling locomotion. The only quantitative kinematic studies of sprawling locomotion to date are for the salamander *Dicamptodon tenebrosus* (Ashley-Ross, 1994a,b, 1995), in which the kinematics and motor patterns of a walking trot have been described in detail and provide a good general picture of sprawling locomotion in an amphibian. Kinematic data for other sprawling tetrapods are scarce. Most studies of limb movements in lizards and crocodylians have focused primarily

on stride and gait characteristics (Snyder, 1952; Urban, 1965; Daan and Belterman, 1969; Sukhanov, 1974; Rewcastle, 1981, 1983; Brinkman, 1981; Peterson, 1984; Avery *et al.* 1987; White and 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; Gatesy, 1991; Bels *et al.* 1992; Reilly, 1995). From these studies, a basic understanding of sprawling gaits and a gross description of limb movements have emerged, but they are based largely on anecdotal and qualitative descriptions of single strides of animals running past a stationary camera. To date, the only study presenting kinematic data for limb movements in sprawling reptiles is Gatesy's (1991) analysis of hindlimb and pelvic kinematics for three consecutive strides of the 'high walk' of an alligator, which he concludes is a semi-erect posture. Thus, although the hindlimb is widely considered to provide the propulsive force in sprawling locomotion (Snyder, 1952; Gray, 1968;

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Sukhanov, 1974) and comparative data on sprawling kinematics are necessary for convincing inferences about the evolution of erect postures, no study to date has quantified limb movements in a true sprawling reptile. This study provides the first quantitative kinematic analysis of sprawling locomotion in a reptile. Movements of the hindlimb, pelvis and vertebral column are described for the lizard *Sceloporus clarkii* using a trot on a treadmill moving at constant speed. The results are compared and contrasted with the general understanding of lizard locomotion based on qualitative work to date. The kinematics of sprawling locomotion in lizards are contrasted with that of salamanders and used to examine fundamental differences in the functional morphology of hindlimb locomotion among tetrapods.

Materials and methods

Kinematic recordings were obtained from *Sceloporus clarkii* (Girard) collected in Molino Basin, Santa Catalina Mountains, 10 miles north of Tucson, Arizona. Kinematic data for two lizards locomoting at 0.833 m s^{-1} were analyzed to describe limb and axial movements during locomotion. *Sceloporus clarkii* was used because it is believed to use generalized sprawling (Sukhanov, 1974) and because this species is morphologically generalized, possessing the primitive morphology for the family Phrynosomatidae (Miles, 1994). Detailed descriptions of the hindlimb motor patterns at the same speed are presented in Reilly (1995).

Kinematic analysis

The lizards were filmed under stroboscopic lights at $200 \text{ fields s}^{-1}$ 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 running lizards were filmed (using mirrors) on a 70 cm long canvas treadmill against 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 room temperature and body temperature of the lizards during running was $27\text{--}30^\circ\text{C}$. Reflective landmarks were painted on the lizards to mark the vertebral column and the pelvis, acetabulum, knee, ankle and the 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 (posterior midline of skull) and the pectoral girdle (midline between the arms). Four 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 0.833 m s^{-1} (3 km h^{-1}) and a total of 10 strides of the right leg during which the lizards ran parallel to the treadmill and matched the treadmill speed were used in the analysis. Five strides from each of two individuals

(snout–vent lengths 91 and 92 mm) were digitized. The kinematics of the two individuals were very similar and, therefore, data for individual 1 were used to produce mean kinematic profiles and to describe the kinematics of hindlimb movement. Individual 1 was chosen because the five strides analyzed for this study were from the nine strides used to describe motor patterns in Reilly (1995) and, thus, direct comparisons of kinematics and motor patterns can be made. For each video field for each stride, the coordinates of each landmark were digitized using Measurement TV (Updegraff, 1990). The coordinate data were then used to calculate two-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 the crus (in lateral view) through the stride as illustrated in Fig. 1. Because the limb



Fig. 1. Kinematic landmarks and angles used to describe limb movements in *Sceloporus clarkii*. The landmarks are as follows: (L) lumbar dot, over the penultimate trunk vertebra (dorsal to the pubic symphysis); (P) 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 fourth 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 (not shown) are described in the text.

moves almost entirely in the horizontal plane (Snyder, 1954; see displacement loop data in Results) and the crus never passes under the knee, two-dimensional angles were used to provide an accurate measure of the minima and maxima and excursions of joint movements during locomotion.

To illustrate limb kinematic patterns, mean kinematic profiles were generated by plotting the mean angles (\pm S.E.M.) for each video field for one individual ($N=5$). Strides were aligned by treating the time of right-foot placement (foot down) as time zero. 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 describe the gait, the timing of footfalls was measured for each foot for each stride (for a complete cycle for each of the four feet), and an overall mean gait diagram for one individual was plotted using mean footfall values for five strides.

Kinematic variables

Limb and pelvic movements

To assess hindlimb kinematics quantitatively, a series of angular and timing variables was obtained from each stride to describe the pelvic and limb movements (Table 1). The variables were chosen to capture the angles and timing of minimum and maximum positions of the pelvis (P) and each of the three 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 limb 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 three 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' (PROT) and 'retraction' (RET) when the foot is being moved anteriorly and posteriorly, respectively (these are sometimes termed recovery and transport phases, respectively). Because protraction and retraction of the limb did not consistently correspond to the stance and swing phases (maximum protraction occurred at a mean of 6 ms before foot down: compare THMAXPROT with STRIDEDUR values in Table 2), we also measured the angle of the hip at maximum limb protraction, the angle of the hip at maximum limb retraction and the angle of excursion (EXC) of the hip during retraction of the limb. The knee is flexed to a minimum (MIN) and then extended to a maximum (MAX) during both the stance and swing phases; therefore, angles were measured to quantify the minimum, maximum and excursion of the knee joint during both phases. The ankle is maximally extended (EXT) just prior to foot down, and this angle was measured. The ankle is then flexed to a minimum during the stance phase and finally extended to a maximum just after foot up, and the period from minimum to maximum ankle angle delineates the power stroke (PS) of the retraction phase. Thus, we measured the minimum, maximum and excursion of the ankle angle during the power stroke. The final angular variable measured

is the maximum angle of rotation of the pelvis relative to the direction of travel (PELVMAX).

Timing variables were measured to describe aspects of the stride and the timing of joint movements. The durations (DUR) of the stance phase, the swing phase and the entire stride were measured (STANCEDUR, SWINGDUR and STRIDEDUR, respectively). The rest of the timing variables are either the times (T) to various joint angles (from time 0 at right foot down) or the durations (DUR) of the angular excursions described above. These are as follows: the time to hip maximum retraction and protraction, and hip retraction duration; the time to minimum and maximum knee positions during the stance and swing phases, and their durations; the time of maximal angle extension prior to foot down and the time to the minimum and maximum ankle angle during the power stroke, and this excursion duration; and the time to the maximum pelvic rotation (TPELVMAX). For reference, detailed descriptions of each variable are presented in Table 1.

