

The Effect of Speed on the Hindlimb Kinematics of the Reeves' Butterfly Lizard, *Leiolepis reevesii* (Agamidae)

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Abstract We recorded locomotor performance of Reeves' butterfly lizards (*Leiolepis reevesii*) on a racetrack and to describe hindlimb kinematic patterns and to evaluate the effect of speed on hindlimb kinematics. The studied lizards predominantly used quadrupedal locomotion at relatively low speeds, but ran bipedally with a digitigrade posture at high speeds. Speed was positively correlated with both stride length and stride frequency, and was negatively correlated with duty factor. Lizards modulated speed probably by a combination of changing frequency and amplitude of limb movements. Within the range of standardized speeds from 50 to 150 cm/s, speed effects on 28 out of a total of 56 kinematic variables were significant. The hip height at footfall increased as speed increased, whereas the amplitude of vertical oscillations of the hip did not vary with speed. The total longitudinal and dorsoventral movements relative to the hip varied with speed for all parts of the limb that were distal to the knee, whereas the lateral movements did not. The knee and ankle angle at footfall varied with speed, but did not at the end of stance. The degree of pelvis rotation during the entire stride cycle did not vary with speed. Our results suggest that pelvic rotation and femoral protraction/retraction have a minor role in modulating speed in *L. reevesii*.

Keywords Agamidae, *Leiolepis reevesii*, kinematics, speed effect, bipedalism

1. Introduction

Locomotor performance of animals reflects underlying variation in morphology, physiology and habitat use and is fitness-related because of its effects on prey capture and predator avoidance (Bennett, 1989; Pough, 1989; Irschick and Garland, 2001; Irschick *et al.*, 2008). Measurement of locomotor performance is the pivotal step to unravel the relationships between morphology, ecology and fitness (Arnold, 1983; Van Damme *et al.*, 2002). Kinematic analysis quantifies the features of gait during locomotion and is developed to characterize the movement patterns and to reveal the mechanisms underlying locomotor performance variation (Russell and Bels, 2001).

Over the past few decades many aspects of locomotor performance have been investigated in a wide range of animal taxa from invertebrates to mammals, and lizards have frequently used as the model organisms to study these relationships (Irschick and Jayne, 1998; Irschick and Garland, 2001; Angilletta *et al.*, 2002; Spezzano and Jayne, 2004; Fuller *et al.*, 2011). For terrestrial tetrapods such as lizards, the limbs play a major role in supporting the body and generating propulsive forces during locomotion (Farley and Ko, 1997; Willey *et al.*, 2004; Reilly *et al.*, 2005). From previous studies of lizards we have known the following. First, most lizards have a typical sprawling limb posture, but the kinematics of limb movements varies among species (Irschick and Jayne, 1999a; Hsieh, 2003; Clemente *et al.*, 2004; Higham and Jayne, 2004; McElroy *et al.*, 2012; Wang *et al.*, 2014). For example, 19 out of 28 linear and angular kinematic variables collected from five morphologically

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distinct lizard species differ significantly among species (Irschick and Jayne, 1999a); other variables such as the footfall pattern, orientation of the digits and tail also varies considerably among species (Reilly and Delancey, 1997a,b; Fieler and Jayne, 1998). Second, the movements of the forelimb are similar to those of the hindlimb at lower speeds, but hindlimbs become more important than forelimbs at higher speeds (Snyder, 1954; Sukhanov, 1974; Russell and Bels, 2001). Third, the kinematics of limb movements can be affected by several factors, including speed, incline and perch diameter (Fieler and Jayne, 1998; Jayne and Irschick, 1999; Irschick and Jayne, 1999a; Higham and Jayne, 2004; Foster and Higham, 2012). In the Common Desert Iguana *Dipsosaurus dorsalis*, for example, stride length, hip height and femoral depression is increased, but stride duration and metatarsal angle is decreased with increasing speed (Fieler and Jayne, 1998). Fourth, bipedal locomotion appears in many lizards, especially agamid and teiid species living in sandy, rocky or open environments (Snyder, 1962; Aerts *et al.*, 2003; Clemente *et al.*, 2008), and those kinematic variables may differ significantly between quadrupedal and bipedal strides (Irschick and Jayne, 1999a). Although limb kinematics has been quantified in a diversity of lizard species, collecting data from more species is still necessary and such an effort will aid the identification of the generalizability of the patterns.

