MECHANICS OF A RAPID RUNNING INSECT: TWO-, FOUR- AND SIX-LEGGED LOCOMOTION

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Summary

To examine the effects of variation in body form on the mechanics of terrestrial locomotion, we used a miniature force platform to measure the ground reaction forces of the smallest and, relative to its mass, one of the fastest invertebrates ever studied, the American cockroach *Periplaneta americana* (mass=0.83 g). From $0.44–1.0 \, \mathrm{m\,s^{-1}}$, *P. americana* used an alternating tripod stepping pattern. Fluctuations in gravitational potential energy and horizontal kinetic energy of the center of mass were nearly in phase, characteristic of a running or bouncing gait. Aerial phases were observed as vertical ground reaction force approached zero at speeds above $1 \, \mathrm{m\,s^{-1}}$. At the highest speeds ($1.0–1.5 \, \mathrm{m\,s^{-1}}$ or 50 body lengths per second), *P. americana* switched to quadrupedal and bipedal running. Stride frequency approached the wing beat frequencies used during flight (27 Hz). High speeds were attained by increasing stride length, whereas stride frequency showed little increase with speed. The mechanical power used to accelerate the center of mass increased curvilinearly with speed. The mass-specific mechanical energy used to move the center of mass a given distance was similar to that measured for animals five orders of magnitude larger in mass, but was only one-hundredth of the metabolic cost.

Introduction

Animals that vary in leg number, leg orientation, body shape and skeletal type show similarities in the mechanics of terrestrial locomotion when the effect of body mass is removed (Full, 1989). Surprisingly, eight-legged ghost crabs (Blickhan and Full, 1987), six-legged *Blaberus* cockroaches (Full and Tu, 1990) and two- and four-legged vertebrates (Cavagna *et al.* 1977; Heglund *et al.* 1982*a,b*) can have similar patterns of ground reaction force and energy fluctuations of the center of mass, maximum stride frequencies and mechanical power outputs.

Eight-legged sideways-moving crabs use walking and running gaits comparable to those described in birds and mammals (Blickhan and Full, 1987). Ghost crabs

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use an inverted pendulum-like mechanism at slow speeds. At fast speeds, the crab gallops by a series of leaps during which all eight legs leave the ground (Blickhan and Full, 1987; Burrows and Hoyle, 1973). No aerial or flight phase is observed at lower speeds. However, the mechanics of the center of mass are still characteristic of running gaits. Horizontal kinetic and gravitational potential energy fluctuate in phase and the body attains its greatest height at midstance. Full and Tu (1990) used the same mechanical criteria to define the gait of the cockroach B. discoidalis as a running or bouncing gait, despite the absence of an aerial phase. The absence of an aerial phase may not necessarily exclude a gait from being a run or a trot (McMahon, 1985; McMahon et al. 1987).

Four-, six- and eight-legged runners may have mechanically or physiologically equivalent speeds (Full, 1989). Quadrupedal mammals attain a maximum sustainable stride frequency when they switch gait from a trot to a gallop (Heglund et al. 1974). Maximum sustainable stride frequency, as well as the speed at which it is attained, scale as a regular function of body mass (Heglund and Taylor, 1988; Heglund et al. 1974). Ghost crabs (Blickhan and Full, 1987) and cockroaches (B. discoidalis; Full and Tu, 1990) both attain a maximum sustainable stride frequency. Remarkably, when the effect of body mass is removed, ghost crabs, Blaberus cockroaches, rats, dogs and horses have similar values for maximum sustainable stride frequency as well as the speed at which it is attained (Full, 1989).

Mechanical power output of the center of mass increases with speed in two-, four-, six- and eight-legged runners (Cavagna et al. 1977; Heglund et al. 1982a; Full, 1989). When the effects of body mass are removed, the mechanical power output of the center of mass is similar in ghost crabs (Blickhan and Full, 1987), Blaberus cockroaches (Full and Tu, 1990), birds and mammals (Cavagna et al. 1977; Heglund et al. 1982a,b).