The knee displacement loops (from coordinate data) were examined and their lateral widths (in dorsal view) and vertical depths (in lateral view) were measured to determine the amount of adduction of the limb during the stride. Displacement loops circumscribe the movements of the landmark in one plane for a single stride. For example, in dorsal view, a narrow displacement loop when adjusted for the lateral movements of the pelvis 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 during the swing phase, indicating the amount of adduction of the limb.

Axial bending

Axial kinematics were quantified using eight variables describing the maximum amplitudes and longitudinal positions of landmarks along the vertebral column. Because consistent rough standing waves with two nodes were found, 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 measured, and the positions of these nodes relative to the vertebral landmarks were also measured.

Results

Stride and gait characteristics

Representative video frames portraying a single stride of the right hindlimb are shown in Fig. 2, and stride timing data are presented in Table 2. At 0.833 m s^{-1} , *Sceloporus clarkii* moves using coordinated footfalls of diagonal limb couplets. For the two individuals ($N=10$ strides), the stride duration time (foot down to foot down) of the right limb averaged 171.5 ms. The stance phase duration (transport phase, time from foot down to

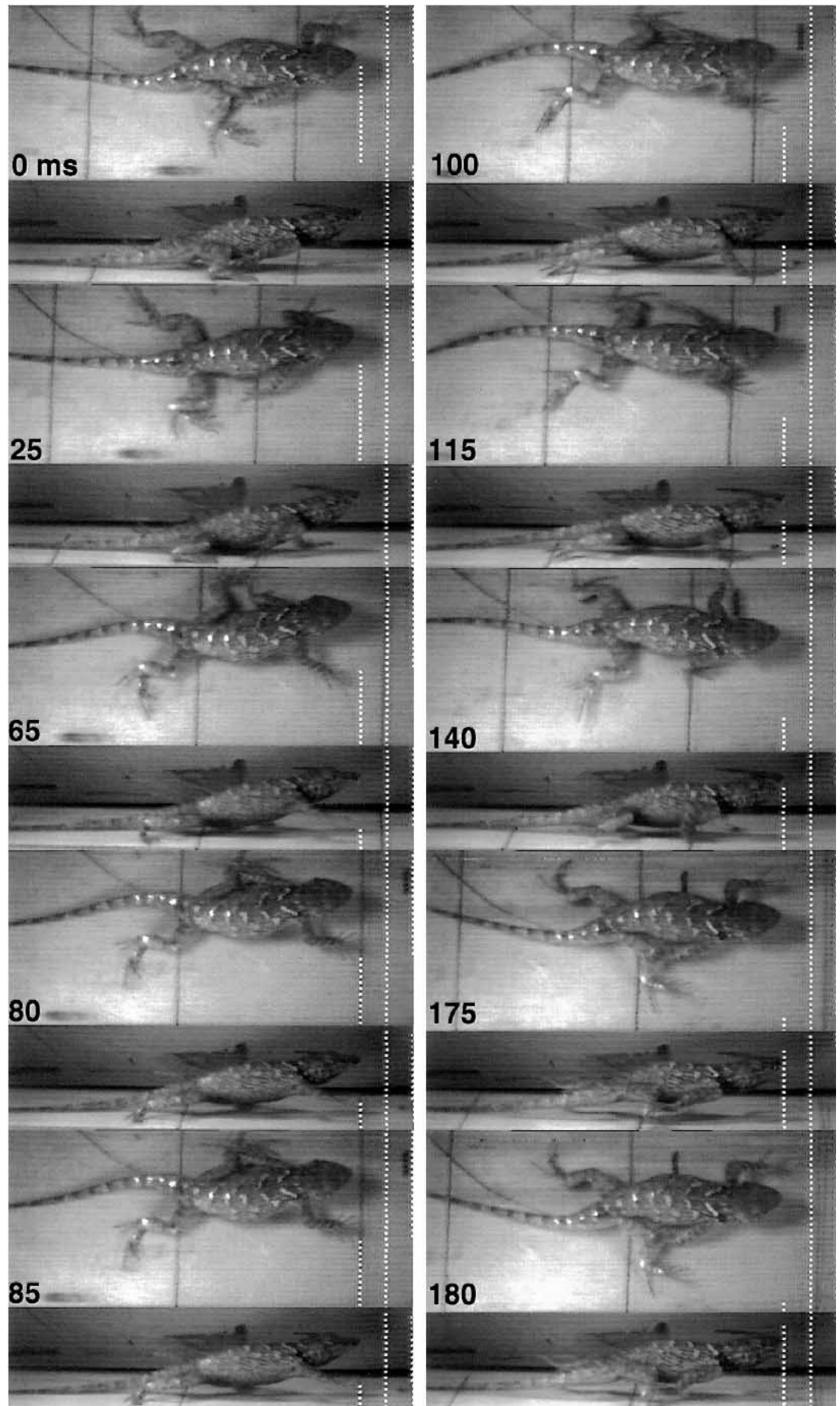


Fig. 2. Images from high-speed video illustrating one stride of *Sceloporus clarkii* moving at 0.833 m s^{-1} using a fast walking trot. Each frame consists of a dorsal view (upper half) and a lateral view (lower half) of the moving lizard. Time is indicated on each frame in milliseconds. Time 0 is the initial foot down, foot up is at 100 ms, and the following foot down is at 180 ms. Note that the crus and foot do not rotate under the knee and that the limb remains well extended throughout the stride.

foot up) averaged 95 ms and the swing (or recovery) phase duration averaged 76.5 ms. The mean percentage of the stride that the right foot is in contact with the substratum (duty factor) averaged 55.4%, and the right forefoot follows the right hindfoot at an average of 51% of stride duration. Thus, based on mean data for the right hindlimb, the gait is categorized as a fast walking trot according to the terminology of Hildebrand (1976).

Limb and pelvic kinematics

Mean kinematic profiles for the angular movements of the

hindlimb joints and pelvic rotation are presented in Fig. 3. Mean values for timing and angular variables are presented in Tables 2 and 3. Using the mean kinematic profiles and mean angular and timing data, a quantitative description of the hindlimb kinematics can be made relative to the overall limb movements and footfall patterns. To visualize the relationship between limb kinematics and general limb movements better, we describe an average stride and illustrate this with stick figures describing key movements of the limb correlated with a bar diagram showing key features of the gross movements of the limb during locomotion (Fig. 4).

Table 1. *Description of the kinematic variables used in this study*

ADN	Ankle angle at foot down
ADURPS	Power stroke excursion duration of the ankle from its minimum to maximum angle
AEXCPS	Power stroke excursion 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 duration 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

Ankle angles are measured from the lateral view and the other angles from the 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 value of a given angle, indicating the timing of the full range of motion of the joint.

