The Journal of Experimental Biology 200, 2177–2188 (1997)
Printed in Great Britain © The Company of Biologists Limited 1997
JEB0769

MECHANICS OF LOCOMOTION IN LIZARDS

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Accepted 8 May 1997

Summary

Lizards bend their trunks laterally with each step of locomotion and, as a result, their locomotion appears to be fundamentally different from mammalian locomotion. The goal of the present study was to determine whether lizards use the same two basic gaits as other legged animals or whether they use a mechanically unique gait due to lateral trunk bending. Force platform and kinematic measurements revealed that two species of lizards, *Coleonyx variegatus* and *Eumeces skiltonianus*, used two basic gaits similar to mammalian walking and trotting gaits. In both gaits, the kinetic energy fluctuations due to lateral movements of the center of mass were less than 5 % of the total external mechanical energy fluctuations. In the walking gait, both species vaulted over their stance limbs like inverted pendulums. The fluctuations in kinetic energy and gravitational potential energy of the center of mass were approximately 180 ° out of phase. The lizards conserved as much as 51 % of the external mechanical energy required for locomotion by the inverted pendulum mechanism. Both species also used a bouncing gait, similar to mammalian trotting, in which the fluctuations in kinetic energy and gravitational potential energy of the center of mass were nearly exactly in phase. The mass-specific external mechanical work required to travel 1 m ($1.5\,\mathrm{J\,kg^{-1}}$) was similar to that for other legged animals. Thus, in spite of marked lateral bending of the trunk, the mechanics of lizard locomotion is similar to the mechanics of locomotion in other legged animals.

Key words: biomechanics, walking, running, mechanical work, mechanical power, lizard, *Coleonyx variegatus*, *Eumeces skiltonianus*.

Introduction

A variety of legged animals, including mammals, birds and arthropods, use two basic patterns of locomotor mechanics (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987; Full and Tu, 1990). These legged animals use an inverted pendulum gait at low speeds and a bouncing gait at high speeds. The inverted pendulum gait corresponds to walking and is characterized by a pendulum-like exchange between the kinetic energy and the gravitational potential energy of the center of mass. In this gait, the legs behave like stiff struts, and the center of mass of the body vaults over the stance limbs (Cavagna *et al.* 1963, 1976, 1977; Heglund *et al.* 1982; Alexander, 1988, 1991). The vertical position of the center of mass reaches its mid-stance maximum at nearly the same time as the forward velocity of the center of mass reaches its minimum. As a result, the fluctuations in kinetic energy and gravitational potential energy are almost exactly out of phase with each other, allowing pendulum-like exchange between them. This pendulum-like exchange has been shown to reduce the mechanical energy requirements by as much as 70 % during walking gaits (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987; Willems *et al.* 1995).

At higher speeds, legged animals use bouncing gaits including trotting, galloping, hopping and running. In bouncing gaits, the legs behave like compliant springs (McMahon *et al.* 1987; Blickhan, 1989; McMahon and Cheng, 1990; Farley *et al.* 1991, 1993; He *et al.* 1991; Alexander, 1992; Blickhan and Full, 1993; Farley and Gonzalez, 1996; Ferris and Farley, 1997). The compliance of the legs causes the center of mass to reach its lowest point at the middle of the stance phase. In this case, the fluctuations in kinetic energy and gravitational potential energy of the center of mass are in phase with each other. This is similar to the pattern of mechanical energy fluctuations in a spring-mass system or a bouncing ball. There are no substantial energy savings by pendulum-like exchange between the kinetic energy and gravitational potential energy because they are in phase with each other. However, bouncing gaits are characterized by substantial energy savings through elastic energy storage in muscles, tendons and ligaments (Cavagna *et al.* 1964; Alexander, 1988, 1991).

These two basic gaits, the inverted pendulum gait and the bouncing gait, have been shown to be used by a variety of animals including humans, dogs, kangaroos, rats, quail and ghost crabs (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987). However, it is not known whether

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legged animals that bend their trunks laterally during locomotion use these two basic gaits. As lizards move along the ground, their trunks undergo substantial lateral bending with each step (Sukhanov, 1974; Avery *et al.* 1987; Ritter, 1992, 1995). To the naked eye, lizard locomotion appears to be fundamentally different from mammalian locomotion because of the dominance of lateral trunk bending. This idea is supported by the observation that many lizard species have reduced limbs or are limbless and rely on lateral bending for forward propulsion (Gans, 1975, 1986; Withers, 1981; Renous *et al.* 1995). Thus, it seems possible that lateral trunk bending is as important as limb function in determining locomotor mechanics and performance in lizards. In mammals, the limbs are of primary importance in determining the inverted pendulum mechanics of walking and the spring-like mechanics of bouncing gaits. It is not known whether the limbs of legged lizards play a similar role to the limbs of mammals, resulting in inverted pendulum and bouncing gaits. It is possible that the limbs play a very different role in lizards, as they do in some legged robots, acting to keep the center of mass at a constant vertical height throughout the stance phase (Alexander, 1990).

The goal of the present study was to examine the mechanics of legged locomotion in lizards, animals that bend their trunks laterally during locomotion. Specifically, we examined whether two species of lizards use the two basic gaits known to be used by other legged animals: an inverted pendulum gait and a bouncing gait. In addition, we examined whether lizards require substantial external mechanical power to accelerate the center of mass in the lateral direction as the trunk bends laterally. To achieve these goals, we used force platform and kinematic measurements to examine the mechanical power required to lift and accelerate the center of mass during locomotion in two species of small lizards, *Coleonyx variegatus* (western banded gecko) and *Eumeces skiltonianus* (western skink). These two species have similar body masses, but *C. variegatus* has 2.7-fold more massive limbs than *E. skiltonianus*. *E. skiltonianus* is from a family (Scincidae) that has many limbless species that rely completely on lateral bending of the trunk for forward propulsion (Gans, 1975, 1986; Withers, 1981). A comparison of *C. variegatus* and *E. skiltonianus* may provide insight into the importance of limb morphology in determining the biomechanics of lizard locomotion.

Materials and methods

Animals

Data were obtained from four individuals of the western banded gecko *Coleonyx variegatus* (Baird), ranging in body mass from 3.3 g to 4.5 g (mean 3.7 g) and with a snout–vent length of approximately 5.6 cm. Data were also obtained from three individuals of the western skink *Eumeces skiltonianus* (Baird and Girard), ranging in body mass from 4.7 g to 5.1 g (mean 4.9 g) and with a snout–vent length of approximately 5.2 cm. Limb mass relative to body mass was approximately 2.7-fold larger in *C. variegatus* (total limb mass=16 % of body mass) than in *E. skiltonianus* (total limb mass=6 % of body mass). We attempted to obtain data from six individuals of each species but the additional individuals did not move across the force platform at a constant speed. Individuals of *E. skiltonianus* were collected in San Bernardino County, CA, USA. Individuals of *C. variegatus* were collected in Riverside County, CA, USA.