Even though the similarities in pedestrian locomotor mechanics are striking, the small number of diverse locomotor designs tested (i.e. one insect, one crustacean, four birds and nine mammals) prevents the quantification of differences in mechanics due to variation in morphology and physiology. In the present study we examine a six-legged pedestrian adapted for high-speed locomotion, the American cockroach Periplaneta americana. McConnell and Richards (1955) reported speeds for P. americana of $1.3\,\mathrm{m\,s^{-1}}$, equivalent to nearly 40 body lengths per second. Delcomyn (1971) measured stride frequencies that approach the wing beat frequencies used during flight (25 Hz). Morphological features, such as long, narrow legs relative to body size, are consistent with this high-speed locomotor capacity. Study of the locomotor mechanics of the American cockroach allows comparison with our previous research on the much slower cockroach B. discoidalis (Full and Tu, 1990). Maximum speed for B. discoidalis is less than half that found for P. americana. Moreover, B. discoidalis is simply a more awkward runner (i.e. more apparently wasted motion such as pitching and rolling) than the American cockroach.

Specifically, we address three hypotheses. First, insects are confined to statically stable walking gaits. Rejection of this hypothesis would support the conclusion of

Full and Tu (1990) that insects use a gait that is mechanically similar to the bouncing gait of running ghost crabs and two- and four-legged vertebrates. Second, *P. americana* have physiologically or mechanically equivalent speeds to those used by other pedestrians, as defined by gait and stride frequency changes. Third, the mechanical power output of *P. americana* is similar to that generated by *B. discoidalis* and other pedestrians, despite variation in morphology (i.e. adaptation for high-speed locomotion).

Materials and methods
Animals

Periplaneta americana (0.83 ± 0.07 g, S.D., $N=8$) were obtained from Carolina Biological Supply Company. Cockroaches were housed in individual containers with a layer of cedar shavings. Animals were given water and Purina Puppy Chow *ad libitum*. All animals were kept on a local photoperiod at ambient temperatures (24 ± 2°C). Trials were conducted at 23–26°C.

Force measurements

We measured vertical, horizontal and lateral ground reaction forces using a force platform (Full and Tu, 1990). A model aircraft plywood plate (10.7 cm$\times6$ cm$\times0.06$ cm) was mounted on four brass beams. Semiconductor strain gauges bonded to spring blades cut from the brass supporting beams responded to forces acting on the plywood cover. The force platform was inserted into the floor of a Plexiglas and cardboard track. Force signals were filtered using a Butterworth filter at a cut-off frequency of 210 Hz (unloaded natural frequency of the plate$=400$–650 Hz).

To measure lateral forces, we rotated the force platform by 90°. Strain gauges which measured force in the horizontal direction were placed in position to measure lateral forces. Vertical and lateral forces were measured simultaneously for each trial.

Data acquisition

Signals from each force platform channel were amplified (Vishay, Measurements Group) and collected by an analog to digital converter (C-100, Cyborg) interfaced with a computer (IBM PC/AT). Force signals were sampled at a frequency of 1000 samples s^{-1}. Integration of force records was performed using data acquisition and analysis software (Discovery, Cyborg). Energy fluctuations were calculated using macros in linked electronic spreadsheets (Lotus 1–2–3).

Kinematic analysis

Dorsal and lateral views were filmed simultaneously using video cameras capturing 60–300 frames s^{-1} (Video Logic CDR460 and 660). Video frames were

grabbed and the coordinates of the leg positions at each frame were digitized into a computer (IBM PC/AT) using a video analysis system (Peak Performance Technologies Inc.). During the digitizing process, the video frame number corresponding to the first step on the force platform was recorded. This frame was synchronized to the forces by matching it to the first interval that showed an increase in vertical ground reaction force. Thirty high-speed trials (i.e. $>1.0 \, \mathrm{m \, s^{-1}}$) were videotaped specifically to clarify leg movement and position. Ground reaction forces were not measured and these trials were not included in the dynamics analysis.