The Reeves' Butterfly Lizard (*Leiolepis reevesii*) is a medium-sized, oviparous agamid that ranges from Guangdong, Guangxi, and Hainan Provinces of South China to Vietnam (LH Lin *et al.*, 2010). This species is a typical fast-moving predator with a diet consisting primarily of arthropods, and mainly inhabits sunny sandy coastal regions covered by grass patches. While sexual dimorphism, female reproduction, hatchling phenotypes, activity patterns and population genetic structure have been well studied (CX Lin *et al.*, 2004, 2007; Wang *et al.*, 2005; LH Lin, 2010; Du *et al.*, 2011), locomotor performance has never been examined in the species. In the present study, we quantified the hindlimb kinematics of *L. reevesii* at different speeds. Our study aims were to: (1) describe in detail the hindlimb movements during locomotion, (2) evaluate the effects of speed on hindlimb kinematics, and (3) compare the kinematic patterns with those so far reported for other lizards.

2. Materials and Methods

We collected adult *L. reevesii* larger than 82 mm snout-

vent length (SVL) in October 2007 from Sanya (18°15' N, 109°30' E), Hainan, South China. Lizards were transported to our laboratory in Hangzhou, where they were individually maintained in 660 mm × 500 mm × 400 mm (length × width × height) cages placed in a room where temperatures were never higher than 28 °C. Each lizard was weighed (to the nearest 0.01 g) and measured (to the nearest 0.01 mm) for SVL, tail length, forelimb length (humerus plus ulna) and hindlimb length (femur plus tibia). Each cage had a substrate of sand (~150 mm depth), with pieces of clay tiles and litter layers provided as shelter and basking sites. A 100 W light bulb suspended above one end of each cage and on a cycle of 12 h light: 12 h dark allowed lizards to thermoregulate body temperature for 12 h daily. Lizards were fed mealworm larvae (*Tenebrio molitor*) and house crickets (*Acheta domesticus*) every other day. Eight individuals (four females and four males) of similar sizes (SVL: 84.1 ± 0.8 mm; body mass: 13.0 ± 0.5 g) were used in this study.

Lizards were marked by painting white non-toxic dots on the centre of pelvis girdles, the joints of hindlimb (hip, knee and ankle), and the base, middle and tip of the long fourth toe, to facilitate digitizing the video images. All locomotor trials were conducted in another room at 34 ± 0.5 °C close to the mean level of thermal preference recorded in *L. reevesii* (LH Lin *et al.*, unpublished data). To minimize the possible influence of diel variation in locomotor performance, trials were conducted between 14:00–17:00. Prior to each trial, lizards were kept in the room at 34 °C for 1 h, and then individually chased down a 2 m × 0.2 m × 0.3 m (length × width × height) wooden racetrack. Locomotor performance was recorded laterally with a PCO1200 high-speed digital camera (Cooke, USA) at constant 250 frames per second. The panel facing the camera was a piece of transparent glass, and the back and bottom panels were painted with 1 cm reference lines. A mirror fixed on a wooden support at an angle of 45° provided a simultaneous dorsal view of lizards. Two 500 W lights, placed approximately 2 m in front of the racetrack, provided illumination. Each lizard was tested 5–6 times, with a minimum of 15 min rest between successive trials. The sequences where the animals ran straight and continuously were retained, and examined later on a frame-by-frame basis using MaxTRAQ software (Innovision Systems, USA).

We defined three axes following Jayne and his colleagues to describe the position and movement of each lizard (Fieler and Jayne, 1998; Jayne and Irschick, 1999; Irschick and Jayne, 1999a). The x axis was the horizontal dimension parallel to the overall direction of travel and

the tread surface, the y axis perpendicular to the tread surface, and the z axis perpendicular to the x - y plane. The marker points were digitized for each frame from the lateral or dorsal view. The measured kinematic variables were similar to those recorded in previous studies (Fieler and Jayne, 1998; Jayne and Irschick, 1999; Irschick and Jayne, 1999a; Clemente *et al.*, 2004). Six variables describing movements of the whole hindlimb were stride length (distance traveled between successive footfalls), frequency (the reciprocal of the duration between successive footfalls), speed (stride length multiplied by stride frequency), step length (the distance traveled by the body along the x axis while the foot touched the ground), step duration, and duty factor (step duration/stride duration). Three variables describing the height of the hip relative to the racetrack surface were hip height at the time of footfall ($Y_{\text{hip,footfall}}$), $Y_{\text{hip,footfall}}$ minus minimum hip height during the stance portion of the cycle ($\Delta Y_{\text{hip,stance}}$), and the total vertical oscillation of the hip for the entire stride cycle ($\Delta Y_{\text{hip,total}}$). At footfall, the effective limb length was measured as the straight line distance from the hip to the ankle in both three and two dimensions (in the lateral view). To facilitate visualizing movements of the limb relative to the hip, the x , y and z coordinates were standardized so that the hip was positioned at the origin in the three-dimensional space. Within each stride cycle, the minimum (X_{min} , Y_{min} and Z_{min}) and maximum (X_{max} , Y_{max} and Z_{max}) values, and the difference between the maximum and minimum (ΔX , ΔY and ΔZ) values for each marker of the limb were determined. The angles of three joints (the knee, ankle and fourth toe) within the hindlimb at footfall and at the end of stance were also determined. The knee angle was the angle between the femur and the tibia, the ankle angle was the angle between the tibia and metatarsal on the dorsal side of the foot, and the toe angle was the angle between the metatarsals and a straight line extending from the base to the tip of the fourth toe. Additionally, the angle between the x axis and a line connecting the left and right hips was measured to indicate the orientation of the pelvis, and the difference between maximum and minimum values of these angles to indicate the amount of pelvis rotation.