The lizards were housed in an environmental room (24 °C) illuminated for 13 h per day. In addition, each cage containing an individual of *C. variegatus* had direct ultraviolet lighting from a fluorescent tanning lamp and a heat strip to allow behavioral thermoregulation over a gradient of 24–40 °C. The field active body temperature is 30 °C for *E. skiltonianus* and approximately 23 °C for *C. variegatus* (Brattstrom, 1965; Cunningham, 1966). Both species were fed a diet of mealworms, crickets and a vitamin/mineral supplement, and they were given water daily.

Measurements

Synchronized force platform and video data were obtained as the animals moved along a track and across a force platform (0.11 m×0.06 m). The 1 m track had acrylic walls and a running surface of extremely fine sandpaper. This surface gave the animals sufficient friction to prevent slipping. All experiments were carried out at an ambient temperature between 24 and 25 °C. The force platform was built into the floor of the track and its surface was flush with the running track surface. After crossing the force platform, the lizards ran into a darkened box placed 0.5 m beyond the force platform.

The force platform was capable of measuring simultaneously the vertical, horizontal (fore–aft) and lateral components of the ground reaction force. The design and performance of the force platform have been described in detail previously (Full and Tu, 1990; Full *et al.* 1991). The force platform consisted of a balsa-wood platform that was mounted on four brass beams. Each beam had semi-conductor strain gauges bonded to spring blades (Full and Tu, 1990). The force platform gave a linear response over a range of forces from 0.001 N to 0.1 N. The mean body weight of the smaller species, *C. variegatus*, was 0.037 N and, thus, the force platform could resolve forces equal to 2.7 % of its body weight. The peak ground reaction force never exceeded 0.1 N in either species. The unloaded natural frequency of the force platform was approximately 500 Hz.

After data collection, the force platform data were corrected for cross-talk between the vertical, horizontal and lateral channels. The correction factors were determined from measurements of cross-talk when the force platform was loaded with known vertical, horizontal and lateral forces. These calibrations revealed that there was a small but systematic amount of cross-talk between the channels that caused errors ranging from 1 to 13 % before correction, depending on the combination of channels examined. The effect of cross-talk was corrected in computer software, and the calibration trials showed that the force platform measurements were accurate to within 1 % after the software cross-talk correction.

The force platform signals were amplified using bridge amplifiers (Vishay, Measurements Group) and sampled at 1000 samples s^{-1} using a computer (IBM PC/AT) and an analog-to-digital converter (C-100, Cyborg). The signals were collected using data-acquisition and analysis software (Discovery, Cyborg). The data were digitally low-pass filtered using a fourth-order zero-lag Butterworth filter with a cut-off frequency of 185 Hz.

As the lizards ran across the force platform, they were videotaped at 1000 fields s^{-1} in lateral view (Kodak Ektapro 1000, Image Intensified). A mirror was placed behind the force platform so that all four limbs could be viewed in the video recording of the animal on the force platform. This information allowed us to identify an integral number of strides for analysis. We also used the video recordings to examine the footfall pattern during a stride.

Data analysis

The animal's mean forward speed was calculated from the video recordings by dividing the force platform length (0.11 m) by the time taken to cross the force platform. We calculated the change in speed during an integral number of strides from the net horizontal impulse divided by body mass. If the change in speed exceeded 25 % of the mean speed, the trial was discarded. The lizards rarely moved at a steady speed, and only one out of every 200 trials that we collected met this criterion. This may have been because of the unnatural laboratory conditions or may reflect the normal locomotor patterns of lizards. For all of the trials that were included in the study, the change in speed was 5.7±11.6 % (mean ± S.D.). It is likely that error was introduced by accepting trials in which there was net acceleration or deceleration because the external mechanical power output at a given speed is probably affected by acceleration. However, the mean acceleration in the trials that we accepted (0.39±0.43 m s^{-2}, mean ± S.D.) was two orders of magnitude smaller than the mean acceleration during the acceleration phase of sprinting (>10 m s^{-2}) (Eckel and Farley, 1996). Thus, within the spectrum of locomotor behavior of these animals, the trials included in this study are close to steady-speed locomotion.

For the trials that met the criterion for inclusion in the present study, the video recordings were used to calculate the step frequency from the inverse of the time between the footfall of one hindlimb and the footfall of the contralateral hindlimb. The video recordings were also used to determine the footfall pattern during each trial and to calculate the phase shift between when a forelimb and its contralateral hindlimb hit the ground. This phase shift was calculated from the ratio of the time interval between these events and the stride period. This value was multiplied by 360 ° to give the phase shift in degrees. A phase shift of 0 ° means that the diagonal pair of limbs hit the ground synchronously, as in a mammalian trot, and a phase shift of 90 ° corresponds to a mammalian walk.

For an integral number of strides within each trial, we calculated the velocity and displacement of the center of mass in each direction from the force platform measurements as described in detail elsewhere (Cavagna, 1975; Blickhan and Full, 1993). The kinetic (E_k) and gravitational potential (E_p) energy of the center of mass were calculated from the velocity and vertical displacement of the center of mass, respectively (Cavagna, 1975; Blickhan and Full, 1993; Willems *et al.* 1995). The instantaneous total external mechanical energy (E_{cm}) was calculated from the sum of the horizontal, vertical and lateral kinetic energies and the gravitational potential energy at each instant.

We determined the mechanical power required to move the center of mass in the horizontal, vertical and lateral directions. By examining each direction separately, we were able to assess the importance of lateral bending of the trunk in terms of the external mechanical power output. For the horizontal and lateral directions, the mechanical power was calculated from the sum of the positive increments in the horizontal kinetic energy or the lateral kinetic energy, respectively, divided by the time period. For the vertical direction, the mechanical power was calculated from the sum of the positive increments in the vertical kinetic energy and gravitational potential energy divided by the time period. The total external mechanical power required to lift and accelerate the center of mass was calculated from the sum of the positive increments of E_{cm} divided by the time period. The mass-specific external mechanical work required to travel 1 m was determined by taking the slope of the mass-specific total external mechanical power *versus* speed relationship.

A key parameter in determining whether a gait is an inverted pendulum gait or a bouncing gait is the phase between the fluctuations in gravitational potential energy and kinetic energy (Cavagna *et al.* 1977; Heglund *et al.* 1982; Full and Tu, 1990). Inverted pendulum gaits are characterized by these energies being approximately one half-cycle out of phase with each other (a phase of approximately 180 °), and bouncing gaits are characterized by these energies being approximately in phase with each other (a phase of approximately 0 °). The phase between the gravitational potential energy and the kinetic energy of the center of mass was calculated by determining the fraction of the stride time between the time when the kinetic energy reached its minimum and the time when the gravitational potential energy reached its minimum. The fraction of the stride time was multiplied by 360 ° to give the phase in degrees.