See text for further explanation.

The limb remains well extended throughout the stride such that the crus and foot remain extended laterally to the knee joint in dorsal view and are never obscured by the proximal portion of the limb (Fig. 2). Representative dorsal and lateral displacement loops are presented in Fig. 5. In dorsal view, displacement loops for the knee formed approximately crescent-shaped loops (mean loop width 15.9 ± 3.3 mm, mean \pm S.D.) that, when adjusted for the lateral amplitude of pelvic movements (mean 9.7 ± 1.7 mm), indicate an approximately 6 mm lateral loop width. In lateral view, knee displacement loops form nearly overlapping anteroposterior lines (mean loop depth 10.1 ± 2.2 mm). Thus, on the basis of the small extent of knee excursion in both views, *Sceloporus clarkii* has a sprawling movement of the femur with little or no adduction during the stance phase relative to the swing phase. Stance and swing phases are by definition determined by the footfall times (Fig. 4, left-hand bar diagram). Overall limb retraction and

protraction are defined by the direction of movement of the foot and especially by the tips of the toes (Fig. 4, center bar diagram). Posterior movement of the toes indicates limb retraction and anterior movement of the toes indicates limb protraction. The limb retraction phase (Fig. 4, right-hand bar diagram) may be broken down further as described below.

The kinematic data reveal that the maximal anterior rotation (protraction) of the entire right limb based on the direction of movement of the toes occurs just prior to foot down. The times to the maximal pelvic rotation to the left (at 175 ms, Fig. 3), maximal hip protraction (at 174 ms), maximal knee extension (at 176 ms) and maximal ankle extension (at 163 ms) all occur just prior to the time of foot down (at 180 ms, Table 2). Thus, retraction of the limb as a whole, retraction of the femur and flexion of the knee and ankle all begin prior to foot down. Therefore, the foot hits the substratum while moving posteriorly, and the onset of limb retraction does not exactly

Fig. 3. Mean profiles for right hindlimb joint kinematics (in degrees versus time in ms) and footfall patterns (bottom plot) in *Sceloporus clarkii* using a fast walking trot at 0.833 m s^{-1} . Angular means \pm S.E.M. are shown for five strides from one individual. The x-axis indicates time in ms from right foot down (time 0). The ankle angle is measured in lateral view and data are omitted during the time that the limb is swung towards the camera during the swing phase. The other angles are in dorsal view. The pelvic angle swings from the right (positive values) to the left (negative 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 first and second vertical lines on each plot indicate the mean time of the end of the stance phase (foot up) and the end of the swing phase (foot down) respectively. Footfall patterns (scaled to stride duration) are presented in the bottom plot with lines indicating stance phases for all four feet based on mean footfall and foot up times for five strides from one individual.

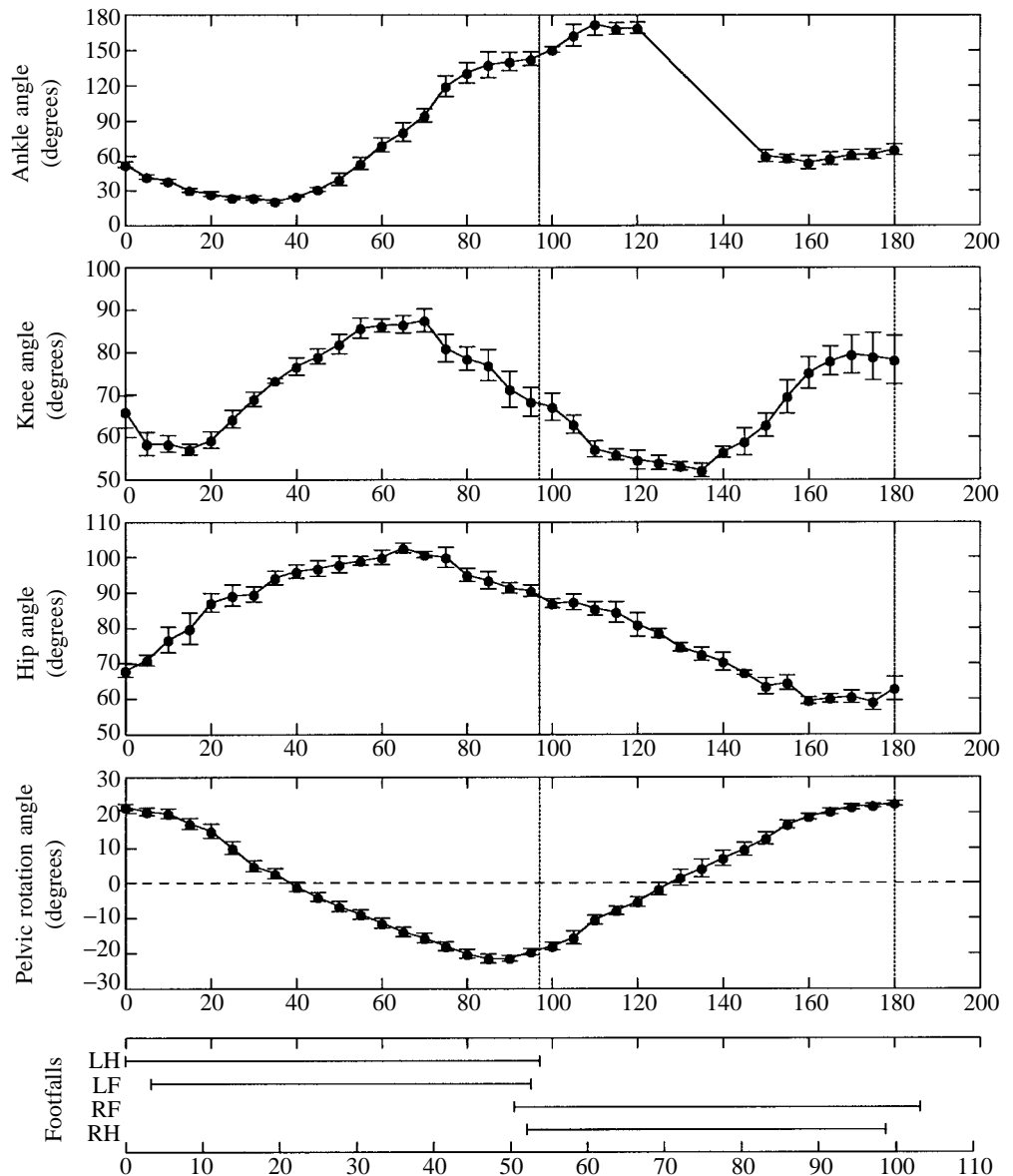


Table 2. Kinematic timing data for two *Sceloporus clarkii* running at 0.833 m s^{-1}