Speed

The average speed of the animal was calculated by dividing the length of the force plate plus the body length of the animal by the duration of the vertical force recording. This method gives results consistent with speed determinations made from the high-speed video recordings.

Stride period, frequency and length

Synchronization of the video and force recordings showed that, at all speeds, maxima and minima of the vertical force recording clearly defined each stride period (i.e. one complete cycle of protraction and retraction of a leg). Stride frequencies were calculated from the duration of the stride or strides selected from the trials used for energy analysis. Stride length was calculated by dividing the average speed by stride frequency.

Velocity and displacement of the center of mass

Segments of the force recordings were selected for analysis if they contained one or more complete strides in which the sum of the increases and decreases in speed were within 10 % of the average speed of the animal (see Full and Tu, 1990). The horizontal and lateral velocity of the center of mass were calculated by integrating the horizontal and lateral force recordings, respectively. The vertical velocity of the center of mass was calculated from integration of the vertical force recording minus the body mass. An additional integration of the vertical velocity yielded the vertical displacement of the center of mass. The average speed of the animal was used as the integration constant for the horizontal velocity of the center of mass. The integration constants for the vertical and lateral component of velocity and for the vertical displacement of the center of mass were assumed to be zero.

Energy calculations

Calculations of the energy fluctuations of the center of mass were performed as in Blickhan and Full (1987), Cavagna (1975), Heglund et al. (1982a) and Full and Tu (1990). The horizontal, lateral and vertical kinetic energy changes of the center of mass (E_k) were calculated from the velocity changes of the center of mass. Gravitational potential energy of the center of mass (E_p) was calculated from the vertical displacement. The power output of each individual component was

determined by summing the positive increments over an integral number of strides and dividing by the duration of the strides. At each sampling period (i.e. 1 ms) the vertical, lateral and horizontal kinetic and gravitational potential energies were summed to obtain the total energy of the center of mass (E_{cm}). The power generated to lift and accelerate the center of mass ($\dot{E}_{cm}$) was calculated from the sum of the positive increments of E_{cm} over an integral number of strides divided by the duration of the strides.

Results

Speed, gait and ground reaction forces

P. americana moved either rapidly, in response to prodding, or slowly when left undisturbed. They did not travel at intermediate speeds (see Kozacik, 1981). Locomotion at low speeds (less than 0.15 m s^{-1}) was intermittent. The cockroaches sustained a constant horizontal speed only when moving at speeds between 0.44 and 1.5 m s^{-1}.

At all speeds, *P. americana* ran using two alternating set(s) of one, two or three legs. Despite variation in the number of legs contacting the ground, the pattern of ground reaction force production during each step was consistent over the entire speed range. During each step, the animal accelerated its center of mass upwards, forwards and to one side. The propulsive phase of one stride corresponded to a maximum or minimum in vertical, horizontal and lateral forces (Fig. 1A,B). As the center of mass fell, vertical force increased and the insect decelerated its body in the horizontal direction (Fig. 1A,E, t_1). Peak vertical ground reaction force was 1.5–1.9 times the weight of the cockroach. As the animal accelerated its center of mass forwards and upwards, vertical force decreased to values less than body weight (Fig. 1A,E, t_2).

At speeds less than 1.0 m s^{-1}, *P. americana* ran using an alternating tripod stepping pattern. The right front, left middle and right hind legs all moved simultaneously, while each moved out of phase with its contralateral pair.

Vertical force frequently decreased to less than 10 % of the animal's weight and approached zero at speeds above 1 m s^{-1}. *P. americana* attained an aerial phase at the fastest speeds (1.0–1.5 m s^{-1}; Fig. 2). High-speed video recordings (300 frames s^{-1}) showed that, at these high speeds, the insect raises its body off the substratum (from 0.5 to 1.0 cm) and increases its body's angle of attack (from 0 to 30° relative to the horizontal). In half of the high-speed runs ($N=13$), cockroaches used only four legs (i.e. middle and hind legs). In the other half of the high-speed runs, cockroaches ran bipedally, propelling themselves exclusively with their hind legs (Fig. 2).