We quantified the magnitude of energy exchange due to the pendulum mechanism by comparing the magnitude of the mechanical work that would have been required to maintain a constant speed if there were no exchange with the amount of mechanical work actually performed (ΣE_{cm}). The magnitude of the mechanical work required to maintain a constant speed if there were no exchange was equal to the sum of the positive increments in kinetic energy ($\Sigma\Delta E_k$) and gravitational potential energy ($\Sigma\Delta E_p$) (see Figs 4, 5). Percentage recovery was calculated as the amount of mechanical energy saved by the pendulum mechanism (Cavagna *et al.* 1963, 1976, 1977; Blickhan and Full, 1987; Full and Tu, 1990; Heglund *et al.* 1982; Willems *et al.* 1995):

$$\% \text{ Recovery} = [(\Sigma\Delta E_k + \Sigma\Delta E_p - \Sigma E_{cm})/(\Sigma\Delta E_k + \Sigma\Delta E_p)] \times 100\,. \quad (1)$$

The magnitude of the recovery of mechanical energy by the inverted pendulum mechanism depends on several factors: the phase of E_p and E_k, the shapes of the E_p and E_k *versus* time relationships, and the relative magnitudes of the fluctuations in E_p and E_k.

Results

Footfall pattern

We began by examining the footfall pattern during locomotion for comparison with the footfall pattern in quadrupedal mammalian gaits. Diagonal limbs moved approximately synchronously at all locomotor speeds in both species (Fig. 1). This synchronous movement was reflected in diagonal limb phase values of approximately 0 ° over the entire range of speeds (Fig. 1). The maximum diagonal limb phase was 40 °, and it occurred at a low speed in *C. variegatus*. This means that the forelimb hit the ground 11 % of the stride time before the hindlimb. In mammals, a trotting gait has a diagonal limb phase of 0 ° while a walking gait has a diagonal limb phase of 90 ° (Hildebrand, 1985). Thus, the footfall pattern observed in *C. variegatus* and *E. skiltonianus* was most similar to a mammalian trotting pattern over the entire range of speeds (Fig. 1). This pattern of nearly synchronous movement of diagonal limbs at low and high speeds has been observed previously in other lizard species (Snyder, 1952; Sukhanov, 1974).

Ground reaction force, velocity of the center of mass and vertical displacement of the center of mass

Two patterns of ground reaction force and movements of the center of mass were observed. The first pattern was similar to the walking or ‘inverted pendulum’ pattern that has been observed previously in other legged animals (Figs 2A, 3A). The second pattern was similar to the trotting or ‘bouncing’ pattern observed in other legged animals (Figs 2B, 3B). In Figs 2 and 3, a single step is shown, from the time when one pair of diagonal limbs first touched the ground until the time when the other pair of diagonal limbs hit the ground. The most important difference between these gaits was the pattern of fluctuation in the vertical displacement of the center of mass during the step. In some trials, the center of mass reached its highest point at mid-step (Figs 2A, 3A). This pattern is characteristic of walking gaits in other legged animals. In other trials, the center of mass reached its lowest value near the middle of the step (Figs 2B, 3B). This pattern is similar to that seen in other legged animals using bouncing gaits such as trotting, hopping and running.

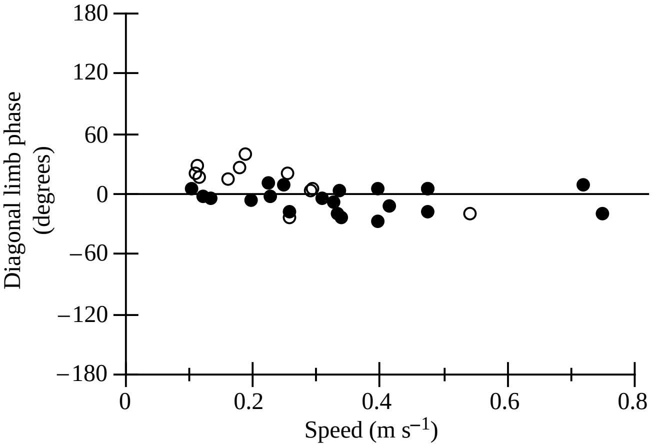

Fig. 1. Diagonal limb phase shift *versus* speed. A phase shift of 0 ° indicates that the forelimb and hindlimb in each diagonal pair hit the ground at the same time. A phase shift of 90 ° indicates that the forelimb hits the ground a quarter of the stride time before the contralateral hindlimb hits the ground. The open symbols represent trials by *Coleonyx variegatus* and the filled symbols represent trials by *Eumeces skiltonianus*.

In both species, the peak ground reaction force was higher in the trotting gait (Figs 2B, 3B) than in the walking gait (Figs 2A, 3A). In walking, the vertical ground reaction force did not exceed 1.05 times body weight. In trotting, the peak vertical ground reaction force was up to 1.6 times body weight. In both the walking and the trotting gaits, the vertical ground reaction force was never zero, indicating that there was no aerial phase. Thus, there was always at least one pair of diagonal limbs in contact with the ground in both the walking and the trotting gaits. In both gaits, the horizontal ground reaction force was negative during the first half of the step, pushing backwards on the lizard, and then became positive during the second half of the step. This pattern of horizontal ground reaction force is similar to that seen in a wide variety of legged animals during both walking and bouncing gaits (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987; Full, 1989; Full and Tu, 1990, 1991). The lateral ground reaction force fluctuated around zero in both gaits, and the magnitude of the fluctuations was greater in the trotting gait than in the walking gait (Figs 2, 3).

The fluctuations in the velocity of the center of mass were similar during the trotting gait, and the walking gait in both species (Figs 2, 3). These velocity fluctuations were largest in the horizontal direction. The horizontal velocity of the center of mass decreased during the first half of the step and increased during the second half of the step in both gaits (Figs 2, 3). The fluctuations in the lateral velocity of the center of mass were slightly smaller than the fluctuations in the horizontal velocity of the center of mass (Figs 2, 3). The lateral velocity of the center of mass was in one direction for the first half of the step, passed through zero near the middle of the step, and was in the opposite direction for the second half of the step (Figs 2, 3). There were no substantial differences between the species in terms of the fluctuations in the horizontal and lateral velocity of the center of mass.

Fluctuations in the mechanical energy of the center of mass

The fluctuations in the mechanical energy of the center of mass during locomotion can be divided into fluctuations in kinetic energy and fluctuations in gravitational potential