Variable	Time (in ms)	
	Individual 1	Individual 2
SWINGDUR	83±5 (0.46)	70±2 (0.43)
STANCEDUR	97±3 (0.54)	93±4 (0.57)
STRIDEDUR	180±4 (1.00)	163±5 (1.00)
THMAXPROT	174±5 (0.97)	146±4 (0.90)
THMAXRET	66±6 (0.37)	58±6 (0.36)
HRETDUR	72±6 (0.40)	75±6 (0.46)
TKMINST	19±2 (0.11)	24±3 (0.15)
TKMAXST	71±5 (0.39)	81±4 (0.50)
KDURST	52±4 (0.29)	57±5 (0.35)
TKMINSW	139±4 (0.77)	112±6 (0.69)
TKMAXSW	176±4 (0.98)	155±4 (0.95)
KDURSW	37±3 (0.21)	43±5 (0.26)
TAMINPS	36±3 (0.20)	26±4 (0.16)
TAMAXPS	117±4 (0.57)	98±4 (0.60)
ADURPS	67±3 (0.37)	72±6 (0.44)
TAMAXEXT	163±5 (0.91)	147±4 (0.90)
TPELVMAX	85±5 (0.46)	78±5 (0.48)

Means ± S.E.M. are presented for five strides from each individual with mean values scaled to the stride duration in parentheses.

Variables are defined in Table 1.

coincide with the onset of the stance phase (Fig. 4). Because the limb is actually beginning to retract at the end of the swing phase, we term the period of limb retraction prior to foot down the terminal swing retraction phase (TSR, Fig. 4). Which component of the limb is moving posteriorly during retraction prior to foot down is indicated by the differences in the joint angles at their maximal forward positions and their angles at foot down (Table 3). The ankle and knee angles did not change, whereas the hip angle decreased by 5° , indicating that the terminal swing retraction of the limb is produced by retraction of the femur alone. The foot hits the ground either heel first ($N=4$) or as a unit (plantigrade, $N=6$). When the foot hits the ground (Fig. 2, 0 ms), the fifth toe points laterally and the other four toes point anteriorly, with the direction of movement centered approximately on the third toe; the line through the tips of toes 1–4 is at approximately 45° to the right of the direction of travel.

Retraction of the limb involves pelvic rotation, rapid retraction of the femur and flexion followed by extension of the knee and ankle joints (Fig. 3). During retraction, the pelvis rotates from 21° to the left just before foot down to 21° to the right 85 ms after foot down. The femur is retracted through an arc of 47° in 72 ms, reaching its maximum retraction 66 ms after foot down. The knee is flexed by 27° in 23 ms, reaching its maximum flexion 19 ms after foot down. The knee then extends by 35° in 52 ms to reach its maximal extension 71 ms after foot down. The ankle (in lateral view) flexes by 36° in 53 ms to reach its minimum flexion 36 ms after foot down. The ankle then extends by 125° in 61 ms, at which time the toes leave the substratum, and then continues to extend by another

43° in 20 ms to reach its maximum flexion of 189° at 117 ms after foot down (which is 20 ms after foot up). Following mammalian terminology (Craig and Oatis, 1995), we term the period from foot down to minimum ankle angle the preparatory phase and the period from minimum ankle angle to its maximal extension the propulsive phase. Therefore, the overall limb retraction phase (Fig. 4, right-hand bar diagram) is composed of the terminal swing retraction phase (5 ms), the preparatory phase (36 ms) and the propulsive phase (117 ms). In terms of the stance phase, the pelvis is maximally rotated to the right at 88 % of the stance phase, the femur is maximally retracted at 68 % of the stance phase and the knee is maximally extended at 73 % of the stance phase; thus, the pelvis begins to rotate to the left, the femur begins to protract and the knee begins to flex well before the foot leaves the ground and plantar flexion of the foot is completed. The ankle, in contrast, is extended for the latter two-thirds of the stance phase and continues to extend for 20 ms after foot up. Thus, although the pelvis, femur and knee begin to pull the ankle forward, subsequent extension of the ankle joint causes the flexion of the foot (and thus posterior movement of the toes) to continue well into the swing phase, such that overall retraction of the limb continues for 24 % of the swing phase. As the foot is retracted, the entire force of the limb propulsion is conveyed to the claws of toes 1–4, which are still aligned at 45° to the right of the direction of travel (Fig. 2, compare 0 ms with 25 ms). As plantar flexion proceeds, the lizard rolls

Table 3. Mean hindlimb movement data for angles describing the positions of and excursions of limb joints for two *Sceloporus clarkii* using a walking trot at 0.833 m s^{-1}

Variable	Angle (degrees)	
	Individual 1	Individual 2
HDN	63±3	47±3
HUP	91±2	89±2
HMAXPROT	58±1	43±2
HMAXRET	105±1	76±4
HRETEXC	47±2	32±6
KDN	82±2	80±4
KUP	73±5	83±3
KMINST	56±2	65±4
KMAXST	91±2	97±1
KEXCST	35±4	31±4
KMINSW	50±1	58±6
KMAXSW	83±4	85±7
KEXCSW	32±4	27±7
ADN	58±4	67±7
AUP	146±7	142±8
AMINPS	21±2	42±4
AMAXPS	149±5	156±6
AEXCPS	127±4	114±3
AMAXEXT	57±2	79±12
PELVMAX	21±2	19±2

Values are means ± S.E.M., $N=5$.

Variables are defined in Table 1.