All data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using Bartlett's test prior to parametric analyses. We used linear regression, mixed model analysis of variance (ANOVA) with speed as the fixed factor and individual as the random factor and Tukey's test to analyze the corresponding data. Throughout this

paper, values are presented as mean \pm standard error, and the significance level is set at $\alpha = 0.05$.

3. Results

3.1 General description of a stride Within a single stride, the hip moved forward with a nearly constant speed as the hindlimb oscillated relative to the hip, simultaneously the limb and hip oscillated vertically relative to the racetrack surface. During the stance phase, the height of the hip and knee decreased immediately after footfall, and then gradually increased, with the amplitude of vertical movements of the knee being larger than that of the hip; the segments of the foot from proximal to distal sequentially left the racetrack surface after the ankle began to move up. During the swing phase, the height of the knee increased for approximately the first two-thirds of the phase and then decreased; the heights of all parts of the limb rapidly decreased during the end of phase.

Figure 1 shows the lateral and dorsal views of the paths traveled by the different portions of the limb relative to the hip at a forward speed of 140 cm/s. Within a single stride, the most anterior (X_{max}) and posterior (X_{min}) positions of the knee had extremely similar magnitudes, whereas the magnitude of X_{min} for other portions of the limb was commonly larger than (about 1.5 times) that of

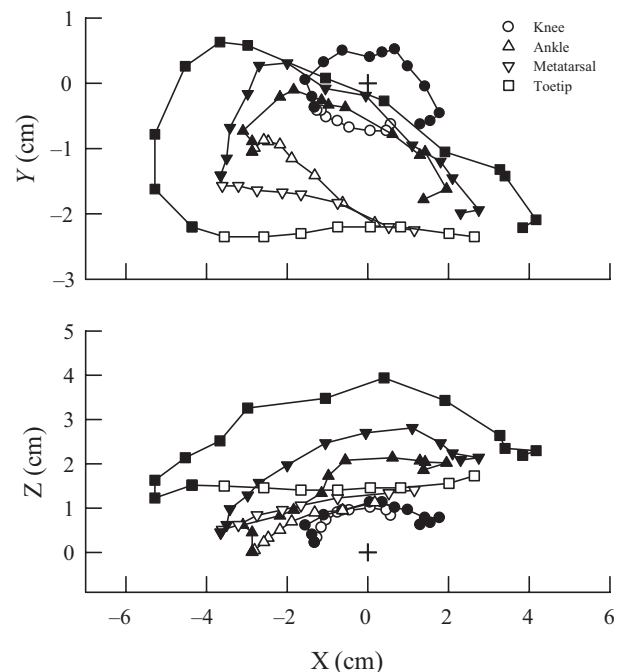


Figure 1 Lateral (x versus y) and dorsal (x versus z) view of paths made by the knee, ankle, metatarsal and toetip landmarks relative to the hip during one stride at a forward speed of 140 cm/s. The hip is located at point 0, 0, marked by a cross. The open and filled symbols represent the stance and swing portions of the stride, respectively.

X_{\max} , Z_{\max} generally occurred at the mid-swing phase with the portions of the limb having the fastest velocities in the x direction. The slowest velocities of the portions of the limb generally occurred at the transition steps between stance and swing, and between swing and stance.

3.2 Effects of speed on kinematics variables Individual lizards of *L. reevesi* predominantly used quadrupedal locomotion at the relatively low speeds (50–100 cm/s, duty factor > 0.5), but increasingly more frequently used bipedal locomotion as speed increased (Figure 2). Speed was positively correlated with both stride length ($r = 0.82$, $F_{1,67} = 133.82$, $P < 0.001$) and frequency ($r = 0.84$, $F_{1,67} = 156.35$, $P < 0.001$), and negatively correlated with duty factor ($r = -0.84$, $F_{1,67} = 164.75$, $P < 0.001$). The stride length increased, and duty factor decreased, as speed increased (Figure 3).