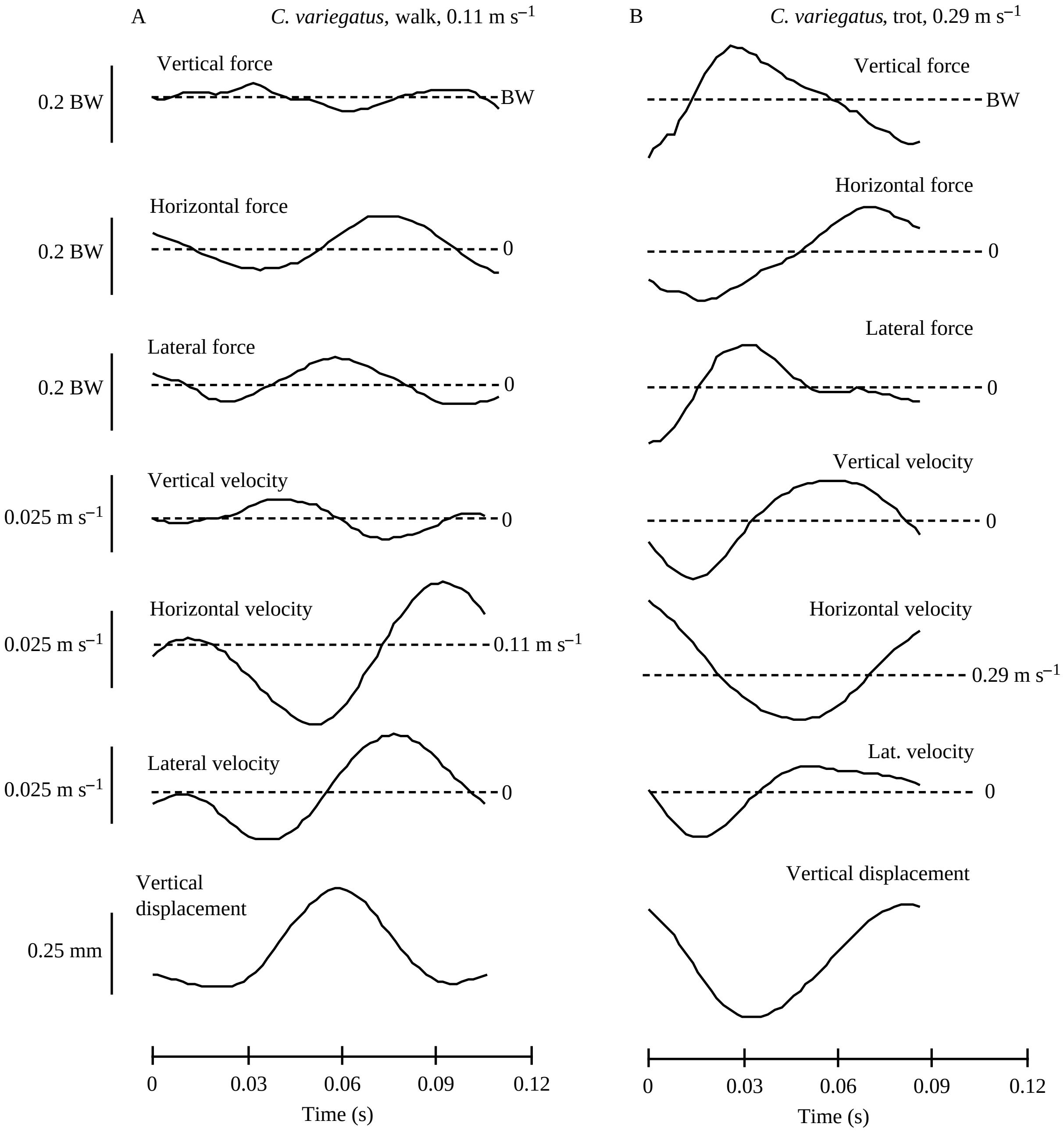

Fig. 2. Ground reaction force, velocity of the center of mass and vertical displacement of the center of mass *versus* time in *C. variegatus* for a walk (A) and a trot (B). A single step of each gait is shown for one individual, beginning when one diagonal limb pair hits the ground and ending when the other diagonal limb pair hits the ground. BW, body weight (0.034 N).

energy. In both the walking and the trotting gaits, the total kinetic energy of the center of mass decreased during the first half of the step, reached its minimum at mid-step, and increased during the second half of the step (Figs 4, 5). There were contributions to the total kinetic energy of the center of mass from the horizontal, vertical and lateral components of the velocity. The fluctuations in the horizontal component of the kinetic energy were substantially larger than the fluctuations in the lateral or vertical components of the kinetic energy. In both species using both gaits, the fluctuations in the horizontal kinetic energy were more than 20 times greater than the fluctuations in the lateral kinetic energy of the center of mass (Figs 4, 5).

In both species, we observed two distinct patterns of fluctuations in gravitational potential energy during a step (Figs 4, 5). In the first pattern, the gravitational potential energy reached a maximum near mid-step (Figs 4A, 5A). This pattern corresponds to the inverted pendulum gait observed previously in walking mammals. In this walking gait, the kinetic energy of the center of mass reached its minimum at nearly the same time as the gravitational potential energy reached its mid-step maximum (Figs 4A, 5A). Thus, the