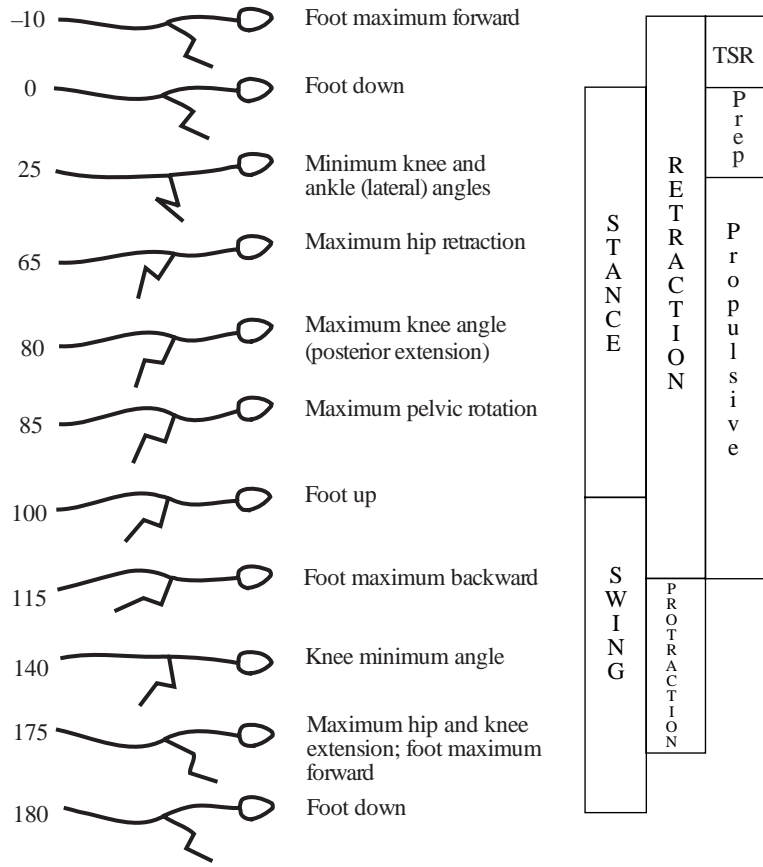


Fig. 4. Relationship between limb kinematics and basic features of the stride. Stick figures on the left are traced directly from high-speed video images of dorsal views, with landmarks indicating the positions of the axial column and limb segments for the key points during the stride that are described in the center. Time is indicated in milliseconds. Basic components of the stride are indicated on the right, with columns for the footfall patterns (left: stance=foot down, swing=foot up), overall direction of limb movement (center) based on the direction of movement of the foot (retraction=posterior movement, protraction=anterior movement), and the subunits of the retraction phase (right). The limb retraction phase is broken down into the terminal swing retraction phase (TSR, foot retraction before foot down), the preparatory phase (Prep, from foot down to minimum ankle angle) and the propulsive phase (from minimum ankle angle to the onset of limb protraction). Note that the stance and swing phases do not directly correlate with limb retraction and protraction phases.

anteromedially off the tips of the medial three toes and moves in a direction approximately 50° to the left of the direction of travel towards the footfall position of the opposite forelimb (compare the position of the lizard with that of the black smudge on the treadmill at 0–85 ms in Fig. 2).

Anterior movements of the limb components parallel posterior movements in that there are uniphasic motions of the pelvis and hip joint, but biphasic motions of the knee and ankle joints. The pelvis begins to rotate to the left 5 ms prior to foot up, rotates through 42° and reaches its maximal rotation to the left just prior to foot down. The hip is protracted to its minimum angle of 58° in 108 ms. The knee flexes by 41° in 68 ms and is then extended by 33° in 37 ms. After the toes leave the substratum, the ankle quickly rotates the foot, so that the dorsal side faces up again, and within 30 ms the ankle flexes to 57°. The ankle remains at approximately this angle for the rest of the protraction phase.

Axial bending patterns

Patterns of axial bending are illustrated in Fig. 6. *Sceloporus clarkii* moving at 0.833 ms⁻¹ exhibits a rough standing wave with nodes appearing at the pectoral and pelvic girdles. Amplitudes at the pectoral and pelvic nodes averaged 5.5±2.2 and 9.7±1.7 mm (mean ± s.d.), respectively. Amplitudes at the snout (11±2.6 mm) and trunk region (13.4±2.2 mm) are similar, but caudal amplitudes are greater (24.2±5.8 mm).

Discussion

Sprawling locomotion in lizards

Gait data for a variety of lizards show that lizards use a lateral sequence walk at very low speeds, a trot at medium-to-fast speeds and a diagonal sequence run at very high speeds, but that the predominant gait by far is the trot (Sukhanov, 1974;

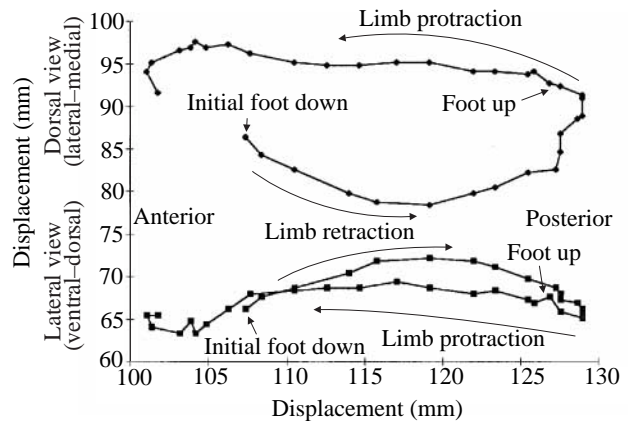
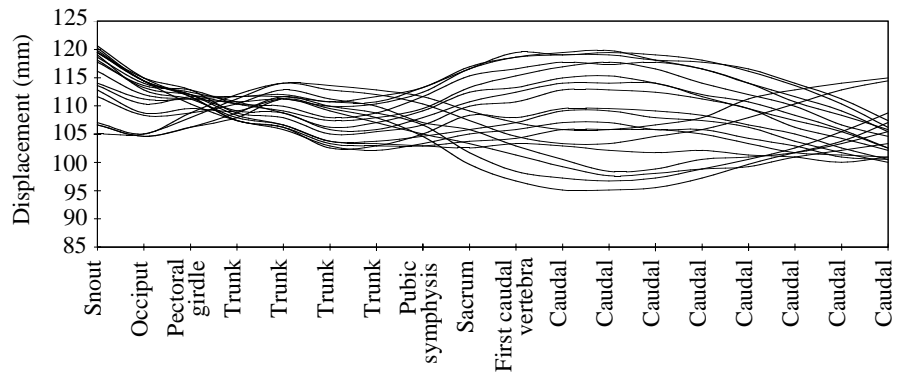


Fig. 5. Typical displacement loops for dorsal and lateral movements of the knee landmark in *Sceloporus clarkii* (individual 1) moving at 0.833 ms⁻¹. Axes are in millimeters and points were digitized from lateral and dorsal views on video frames for one stride. The points reflect movements of the knee because the body remains essentially stationary while the lizard matches the treadmill speed.

Fig. 6. Axial bending patterns for one individual stride of *Sceloporus clarkii* using a walking trot at 0.833 m s^{-1} . Stick figures (lines through the axial landmarks) for every other frame during the stride are superimposed to illustrate the shape of axial bending waves. y -axis values are y values (in mm) from coordinates digitized from the axial landmarks indicated on the x -axis. Note the rough double-node standing wave with nodes on the appendicular girdles.



Hildebrand, 1976; White and Anderson, 1994). At 0.833 m s^{-1} , *Sceloporus clarkii* used a fast walking trot and, therefore, this study describes quantitatively the most common gait used by lizards. In addition, mean maximum sprint speed in *Sceloporus clarkii* averages 1.89 m s^{-1} (on racetracks, Miles, 1994) and the speed over a 2 m track averages 1.24 m s^{-1} (D. B. Miles, unpublished data). Therefore, the locomotor kinematics at 0.833 m s^{-1} describe movements of the hindlimb at an ecologically relevant speed of approximately 67% of average track speed and 44% of maximum sprint speed.