In order to balance experimental design suitable for ANOVA, we restricted our statistical analyses to three standardized speeds ranging from 50 to 150 cm/s ($\pm 10\%$) for remainder of the results. Within this range, speed effects on the five variables describing whole-limb movements were significant. Both stride length ($F_{2,14} = 16.11$, $P < 0.001$) and frequency ($F_{2,14} = 38.41$, $P < 0.001$) increased, while stride duration ($F_{2,14} = 47.84$, $P < 0.001$), step duration ($F_{2,14} = 172.36$, $P < 0.001$) and duty factor ($F_{2,14} = 26.51$, $P < 0.001$) decreased, as speed increased. The speed effect on step length was not significant ($F_{2,14} = 0.71$, $P = 0.508$). The hip height at footfall increased as speed increased ($F_{2,14} = 11.75$, $P < 0.01$), with the mean hip height increasing about 1.1 cm at the changeover of speed from 50 cm/s to 150 cm/s. Neither during the

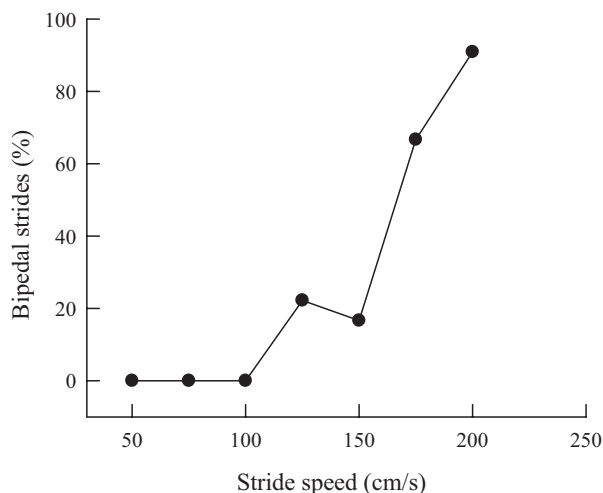


Figure 2 Percentage of bipedal stride for *Leiolepis reevesi* during level locomotion. The strides ($N = 69$ strides from eight individuals) at corresponding speeds (mean value $\pm 10\%$) were used to calculate the percentages.

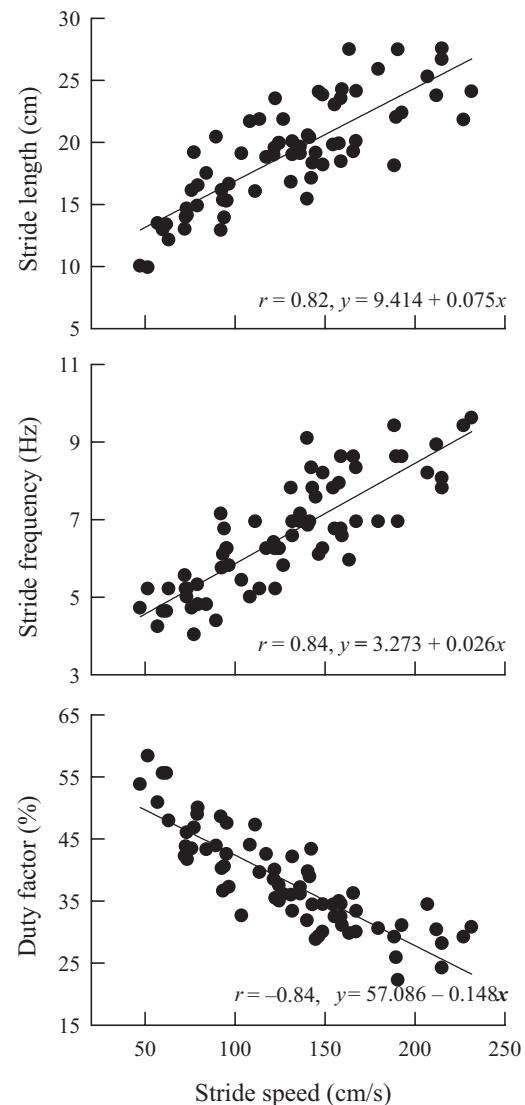


Figure 3 Plots of the regressions for stride length, frequency and duty factor versus forward velocity.

stance phase ($F_{2,14} = 0.15$, $P = 0.858$; mean = 0.3 cm) nor in the entire stride cycle ($F_{2,14} = 1.03$, $P = 0.382$; mean = 1.0 cm) the speed effect on the amplitude of the vertical oscillations of the hip was significant (Figure 4). Effective limb length at footfall increased as speed increased (two-dimensional: $F_{2,14} = 6.05$, $P = 0.013$; three-dimensional: $F_{2,14} = 6.20$, $P = 0.012$) (Figure 5).