At speeds less than 1.0 m s^{-1}, maximum lateral force was observed once during each step at approximately the same time as the maximum vertical force. The direction of the lateral force was determined by the side of the body with two legs of the tripod in contact with the ground. A net lateral force to the left occurred
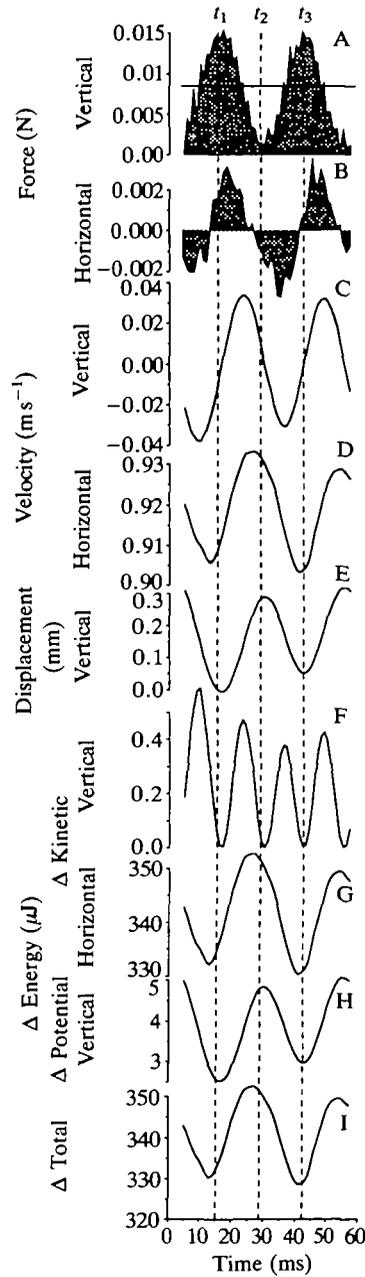
R. J. Full and M. S. Tu

Fig. 1

when the body was supported and propelled by the left hind, left front and right middle legs. Propulsion by the alternate set of legs produced a net force to the right. Lateral force maxima varied in magnitude between one-fifth and three-quarters of the magnitude of the fluctuations in vertical force. Lateral forces were more variable during two- and four-legged high-speed running.

Fig. 1. Ground reaction force, velocity, displacement and energy fluctuations of the center of mass for one stride for *Periplaneta americana* weighing 0.81 g (0.0079 N) running at $0.92\,m\,s^{-1}$. (A) Vertical force recording from the force platform. The horizontal line represents the animal's weight; (B) horizontal force; (C) vertical and (D) horizontal velocity calculated by integration of the force recordings; (E) vertical displacement calculated by integration of the vertical velocity; (F) vertical kinetic energy; (G) horizontal kinetic energy; (H) gravitational potential energy; (I) total mechanical energy of the center of mass (E_{cm}) obtained by summing the vertical kinetic, horizontal kinetic and gravitational potential energy recordings. See text for an explanation of t_1, t_2 and t_3.
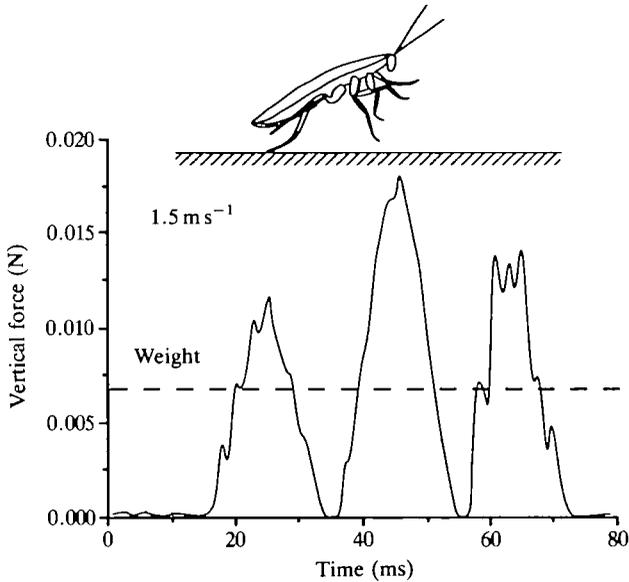

Fig. 2. Vertical ground reaction force pattern for bipedally running American cockroaches. Cockroaches used their hind legs to propel their body. Vertical force decreased to zero showing that the cockroach had all six legs off the ground in an aerial phase. Cockroaches ran with their body elevated from the ground and their head end angled upward (angle of attack=23°).