Quantitative kinematics for *Sceloporus clarkii* reveal several novel observations about the hindlimb cycle in lizards. First, there is a lack of direct correlation of limb retraction/protraction movements with the footfall phases (Fig. 4). Previous studies of lizard locomotion, perhaps owing to slower filming rates and the use of data only for single strides, have not noted that the foot begins to move posteriorly prior to impact and that it continues posteriorly after the end of the stance phase. Thus, the stance phase occurs during a portion of the retraction phase. In addition, the limb protraction phase is only a subset of the swing phase, and the end of the swing phase involves the onset of retraction, so that there is a terminal swing retraction phase (TSR). Data for *Sceloporus clarkii* running at lower speeds (Reilly and DeLancey, 1997) show that, when scaled to stride duration, the duration of the TSR tends to decrease at slower speeds and often coincides with foot down and the beginning of the stance phase. Angular data (Table 3) reveal that the TSR is produced by retraction of the femur alone because the ankle and knee angles do not change from maximal limb protraction to foot down.

The second novel observation is that axial bending involves a rough standing wave with two nodes, one centered on each limb girdle. Standing waves have been shown to occur in several lizards (Daan and Belterman, 1968; Peterson, 1984; Ritter, 1992), but these studies used only trunk and girdle landmarks and thus were unable to visualize fully the nodes near the girdles. Axial plots presented by Ritter (1992) clearly show an axial node on the pectoral girdle with lines converging towards the pelvic girdle, indicating a second node just posterior to his pelvic landmarks in several species. Axial bending patterns in *Sceloporus clarkii* verify that a double-node standing wave, albeit approximate, is used in lizards trotting at a constant speed.

Finally, limb kinematics in *Sceloporus clarkii* illustrate the truly sprawling nature of hindlimb locomotion in this species. At 0.833 m s^{-1} (and at speeds down to 0.270 m s^{-1} , Reilly and DeLancey, 1997), the limb is swept forwards and backwards in a more or less extended fashion with the crus and foot remaining extended laterally from the knee joint so that the knee never obscures the distal segments of the limb in dorsal view. Furthermore, the knee displacement loops were narrow, indicating little or no adduction of the femur during the stride. This species is therefore a good model for completely sprawling locomotion because it has the most sprawling limb posture shown to date, but is in contrast to the other species of lizards for which there are data available. On the basis of knee and ankle joint anatomy and oblique lateral views of one *Crotophytus collaris* stride in Snyder (1952), Rewcastle (1983) described the lacertilian foot as passing medial to the knee as it moves past the femur during the propulsive phase. In addition, line drawings of *Teratoscincus scincus* (Sukhanov, 1974) and *Iguana iguana* (Brinkman, 1980) clearly show the foot passing under the knee during limb retraction. However, the foot clearly remains lateral to the knee in *Sceloporus clarkii* (Fig. 2), *S. undulatus*, *S. magister* and *S. occidentalis* (Reilly and DeLancey, 1997) and, thus, *Sceloporus* spp. have a more sprawling posture than the more erect postures observed in other lizards. Therefore, the generalization (Rewcastle, 1983) that the 'lacertilian' foot passes under the knee joint is no longer supported.

Although a general 'understanding' of the basic hindlimb cycle is evident in the literature, it is derived from the gross descriptions of Snyder (1952, 1954), Sukhanov (1974) and Brinkman (1980). Unfortunately, no kinematic data were provided in these studies. Snyder (1952) presents one figure of seven frames from an oblique view of *Crotophytus collaris* 'running' at an unknown speed with no timing information. Sukhanov (1974) subsequently showed that Snyder's (1952) description of the locomotory cycle was confused by mixing gaits. Therefore, it is difficult to evaluate Snyder's (1952) descriptions of limb movements and, because *Crotophytus collaris* is a bipedal lizard, extrapolations to generalized sprawling quadrupeds may be inappropriate. More recently, Rewcastle (1980, 1983) combined elegant anatomical studies of the biomechanics of lizard limb joints to make numerous

inferences about sprawling hindlimb locomotion, but they are again based on Snyder's (1952) limb cycle. Sukhanov's (1974) study of lizard gaits presents several frame-by-frame line drawings of lateral and oblique views of *Eremius velox* and *Teratoscincus scincus* using a fast walking trot at unknown speeds that vary within strides. The only other limb kinematic information published for lizards running is line drawings of the hindlimb bones from seven X-ray frames of an iguana, *Iguana iguana*, moving at 0.35 m s^{-1} (Brinkman, 1980). To date, no angular or timing data on hindlimb kinematics have been published for a lizard running at a constant speed. Thus, our study provides the first quantitative kinematic data with which to test the conclusions of Snyder (1954) and Rewcastle (1980, 1983). As mentioned above, however, *Sceloporus clarkii* uses a more sprawling posture than the other lizards studied to date and, thus, this species may differ in the kinematic details of the limb movements. Nonetheless, given that the present understanding of the lizard limb cycle is presented as a generalization to sprawling locomotion in lacertilians, it is necessary to contrast our quantitative results with specific points made in the literature.

The hindlimb kinematics of *Sceloporus clarkii* differ from Snyder's (1952, 1954) descriptions of the limb cycle in several aspects. First, the foot does not always strike the ground plantigrade. We found that four of ten strides landed heel first. Second, the limb does not progressively flex as it is drawn back. *Sceloporus clarkii* exhibits a period of stasis (approximately 15 ms, Fig. 3) in the knee joint in the middle of the stance phase where the knee maintains approximately 90° . Third, the leg does not 'form nearly a straight line' (Snyder, 1952) at the termination of the propulsive phase. In fact, the leg was far from being completely extended, and the pelvis, femur and knee were already being moved anteriorly. Fourth, the retraction phase does not begin when the foot leaves the ground and it is not coincident with the onset of flexion of the thigh and knee. In a different statement, however, Snyder (1952) was correct in stating that the thigh and crus are flexing as the limb leaves the ground at the end of the stance phase, but he did not mention the continued posterior movement of the foot after it leaves the ground. Finally, the limb did not swing forward in a highly abducted 'overhand' fashion; rather, both the knee and foot follow a relatively horizontal trajectory during the swing phase.