Of the 36 variables describing hindlimb positions and movements relative to the hip, 18 varied with speed (Table 1). The most anterior (X_{\max}) and posterior (X_{\min}) positions of the markers of the foot (ankle, metatarsal and toetip) increased as speed increased, but those positions of the knee did not vary with speed. The total longitudinal movements relative to the hip (ΔX) varied with speed for all parts of the limb distal to the knee (Table 1, Figure 6). The most ventral locations of the limb elements (Y_{\min})

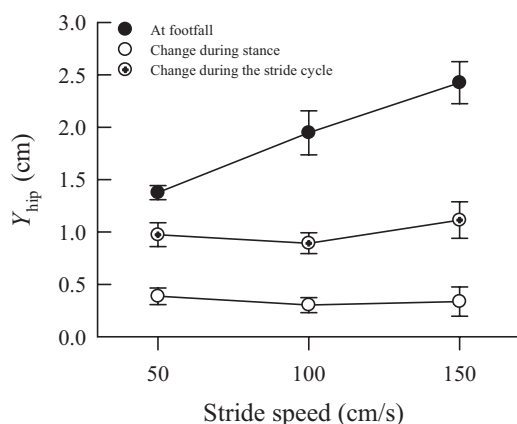


Figure 4 Mean values (\pm SE) for hip height at footfall, the change in hip height during stance and during the entire stride cycle.

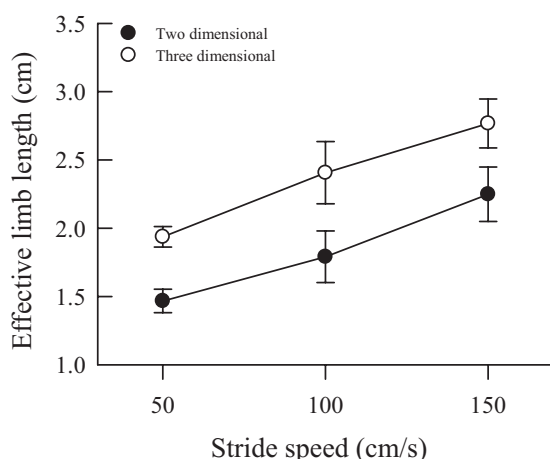


Figure 5 Mean values (\pm SE) for two-dimensional and three-dimensional effective limb lengths at footfall.

varied with speed, but the most dorsal location (Y_{\max}) did not. The pattern of variation with speed for the total dorsoventral movement relative to the hip (ΔY) was similar to that of Y_{\min} (Table 1, Figure 6). The minimum (Z_{\min}) and maximum (Z_{\max}) lateral locations of the limb elements did not vary with speed (Table 1).

At the forward speeds from 50 to 150 cm/s, the knee and ankle angle at footfall varied with speed (knee angle: $F_{2,14} = 10.30$, $P < 0.01$; ankle angle: $F_{2,14} = 13.20$, $P < 0.001$), but did not change significantly at the end of stance (knee angle: $F_{2,14} = 2.55$, $P = 0.114$; ankle angle: $F_{2,14} = 3.44$, $P = 0.061$). At a given speed, the mean values for the joint angles were obviously greater at the end of stance than those at footfall (Figure 7). However, the toe angle did not vary with speed both at footfall ($F_{2,14} = 1.28$, $P = 0.310$) and at the end of stance ($F_{2,14} = 0.83$, $P = 0.456$). The mean value for the toe angle at footfall was greater than that at the end of stance (Figure 7).

The amount of pelvis rotation during the entire stride cycle did not vary with speed ($F_{2,14} = 0.02$, $P = 0.981$).

4. Discussion

As in other lizards such as the Savannah Monitor Lizard *Varanus exanthematicus* (Jayne *et al.*, 1990), the Clark's Spiny lizard *Sceloporus clarkii* (Reilly and Delancey, 1997a) and *Dipsosaurus dorsalis* (Fieler and Jayne, 1998; Jayne and Irschick, 1999), our data showed profound speed effects on the hindlimb kinematics in *L. reevesi*. However, these effects vary among kinematic variables and among species. For example, speed affects five of 38 examined kinematic variables in *S. clarkii* (Reilly and Delancey, 1997a), 37 of 46 kinematic variables in *D. dorsalis* (Fieler and Jayne, 1998), and 28 of 54 variables in *L. reevesi*. Inter-specific differences might result partly from differences in speed range, as revealed by the fact that the fastest speed used to analyze kinematics was approximately 44 % of the maximum speed in *S. clarkii* (Reilly and Delancey, 1997a), and 60% in *D. dorsalis* (Fieler and Jayne, 1998). In *L. reevesi*, the fastest speed (150 cm/s) is approximately 48 % of the maximal running speed ever recorded in the laboratory (about 310 cm/s, Lu personal observation).

Pelvic rotation, femoral retraction and rotation are believed to contribute to the forward movement of animals with sprawling limbs (Brinkman, 1981; Fieler

Table 1 The results of ANOVAs for speed effects on each kinematic variable describing the hindlimb position and movements relative to the hip.