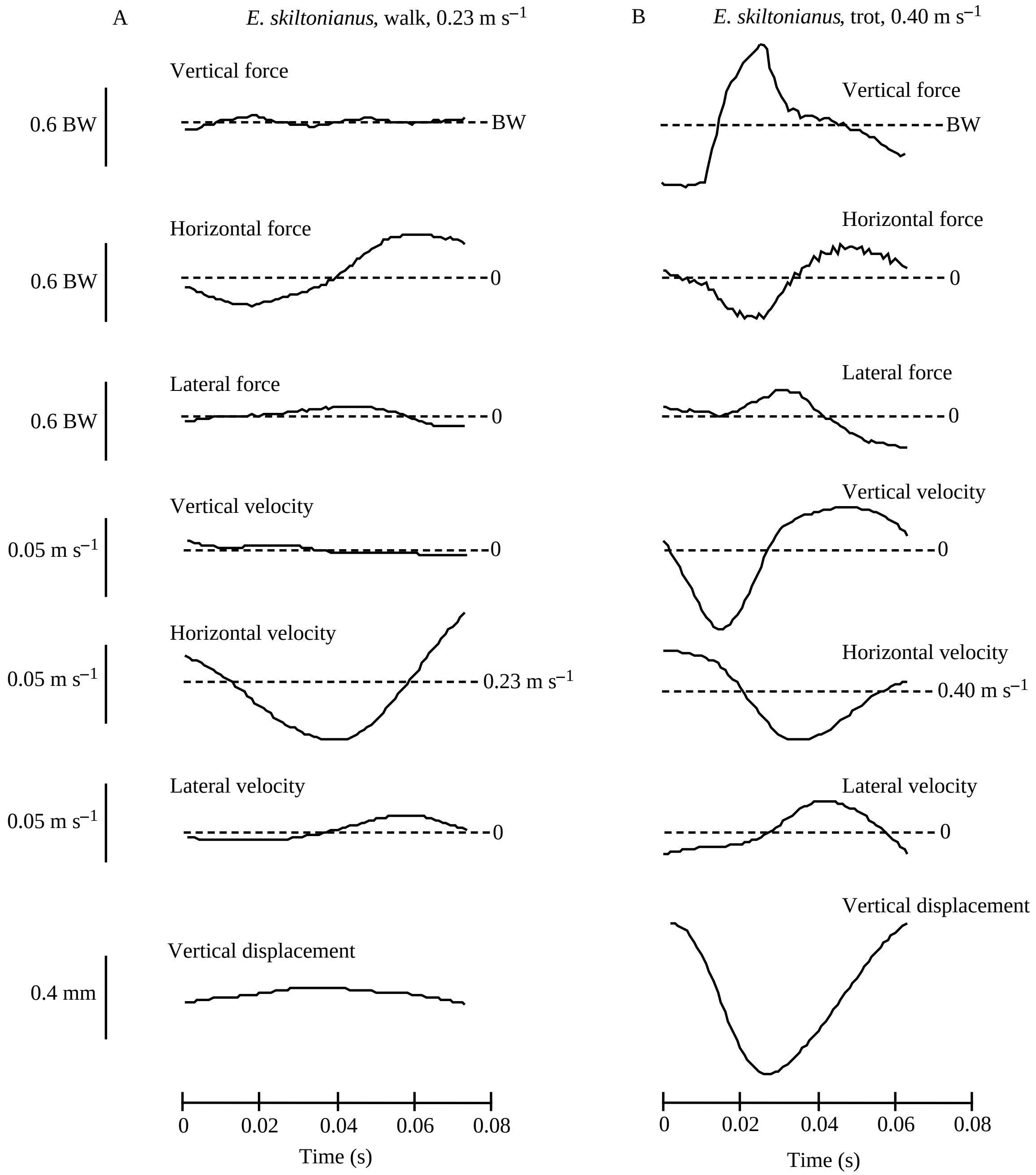

Fig. 3. Ground reaction force, velocity of the center of mass and vertical displacement of the center of mass *versus* time for a walk (A) and a trot (B) in *E. skiltonianus*. A single step is shown for one individual, beginning when one diagonal limb pair hits the ground and ending when the other diagonal limb pair hits the ground. BW, body weight (0.047 N).

'phase' between the gravitational potential energy and kinetic energy fluctuations was approximately 180 ° (Fig. 6). The recovery of mechanical energy by the inverted pendulum mechanism was maximized at the lowest speeds, reaching a maximum value of 51 % (Fig. 7). It is important to note that the recovery of mechanical energy by the inverted pendulum mechanism depends on several factors: the phase, shape and relative magnitudes of the fluctuations in gravitational potential energy and kinetic energy.

The second pattern of gravitational potential energy fluctuations during a step corresponds to the pattern seen in trotting mammals. In this pattern, the gravitational potential energy reached a minimum at mid-step (Figs 4B, 5B). The mid-step minimum in gravitational potential energy occurred at approximately the same time as the minimum in kinetic energy (Figs 4B, 5B). Thus, the phase between the fluctuations in gravitational potential energy and kinetic energy was approximately 0 ° in this gait (Fig. 6).

C. variegatus and *E. skiltonianus* used both walking and trotting gaits at low to moderate speeds but used only a trotting

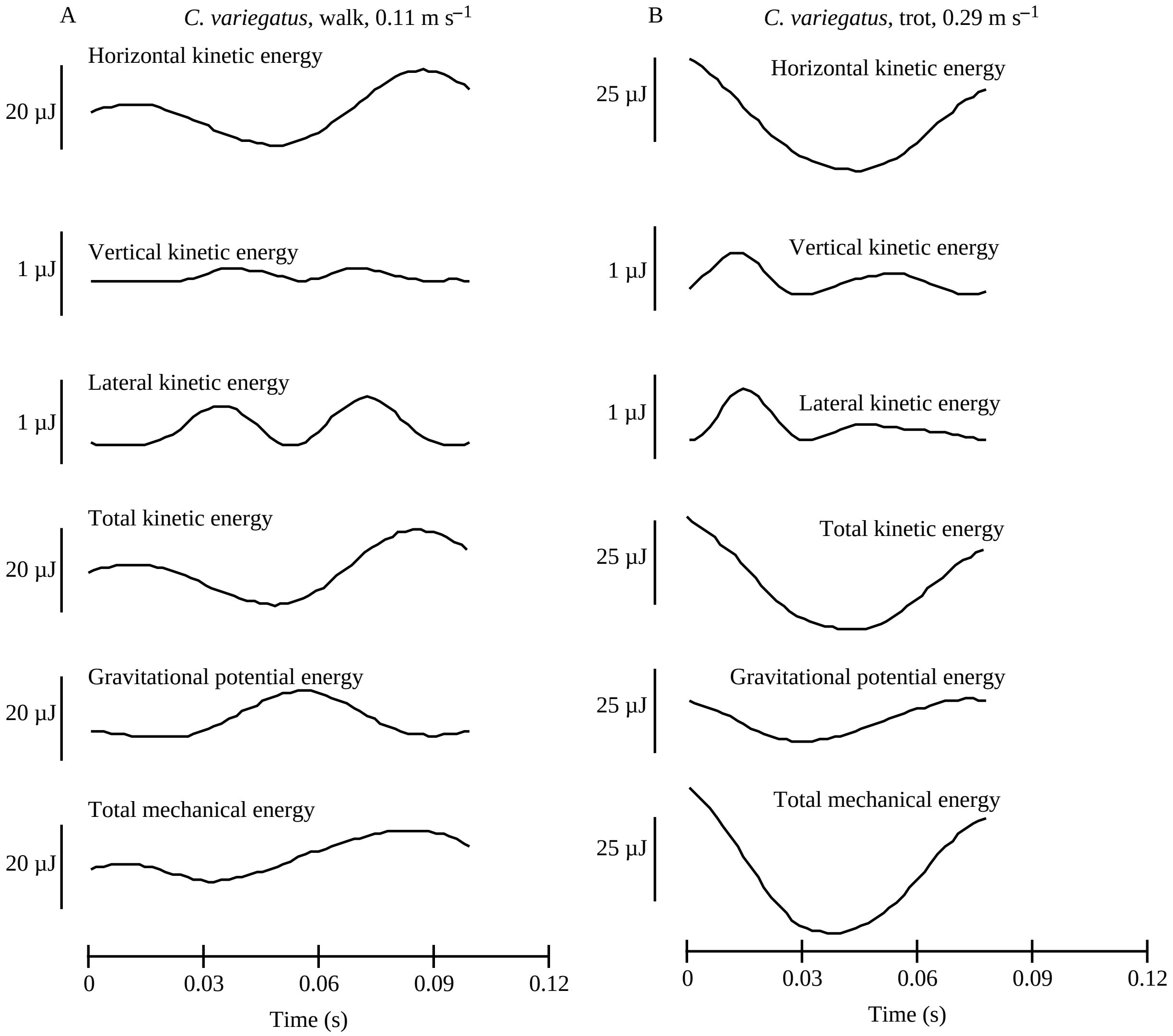

Fig. 4. Kinetic energy, gravitational potential energy and total mechanical energy of the center of mass *versus* time for a walk (A) and a trot (B) in *C. variegatus*. A single step is shown, beginning when one diagonal limb pair hits the ground and ending when the other diagonal limb pair hits the ground. The data are for the same step as shown in Fig. 2.

gait at the highest speeds (Fig. 6). Between 0.10 and $0.52\,\mathrm{m\,s^{-1}}$, the animals used gaits with phases of either approximately 0 ° (trot) or 180 ° (walk) (Fig. 6). Above $0.52\,\mathrm{m\,s^{-1}}$, they always used a trotting gait with a phase of approximately 0 ° (Fig. 6).