Several of Rewcastle's (1980, 1983) interpretations of Snyder's (1952) work were also in contrast to our observations. First, the limb is not 'fully extended' before it hits the substratum, which Rewcastle (1980) inferred from Snyder's (1952) oblique lateral view of *Crotophytus collaris*. Thus, extension of the limb in both the propulsive phase and the swing phase is not as great as previously reported. Second, Rewcastle (1980) and Sukhanov (1974) state that, during limb retraction, the crus flexes on the femur before any femoral retraction occurs, in contrast to *Sceloporus clarkii* where retraction of the femur begins slightly before flexion of the knee and continues throughout knee flexion. Finally, the patterns of foot placement and plantar flexion during the power

stroke in *Sceloporus clarkii* do not fit the model for foot function proposed by Rewcastle (1983) for the lacertilian limb. He states that the 'pes is placed on the substrate with the digits directed anterolaterally' (at approximately 50° lateral to the axis of movement), which is contrary to *Sceloporus clarkii* where the first four toes straddle the axis of movement and the fifth toe projects laterally. Furthermore, Rewcastle (1983) proposes an elaborate model for plantar flexion of the foot, metatarsalia and toes as the foot rolls off the substratum during the power stroke. He states that the more lateral and medial toes leave the ground and the propulsive force of the limb is borne by the mesial digits and, thus, a posteriorly directed force is produced during locomotion. This may occur with more erect-postured lizards or with bipedal lizards, but is simply not the case for *Sceloporus clarkii* running in a quadrupedal trot, where the foot rolls off the mesial three digits as the lizard moves away in an anteromedial direction. The amplitude of the pelvic node indicates that the pelvis moves laterally by approximately 1 cm during the stride, reflecting the degree of medial movement during the propulsive stroke. A similar pattern is seen in *Iguana iguana* (Brinkman, 1980), where the lizard rolls anteromedially off the inner three toes, and both Snyder (1952) and Schaeffer (1941) describe the direction of foot thrust as moving progressively backwards and sideways through the propulsive stroke in *Sceloporus undulatus*, *Cnemidophorus tessellatus* and *Anolis anolis*.

Components of propulsive movement

Previous descriptions of the limb cycle have differed regarding speculations on which components of the limb generate the primary propulsive movement in lizards. Some consider the proximal elements (Hildebrand, 1985; Snyder, 1952; Sukhanov, 1974) as more important in generating propulsive force than the distal elements (Rewcastle, 1981, 1983). Few (Gray, 1968; Edwards, 1977; Ritter, 1992) consider axial bending as a contributing factor. Considering that there have been no quantitative kinematics, motor pattern data (except Reilly, 1995) or force-plate data to identify the propulsive components, our understanding is limited, but some basic inferences can be made from movement patterns. Obviously, axial bending, femoral retraction, knee flexion and extension, and plantar flexion of the foot have important synergistic contributions to force generation during the limb cycle. But which components contribute the most? On the basis of the kinematic data presented here, it appears that coordinated axial bending, femoral retraction and plantar flexion of the foot produce thrust during running. Limb retraction *via* simultaneous axial bending and retraction of the femur with some flexion, then extension, of the knee dominate the first two-thirds of the retraction phase. Bending of the axial skeleton in the region of the pelvis contributes to both limb retraction on one side of the body and limb extension on the other side, and a standing wave with nodes on the girdles ensures that this is true for both fore- and hindlimbs. Axial bending is critical to swinging the limbs on both sides, and it also contributes 20° of pelvic rotation to the overall

movement of the femur in each direction. Extension of the crus appears to be marginally important in generating propulsion because it occurs for only a small portion of the power stroke and involves only a limited extension of the limb.

Several lines of evidence show that a combination of early femoral retraction followed by plantar flexion of the foot may generate most of the propulsive force. Several of the muscles of the hindlimb have been shown to be dedicated specifically to those tasks, and others assist them (Reilly, 1995). Femoral retraction begins before foot down and reaches its maximum retraction in 72 ms; thus, the femoral contribution to propulsion ends at 68% of the stance phase. Extension of the ankle begins at 36 ms (20% of stance phase) and continues until foot up. Retraction of the femur before foot down would reduce braking impulses and the loss of momentum associated with the impact of the foot. Further retraction then rotates the limb to a position where ankle extension begins to contribute to propulsion. Therefore, femoral retraction dominates the first two-thirds the retraction phase, but overlaps ankle extension for 48% of the stance phase. The last third of the retraction phase is dominated by plantar flexion of the foot. Plantar flexion plays a major role in generating thrust, as shown by the significant movement of the lizard in the anteromedial direction after the foot rolls off the substratum (well after maximal femoral retraction and knee extension). However, studies of the effects of running speed indicate that femoral retraction may be the primary effector of propulsive force in *Sceloporus clarkii*. Reilly and DeLancey (1997) have evidence that femoral retraction is the major effector of increasing speed and that ankle extension kinematics do not change over a threefold increase in speed. Furthermore, unique adaptations of the caudifemoralis muscle (see below) point to a critical role of femoral retraction in lizards.

On the basis of observations that the foot rolls off the toes in an anteromedial direction, such that the lizard travels obliquely through the air to land on the opposite foot, it appears that the hindlimb generates both vertical and anteromedial forces that sum from side to side to propel the lizard forward. These speculations closely match data from force-plate studies of the hindlimbs of monitor lizards running at a constant speed, which show that the forces of the substratum acting on the feet are primarily vertical and are combined with speed-dependent anterior and medial forces (A. Christian, personal communication). In addition, thrust appears to be directed posteriorly throughout the stance phase until it shifts to a strong posterolateral thrust as the foot leaves the ground (Fig. 2), which corroborates the hypotheses of Snyder (1952) and Schaeffer (1941). Studies of limb kinematics in relation to ground reaction forces that are lacking in lizards (Biewener, 1989) are needed to describe directly the dynamics of force production during locomotion and to explore how these dynamics change with limb adduction in more erect limb postures.