Kinematic variables	F-values ($df = 2, 14$)			
	Knee	Ankle	Metatarsal	Toetip
X_{\min}	2.56 ^{NS}	4.62*	9.01**	9.21**
X_{\max}	0.67 ^{NS}	12.45***	6.65**	4.68*
ΔX	4.62*	14.28***	12.18***	10.88**
Y_{\min}	6.96**	7.92**	10.14**	10.36**
Y_{\max}	0.94 ^{NS}	1.82 ^{NS}	1.76 ^{NS}	0.87 ^{NS}
ΔY	9.11**	12.12***	17.85***	12.94***
Z_{\min}	2.65 ^{NS}	0.22 ^{NS}	0.73 ^{NS}	0.72 ^{NS}
Z_{\max}	1.94 ^{NS}	2.44 ^{NS}	2.19 ^{NS}	0.34 ^{NS}
ΔZ	2.39 ^{NS}	1.06 ^{NS}	2.56 ^{NS}	0.92 ^{NS}

Note: X_{\max} and X_{\min} are the most anterior and posterior positions relative to the hip, respectively, and $\Delta X = X_{\max} - X_{\min}$; Y_{\max} and Y_{\min} are the most dorsal and ventral positions relative to the hip, respectively, and $\Delta Y = Y_{\max} - Y_{\min}$; Z_{\max} and Z_{\min} are the maximum and minimum lateral positions relative to the hip, respectively, and $\Delta Z = Z_{\max} - Z_{\min}$. NS represents no significant difference; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

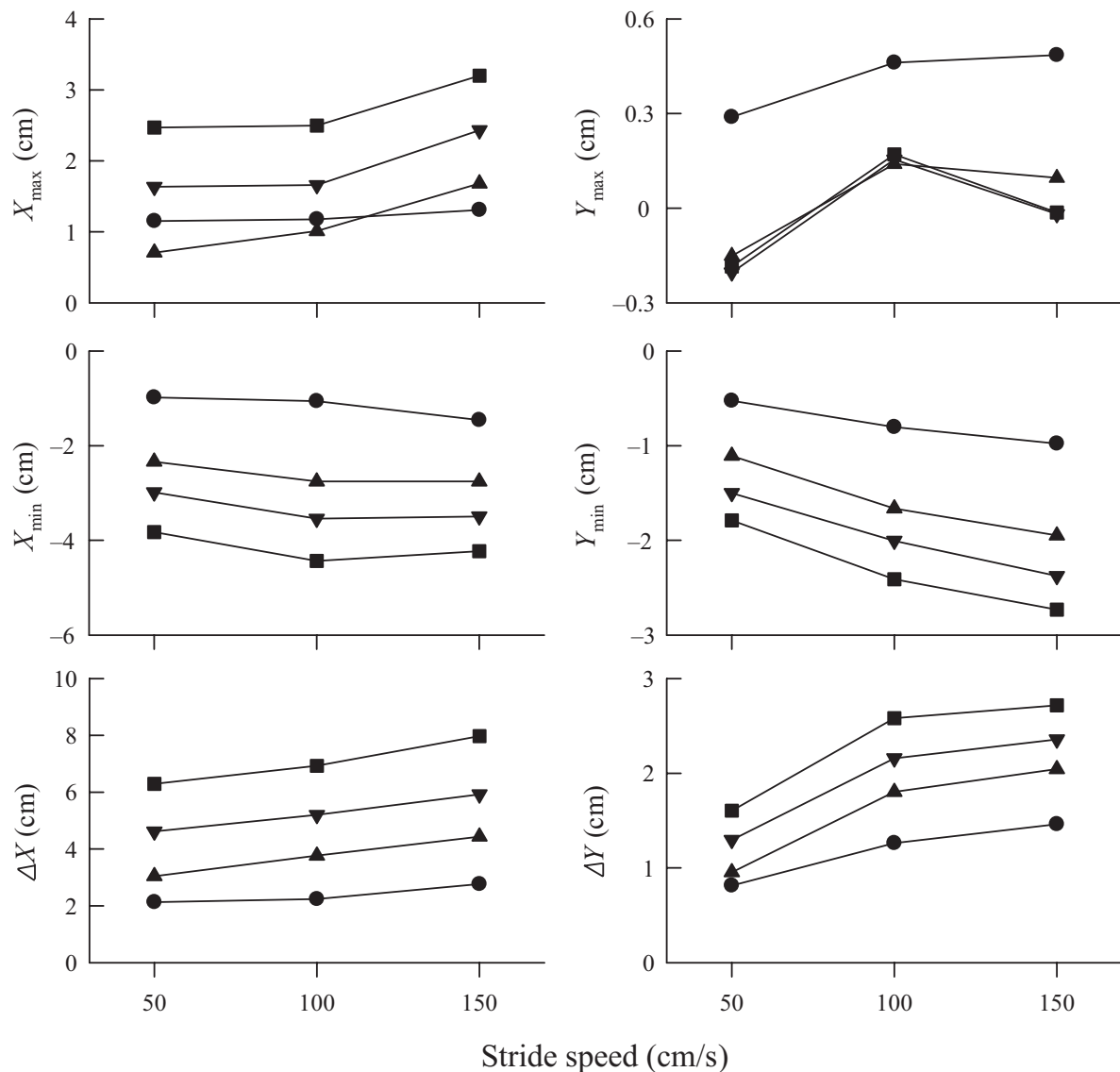


Figure 6 Mean values for positions and movements of the knee, ankle, metatarsal and toetip landmarks relative to the hip. See Figure 1 for key to symbols.