Mechanical power required to lift and accelerate the center of mass

The mechanical power required to lift and accelerate the center of mass is equal to the positive mechanical work required during each step of locomotion (Figs 4, 5) multiplied by the step frequency (Fig. 8). The step frequency increased by nearly threefold between the lowest and highest speeds. It is important to note that the step frequency reported here is twice as high as the stride frequency.

The mechanical power required to accelerate the center of mass in the horizontal direction (P_{horiz}) increased with forward speed (v) and was the largest component of the total mechanical power (Fig. 9; $P_{\mathrm{horiz}}=-0.19+1.4v$, $r^2=0.84$, $P<0.0001$). At all speeds, the mechanical power required to accelerate the center of mass in the lateral direction was less than 5 % of the mechanical power required to accelerate the center of mass in the horizontal direction. Both the lateral component (P_{lat}) and the vertical component (P_{vert}) of the external mechanical power increased with speed ($P_{\mathrm{lat}}=-0.00079+0.012v$, $r^2=0.27$, $P=0.0008$; $P_{\mathrm{vert}}=0.0078+0.155v$, $r^2=0.38$, $P<0.0001$). At the highest speed, the vertical component was approximately 15 % of the horizontal component, and the lateral component was approximately 1 % of the horizontal component.

The total external mechanical power increased over the range of speeds to a maximum value of approximately $0.9\,\mathrm{W\,kg^{-1}}$ at the highest speed (Fig. 9). Its magnitude was similar to the magnitude of the horizontal component because

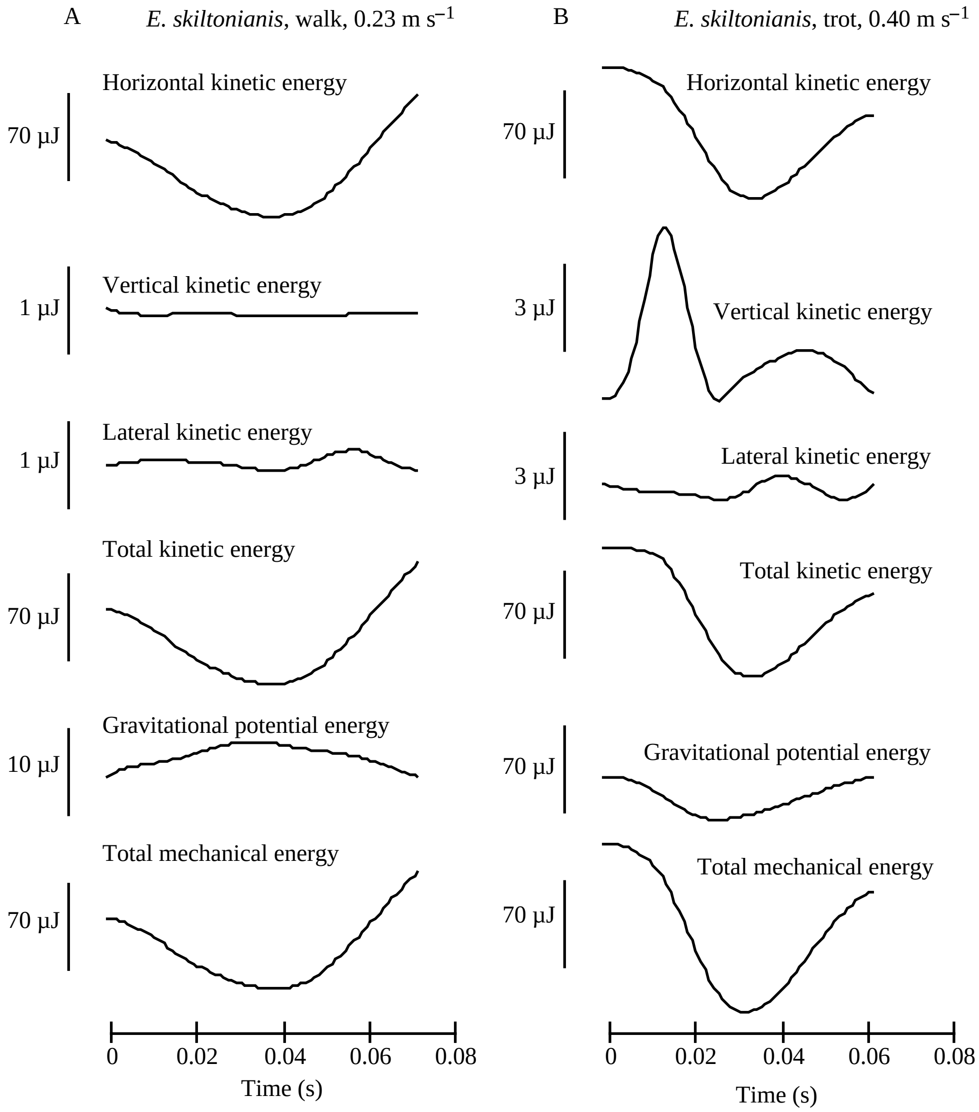

Fig. 5. Kinetic energy, gravitational potential energy and total mechanical energy of the center of mass *versus* time for a walk (A) and a trot (B) in *E. skiltonianus.* A single step is shown, beginning when one diagonal limb pair hits the ground and ending when the other diagonal limb pair hits the ground. The data are for the same step as shown in Fig. 3.

the horizontal component was so much greater than the vertical or lateral components (Fig. 9). The data for the two species appeared to be similar, although we were unable to obtain many moderate- or high-speed trials in which *C. variegatus* moved at a steady speed. The linear least-squares regression for the mass-specific total external mechanical power output *versus* speed was similar regardless of whether the data for the two species were analyzed together or separately (see Fig. 9 legend). It is important to note that the total external mechanical power was not equal to the sum of the horizontal, vertical and lateral components of the power because of recovery of mechanical energy by the inverted pendulum mechanism (Fig. 9).

The slope of the total external mechanical power output *versus* speed relationship is the external mechanical work

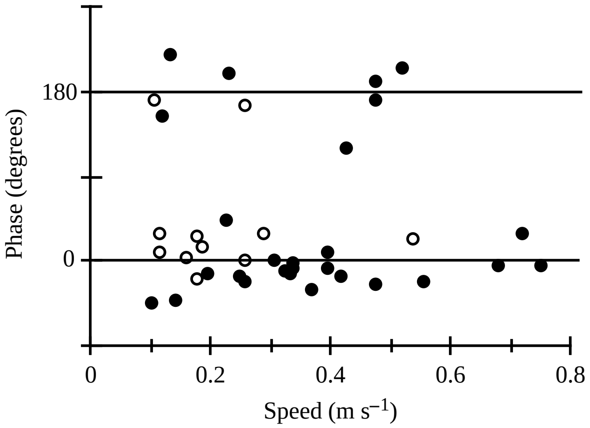

Fig. 6. Phase between the fluctuations in kinetic energy and the fluctuations in gravitational potential energy *versus* speed. When the phase was approximately 180 °, the minimum in kinetic energy occurred at nearly the same time as the maximum in gravitational potential energy. When the phase was approximately 0 °, the minima in kinetic energy and gravitational potential energy occurred at nearly the same time. The open symbols represent trials by *C. variegatus* and the filled symbols represent trials by *E. skiltonianus*.