Comparisons with salamanders

The only quantitative kinematic studies of sprawling

locomotion to date are for the salamander *Dicamptodon tenebrosus* (Ashley-Ross, 1994a,b, 1995), where the kinematics and motor patterns of a walking trot have been described in detail, and an electromyographic study of two hindlimb muscles in *Ambystoma tigrinum* (Peters and Goslow, 1983). These analyses verified that in salamanders the crus and foot rotate under the knee during the stance phase. Thus, salamanders do not show the sprawling limb posture of *Sceloporus clarkii*, but appear to be more similar in posture to other more erect-postured lizards such as *Iguana iguana* and *Crotophytus collaris*. Ashley-Ross (1994a) concluded that extensive femoral movements produced most of the motive force in *Dicamptodon tenebrosus* and, thus, that the 'double crank' mechanism commonly inferred to describe salamander limb movements (Barclay, 1946; Gray, 1968; Edwards, 1977, 1989; Peters and Goslow, 1983) was not strongly supported by quantitative kinematic patterns in this salamander. Comparisons of the quantitative kinematic studies of sprawling locomotion in *Dicamptodon tenebrosus* and *Sceloporus clarkii* reveal similarities and differences in their limb cycle kinematics. *Dicamptodon tenebrosus* moving at 0.254 m s^{-1} (=41% of maximum sprint speed) and *Sceloporus clarkii* moving at 0.833 m s^{-1} (=44% of maximum sprint speed) use essentially identical gaits (a fast walking trot) and have very similar axial movements. Both use a double-node standing wave with the nodes on the girdles, peak pelvic rotation to the left occurs just before right foot down, and peak pelvic rotation to the right occurs just before right foot up. Early aspects of limb and femoral retraction are also similar. In both species, maximum femoral protraction and maximum limb protraction occur just before foot down; thus, both have the terminal swing retraction phase. In addition, both species flex the knee early in the stance phase and extend it in the latter part of this phase. However, because the crus rotates under the knee in *Dicamptodon tenebrosus*, movements of the knee joint during the middle of the stance phase cannot be reliably measured for comparison. Nonetheless, comparative data for maximal extensions of the knee reveal that the salamander extends the knee to nearly full extension during protraction of the limb and at the end of the stance phase (up to 172° compared with a maximum of 91° in *Sceloporus clarkii*). Thus, at the same speed relative to maximum sprint speed, the salamander extends the knee considerably more than the lizard using the same gait. In addition, the timing of knee extension during the latter part of the stance phase differs in these species. In *Dicamptodon tenebrosus*, knee extension continues until foot up, in contrast to the lizard which begins to flex the knee considerably earlier at 73% of the stance phase. The range of femoral retraction and the timing of femoral retraction differ as well. *Dicamptodon tenebrosus* (107°) exhibits more than twice the total femoral excursion of *Sceloporus clarkii* (47°), but note that *Ambystoma tigrinum* has a femoral excursion of 79° ; Peters and Goslow, 1983). Femoral retraction continues until or after foot up in the salamander, in contrast to the lizard where femoral retraction peaks at 68% of the stance phase. Overall, the kinematics of hindlimb locomotion in these two

species differ in that the lizards use a more sprawling posture, move and extend their limbs less, and begin to protract the femur and flex the knee earlier relative to the end of plantar flexion of the foot.

The availability of electromyographic data for two salamanders (Peters and Goslow, 1983; Ashley-Ross, 1995) and a lizard (Reilly, 1995) allows us to identify a fundamental difference in the functioning of the limb during the power stroke in lizards and salamanders. Peters and Goslow (1983) have shown that, in *Ambystoma tigrinum*, early in the stance phase, the body is pulled towards the foot by activity of the knee flexor (the puboischiotibialis muscle) before there is any activity in the femoral retractor (the caudifemoralis muscle) and that the femur then begins to be retracted by activity in the caudifemoralis during the time when the crus is rotated under the knee. The knee flexor is active from just before foot down until just over half-way through the stance phase, and the femoral retractor activates approximately one-third of the way through the stance phase, becoming inactive at approximately two-thirds of the way through the stance phase. Data for *Dicamptodon tenebrosus* support this hypothesis because, even though the femur begins to retract just before foot down and keeps retracting until foot up (Ashley-Ross, 1994a), it exhibits the same motor patterns for these muscles during limb retraction (Ashley-Ross, 1995). Peters and Goslow (1983) discussed similar patterns found in mammalian stepping and concluded that this indicated a functional continuity from the earliest tetrapods to modern mammals. This may be true, but lizards appear to retract the limb differently.

Data for *Sceloporus clarkii* show that the knee bends to its maximum flexion very early (within 20% of the stance phase), coincidentally with the beginning of femoral retraction rather than before it. Thus, knee flexion and femoral retraction occur in synchrony compared with the apparent temporal separation of knee flexion and femoral retraction in salamanders. Electromyographic data for *Sceloporus clarkii* (Reilly, 1995) show that the caudifemoralis is active from just before foot down until half-way through the stance phase, indicating much earlier femoral retraction in lizards. Furthermore, none of the muscles spanning the knee in a position to flex the knee showed a single focused burst of activity during the first 20% of the stance phase. The flexor tibialis internus superficialis was active from well before foot down to half-way through the stance phase, and it could therefore be flexing the knee during the middle of its activity period, but it is more likely to be adducting the limb during retraction. Thus, no specific knee flexor was identified. The functional basis for knee flexion during the stance phase and the coincidence of knee flexion and femoral retraction may be due to the novel structure of the lizard caudifemoralis muscle, as proposed by Snyder (1954). In salamanders, the caudifemoralis is relatively short and inserts only onto the femur. In lizards, it is longer, and an auxiliary tendon extends distally along the femur to insert onto the ligaments, cartilages and muscular insertions on the proximal rear of the crus. Snyder (1954) presents an elegant hypothesis supported by stimulation data that this auxiliary tendon acts to

flex the knee and limb early in the stance phase. As the limb is retracted, the auxiliary tendon acts as a lever with a very long power arm, resulting in rapid flexion of the knee and strong retraction of the limb early in the retraction phase. As limb retraction continues, tension progressively decreases on the auxiliary portion of the caudifemoralis, flexing the knee, and progressively increases on the portion attached to the femur. Therefore, the caudifemoralis produces most of the force for retracting the limb because it dynamically flexes the knee and retracts the femur. This hypothesis is fully supported by the kinematic patterns observed in *Sceloporus clarkii*.

The presence of the novel portion of the caudifemoralis in lizards may be the key morphological difference explaining the fundamental difference in limb retraction kinematics in lizards and salamanders. Interestingly, the possession of the auxiliary caudifemoralis tendon appears to be a synapomorphy for the Sauria. It is present in the Lepidosauria and Crocodylia, but is lost in modern birds owing to the radical changes in their locomotory system (Gatesy, 1990). From a phylogenetic perspective, the apparent retention of the primitive form of the caudifemoralis in mammals may explain the hypothesized continuity of hindlimb form and function in salamanders and mammals (Peters and Goslow, 1983), while the appearance of the novel tendon in the saurians explains the functional differences in the lizard hindlimb. Given the fundamental difference in caudifemoralis structure and hindlimb function, one would expect that there may be fundamental differences in the way that erect postures evolved in the synapsids and theropods. In addition, it is obvious that *Sceloporus clarkii* locomotes with a more stiffened and sprawling limb posture than salamanders and other lizards and may be the most 'sprawling' vertebrate studied quantitatively to date. Major questions are how the lizards with more erect postures use the saurian caudifemoralis and how limb function is modulated with speed and gait changes in taxa with different forms of this muscle. These fundamental questions require quantitative studies of many taxa, with different gaits, and postures before convincing answers can emerge and further inferences about the evolution of tetrapod locomotion can be made.

We thank undergraduates Mike Barnett, Dorothy Glass, Cindy Hamen, Mike Lyons and Pat McCabe for assistance in data collection, digitizing and data analysis. Don Miles and Audrone Bukevicius assisted in many aspects of this research and provided comments on the manuscript. This research was supported by Ohio University Research Challenge Grant RC 95-025 to S.M.R. and NSF BSR 861788 to D.B.M.

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