and Jayne, 1998; Reilly and Elias, 1998; Russell and Bels, 2001). In this study, the degree of pelvis rotation was not affected by speed, with a mean value of about 45° . That speed has no significant role in affecting pelvis rotation has also been reported for *S. clarkii* and *D. dorsalis* (Reilly and Delancey, 1997a; Fieler and Jayne, 1998). However, in the Pacific giant salamander *Dicamptodon tenebrosus*, an amphibian, pelvic rotation is nearly doubled (from 38.5° to 73.3°) as speed increases from 0.77 SVL to 2.90 SVL per second (Ashley-Ross, 1994a). This between-taxa difference probably indicates that the role of pelvic rotation in modulating speed is greater in salamanders than in lizards (Fieler and Jayne, 1998). The amounts of femur protraction and retraction

were normally indicated by negative and positive values of femur retraction angle—the angle between the femur and a line connecting the hips. Despite no direct measurement in this study, the amounts of femur protraction and retraction should be proportional to values of X_{\min} and X_{\max} for the knee (Fieler and Jayne, 1998; Irschick and Jayne, 1998; Spezzano and Jayne, 2004). In *L. reevesi*, the values of X_{\min} and X_{\max} for the knee did not change with speed and were approximately equal to each other (Table 1, Figure 6). That speed does not affect the amounts of femur protraction and retraction, or maximum anterior (X_{\max}) and posterior (X_{\min}) movements of the knee is also found in *D. tenebrosus* (Ashley-Ross, 1994b), *S. clarkii* (Reilly and Delancey, 1997a) and *D.*

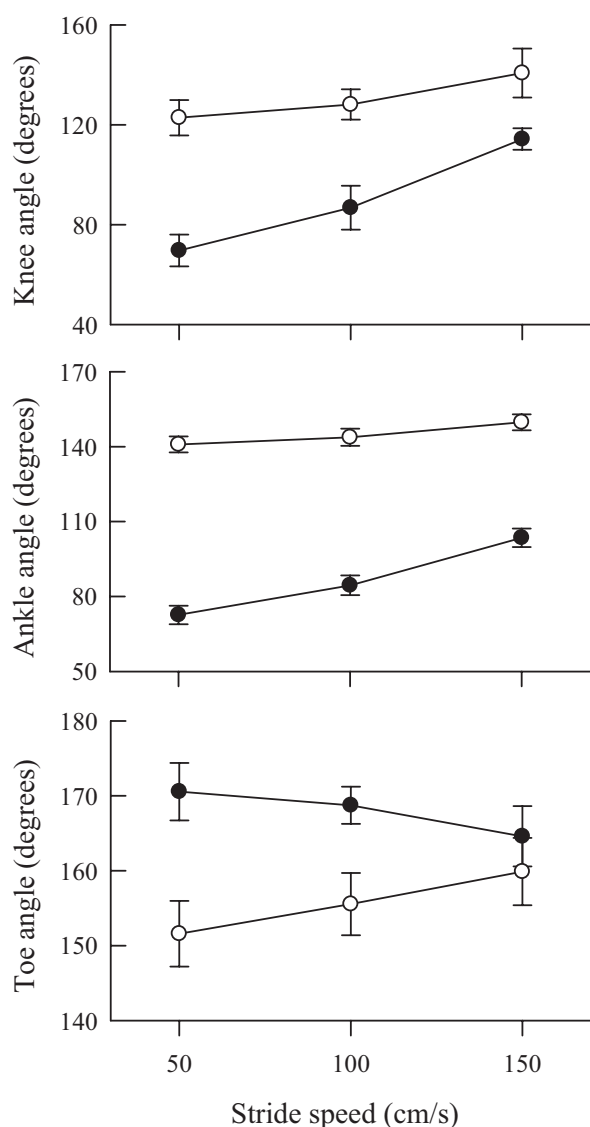


Figure 7 Mean values (\pm SE) for the three-dimensional angles of the knee, ankle and toe at the end of stance (open symbols) and at footfall (filled symbols).

dorsalis (Fieler and Jayne, 1998). In contrast to the knee, the values of X_{\min} and X_{\max} for more distal portions of the limb in *L. reevesii* varied significantly with speed (Table 1). Those movements, such as pelvic rotation and femoral retraction, could theoretically increase stride length and thus speed, but they might play a less important role in modulating speed in *L. reevesii*.