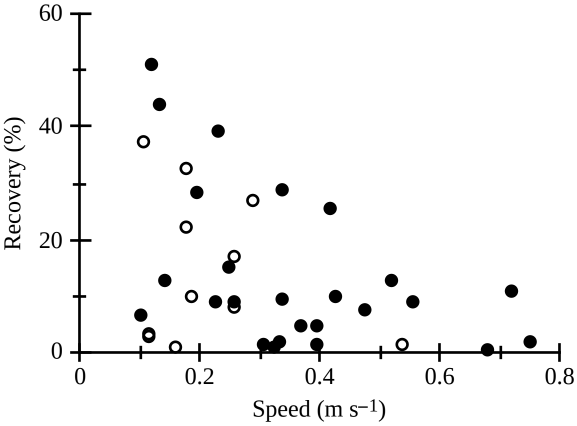

Fig. 7. Recovery of mechanical energy by the inverted pendulum mechanism *versus* speed. The open symbols represent trials by *C. variegatus* and the filled symbols represent trials by *E. skiltonianus.*

required to travel 1 m. For *C. variegatus* and *E. skiltonianus,* 1.5 J kg^{-1} of mechanical work was required to travel 1 m.

Discussion

With each step, a lizard's trunk bends from side to side (Sukhanov, 1974; Avery *et al.* 1987; Ritter, 1992, 1995). Lizard locomotion appears to be fundamentally different from mammalian locomotion because of the substantial lateral trunk bending involved in their gait. Some lizards are limbless and rely on lateral bending for forward propulsion (Gans, 1975, 1986; Withers, 1981; Renous *et al.* 1995). This observation suggests that the limbs may play a less important role in determining the mechanics of locomotion in lizards than in mammals. In mammals, the mechanical behavior of the limbs, acting as stiff struts during walking and compliant springs during running, is of primary importance in determining the mechanics of locomotion.

Our findings show that lizards use the same two basic patterns of locomotor mechanics as mammals: an inverted pendulum gait and a bouncing gait. Both *C. variegatus* and *E. skiltonianus* use an inverted pendulum or walking gait at low speeds. In this gait, the gravitational potential energy of the center of mass reaches a maximum at the middle of the step, at nearly the same time as the kinetic energy reaches a minimum. This walking gait is distinctly different from the bouncing or trotting gait used by both lizards species at high speeds. In the trotting gait, the gravitational potential energy of the center of mass reaches its minimum value at mid-step, at approximately the same time as the kinetic energy reaches its minimum. This bouncing gait is similar to a mammalian trotting gait in terms of the fluctuations in the mechanical energy of the center of mass and the footfall pattern.

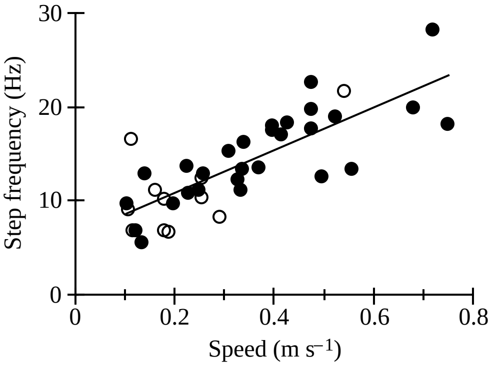

Fig. 8. Step frequency increased by nearly threefold between the lowest and highest speeds. The open symbols represent trials by *C. variegatus* and the filled symbols represent trials by *E. skiltonianus.* The line is the linear least-squares regression (f=6.31+22.8v, where f is step frequency and v is forward velocity, r^2=0.63, P<0.0001).

As a lizard's trunk bends from side to side with each step, the kinetic energy of the center of mass fluctuates because of changes in the lateral velocity of the center of mass. Our results show that the mechanical power required to accelerate the center of mass in the lateral direction represents less than 5 % of the total mechanical power at all speeds (Fig. 9). The highest speed examined was the maximum speed for *E. skiltonianus* and 65 % of the maximum speed for *C. variegatus* for a body temperature of 25 °C (Farley, 1997). These animals are likely to be able to run faster at higher body temperatures (Huey *et al.* 1989). However, it seems unlikely that the mechanical power required to move the center of mass laterally will become a substantial fraction of the total mechanical power at higher speeds because it is such a small component at all of the speeds included in the present study. To investigate further the generality of our findings, it would be useful to examine the mechanical energy associated with lateral undulation in these species at higher temperatures and in lizard species that are particularly fast runners.

The mass-specific total external mechanical work required to travel 1 m is similar in these lizards to that in other legged animals. Past research has revealed that the mass-specific mechanical work required to travel 1 m does not change systematically with body mass (range 0.0008–100 kg), morphology or gait among legged animals. On average, animals require 1.15±0.43 J kg^{-1} (mean ± S.D.) to travel 1 m (Heglund *et al.* 1982; Full, 1989). Our data show that *C. variegatus* and *E. skiltonianus* require 1.5 J kg^{-1} to travel 1 m, a value that falls within the range observed in other legged animals (0.5–1.8 J kg^{-1} m^{-1}; Heglund *et al.* 1982; Full, 1989) in spite of the marked lateral bending of their trunks during locomotion. The data for the lizards in this study are near the upper end of the range, but lateral trunk bending is not the reason. Lateral movements of the center of mass constitute less than 5 % of the total external mechanical power at all speeds (Fig. 9). It is important to note that this analysis only includes the mechanical power required to lift and accelerate the center of mass of the animal. Future research should examine the internal mechanical power required to move the body segments, including the limbs and trunk, relative to the center of mass of lizards during locomotion.

There are substantial differences in morphology and physiology between the two lizard species in this study, but

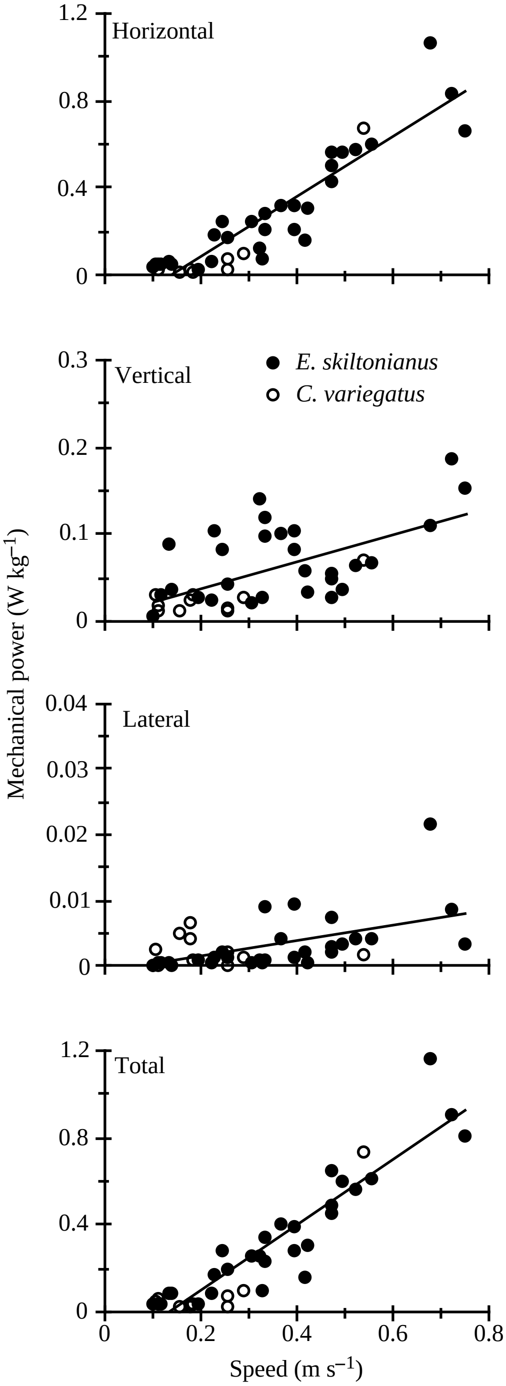

Fig. 9. Mass-specific external mechanical power *versus* speed for *C. variegatus* (open symbols) and *E. skiltonianus* (filled symbols). The largest component was the mechanical power required to accelerate the center of mass in the horizontal direction. At the highest speed, the horizontal component was more than five times greater than the mechanical power required to lift and accelerate the center of mass in the vertical direction and 50 times greater than the component required to accelerate the center of mass in the lateral direction. The lines are the linear least-squares regressions. When the data for *C. variegatus* and *E. skiltonianus* were analyzed together, the linear least-squares regression was $P_{\mathrm{ext}}=-0.20+1.5v$, where P_{ext} is the mass-specific external mechanical power and v is forward velocity ($r^2=0.86$, $P<0.0001$). When the *E. skiltonianus* data were analyzed alone, the linear least-squares regression equation was $P_{\mathrm{ext}}=-0.19+1.5v$ ($r^2=0.84$, $P<0.0001$). Finally, when the *C. variegatus* data were analyzed alone, the linear least-squares regression equation was $P_{\mathrm{ext}}=-0.21+1.5v$ ($r^2=0.78$, $P=0.0003$).

our findings show no substantial differences in locomotion mechanics. First, *E. skiltonianus* has diminutive limbs (total limb mass=6 % of body mass) compared with *C. variegatus* (total limb mass=16 % of body mass). Moreover, *E. skiltonianus* is a member of a family (Scincidae) in which numerous species have extremely reduced limbs or are limbless (Gans, 1975; Withers, 1981). However, our findings show that *E. skiltonianus* uses the same two basic gaits as *C. variegatus* and other legged animals. The second important difference between these species is that the metabolic energy cost of level locomotion is 40 % lower in *C. variegatus* than in *E. skiltonianus* (Farley and Emshwiller, 1996). Although we did not obtain any steady-speed trials at speeds below the maximum aerobic speed for the body temperature used in this study (0.056 m s^{-1}; Farley and Emshwiller, 1996; Autumn *et al.* 1997), our data show no substantial differences in locomotion mechanics between these two species.

Both lizard species in this study, *C. variegatus* and *E. skiltonianus*, can save substantial mechanical energy through the inverted pendulum mechanism during low-speed locomotion. The maximum recovery of energy (51 %) observed in these lizards is similar to the maximum recovery in other quadrupedal walking animals including dogs (50 %) and rams (35 %) (Cavagna *et al.* 1977). For the lowest range of speeds in our study (0.1–0.2 m s^{-1}), there was substantial variation in percentage recovery, with a mean value of 19.5 %. The animals in our study never moved across the force platform at speeds below the maximum aerobic speed. In other animals, energy recovery by the inverted pendulum mechanism is maximized at low sustainable speeds (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987; Willems *et al.* 1995), and it seems likely that energy conservation is most important during low-speed sustained locomotion.

Quadrupedal mammals typically walk at low speeds, trot at moderate speeds and gallop at the highest speeds. Near each gait transition, a mammal is capable of using either gait (Hoyt and Taylor, 1981; Farley and Taylor, 1991). Our findings show that these lizards can walk or trot at speeds between 0.1 m s^{-1} and approximately 0.5 m s^{-1}. Above approximately 0.5 m s^{-1}, they only trot. We did not observe a range of very low speeds at which *C. variegatus* and *E. skiltonianus* only walked. However, it is important to note that the trials obtained for this study were above the maximum aerobic speed (Farley and Emshwiller, 1996; Autumn *et al.* 1997) and approached the maximum sprinting speed of approximately 0.8 m s^{-1} for a body temperature of 25 °C (Farley, 1997). As a result, it is possible that there is a range of low and sustainable speeds, normally used by these species when they are undisturbed in their natural habitat, at which they use only a walking gait.

The maximum speed at which animals are capable of walking can be predicted from the mechanics of the inverted pendulum model for walking (Alexander, 1989; Kram *et al.* 1997). This model predicts that the maximum possible walking speed will be the speed at which the downward force on the center of mass due to gravity is equal to the centripetal force that is required to keep the feet on the ground as the animal vaults over the stance limbs. The ratio of centripetal force to gravitational force is referred to as the Froude number and is equal to $v^2/\boldsymbol{g}L$, where v is forward speed, $\boldsymbol{g}$ is gravitational acceleration and L is leg length or the distance from the ground to the shoulder or hip (Alexander, 1989). When the Froude number is less than or equal to 1, the weight of the animal supplies a large enough downward force to keep the body in a circular arc as it vaults over the stance limbs during walking. When the Froude number is greater than 1, the gravitational force on the center of mass is less than the required centripetal force and, as a result, an animal is not capable of walking. This simple model predicts the observed maximum walking speed in *E. skiltonianus* remarkably accurately. We based our calculations on data from *E. skiltonianus* because we obtained a wider range of speeds for *E. skiltonianus* than *C. variegatus*. On the basis of the leg length of *E. skiltonianus* (0.02 m, average of front and hind limbs), a Froude number of 1 corresponds to a maximum walking speed of $0.44\,\mathrm{m\,s^{-1}}$, a value quite close to the observed maximum speed at which the walking gait was used, $0.52\,\mathrm{m\,s^{-1}}$.

We conclude that, in spite of the obvious lateral bending of their trunks during locomotion, lizards use two basic gaits similar to those of other legged animals: an inverted pendulum gait and a bouncing gait (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan and Full, 1987; Full and Tu, 1990). Lateral bending of the trunk during lizard locomotion requires very little external mechanical power, and the external mechanical work required to travel 1 m is similar in lizards to that in other legged animals such as dogs, humans, quail and ghost crabs (Heglund *et al.* 1982; Full, 1989). These findings show that the mechanics of locomotion in animals with legs is remarkably similar regardless of body morphology, body size and evolutionary history.

The authors thank K. Autumn and R. J. Full for their input to this project. They also thank Dale Denardo for his invaluable assistance with lizard care. This research was supported by grants to C.T.F. from the National Institutes of Health (AR08189) and the University of California Faculty Committee on Research.

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