Theoretically, the changes in limb movement may cause changes in stride length and frequency, thus affecting speed. Our finding that stride length and frequency both increased significantly as speed increased indicated that, like most of species so far studied (Jayne *et al.*, 1990; Ashley-Ross, 1994b; Reilly and Delancey, 1997a; Fieler and Jayne, 1998; Reilly and Elias, 1998;

Zaaf *et al.*, 2001), *L. reevesii* can modulate speed by a combination of changing the frequency and amplitude of limb movements.

Lizards generally exhibit a sprawling limb posture and plantigrade foot posture, but it can vary with speed within an individual species and among different species. For example, some *Sceloporus* lizards have a more sprawling posture than others (Reilly and Delancey, 1997a,b). That the hip height and knee angle at footfall increased with increased speed indicated that hindlimbs became more upright at relatively high speeds in *L. reevesii*. Such finding is consistent with the results reported for *D. dorsalis* (Fieler and Jayne, 1998), *Liolaemus lutzae*, *Tropidurus torquatus* (Rocha-Barbosa *et al.*, 2008) and two padless geckos (*Teratoscincus scincus* and *Eublepharis macularius*; Fuller *et al.*, 2011). Moreover, effective limb lengths increased as speed increased, further indicating that lizards had the ability to modulate the length of the limb behaviorally by the combination of changes in limb movements and dimensions at different speeds. As many other lizards (Fieler and Jayne, 1998; Irschick and Jayne, 1999a,b; Rocha-Barbosa *et al.*, 2008), *L. reevesii* ran in a digitigrade foot posture at relatively high speeds. The gearing and muscle function of the limb may be altered by the changed foot posture, and digitigrady appears to be more associated with high speed running (Fieler and Jayne, 1998; Russell and Bels, 2001).

At relatively high speeds, individual lizards of *L. reevesii* more frequently rely on bipedal locomotion, which is widespread among lizards but the level of bipedalism varies considerably among species. For example, red-tailed spiny-footed lizards (*Acanthodactylus erythrus*) occasionally use a bipedal gait during a trot (Aerts *et al.*, 2003), whereas green basilisks (*Basiliscus plumifrons*; Hsieh, 2003), Brazilian sand lizards (*L. lutzae*; Rocha-Barbosa *et al.*, 2008), Amazon lava lizards (*T. torquatus*; Rocha-Barbosa *et al.*, 2008) and zebra-tailed lizards (*Callisaurus draconoides*; Irschick and Jayne, 1999a,b) display absolute bipedalism. Bipedalism may not be an ancestral trait for lizards, and has evolved independently in different groups of vertebrates (Irschick and Jayne, 1999a,b; Aerts *et al.*, 2003). So far, whether bipedal locomotion has an advantage over quadrupedal locomotion in lizards is still controversial. Snyder (1962) proposed that bipedal locomotion of lizards normally had a larger stride length, and therefore greater speed. Here, the maximal speeds and their stride lengths for bipedal strides were greater than those for quadrupedal strides in *L. reevesii* (stride speed: 178.6 ± 9.6 vs 114.9 ± 7.6 cm per second; repeated measures ANOVA, $F_{1,7} = 30.92$, P

< 0.001 ; stride length: 22.7 ± 1.0 vs 18.1 ± 0.8 cm, $F_{1,7} = 38.40$, $P < 0.001$). These results seem to be consistent with Snyder's (1962) prediction. However, some other studies have shown contrary findings. For example, no significant differences in stride speed and length between bipedal and quadrupedal locomotion are found under both laboratory and field conditions in *C. draconoides* and the Mojave fringe-toed Lizard *Uma scoparia*, which suggested that bipedal stride could not necessarily provide a performance advantage for speed (Irschick and Jayne, 1998, 1999a,b). Several factors, such as acceleration, high torque of the tail about the hip joint, and preventing forelimb interference with the hindlimb movement, have been used to explain why some lizards mainly use bipedal strides during fast movement (Irschick and Jayne, 1999a; Aerts *et al.*, 2003; Clemente *et al.*, 2008). Unfortunately, the acceleration and torque of the tail was not estimated in this study. More fully straightened hindlimbs in fast bipedal strides than in quadrupedal strides have been observed in *L. reevesi* as well as in other lizard species (Irschick and Jayne, 1999a; Rocha-Barbosa *et al.*, 2008). Thus, the increased hip height appears to be related to faster speeds and bipedal gaits. Moreover, high torque of the tail about the hip joint results in increased trunk angles, the body centre of mass closer to the hip, and hence increased forelimb clearance relative to the locomotor surface (Irschick and Jayne, 1999a).

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