Phase relationship between horizontal kinetic and gravitational potential energy

The oscillations in horizontal kinetic and gravitational potential energy (Fig. 1G,H) followed periodic functions that repeated every step. For an individual step, phase shift was defined as zero if the maximum of the gravitational potential energy occurred in phase with the nearest maximum of horizontal kinetic energy. Phase shift was considered negative if the horizontal kinetic energy maximum preceded the nearest maximum of gravitational potential energy. If the horizontal kinetic energy maximum followed the maximum of gravitational potential energy, then the phase shift was considered positive. If the horizontal kinetic and gravitational potential energy maxima were completely out of phase, then the
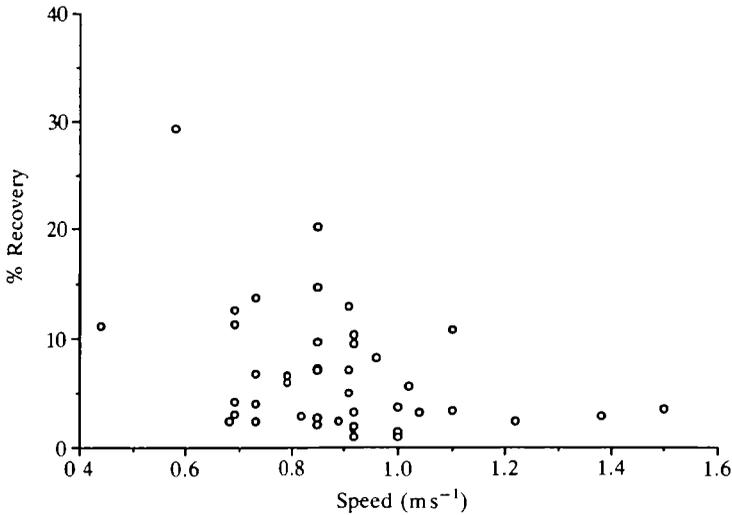
Fig. 3. Percentage energy recovery due to pendulum-like energy exchange as a function of speed.

phase shift would equal $\pm 180°$. For *P. americana*, the magnitude of the changes in the gravitational energy during each step was small, and the overall pattern was often irregular because of small net displacements of the center of mass over a stride. However, the periodicity of the potential energy fluctuations could easily be determined. Kinetic and gravitational potential energy changes of the center of mass tended to occur in phase. The mean phase shift ($-46\pm9.06°$ s.e.) was significantly different from that predicted for a walk (i.e. $\pm 180°$; $t=14.7$; $P<0.001$).

Energy recovery

The magnitude of energy recovery can be calculated by comparing the mechanical energy generated to sustain a constant forward speed if no energy exchange occurred with the amount of energy actually expended. Energy recovery was calculated by:

$$\% \text{ recovery} = \frac{(\Sigma \Delta E_k + \Sigma \Delta E_p - \Sigma \Delta E_{cm})\ 100}{\Sigma \Delta E_k + \Sigma \Delta E_p},$$

where $\Sigma \Delta E_k$, $\Sigma \Delta E_p$ and $\Sigma \Delta E_{cm}$ are the sums of the positive changes in the kinetic, potential and total energy of the center of mass, respectively. If fluctuations in potential and kinetic energy of the center of mass are equal in magnitude and out of phase, recovery will be 100%. The fluctuations in potential and kinetic energy of the center of mass for *P. americana* were nearly in phase. The mean energy recovery was $6.7\pm0.88\%$ s.e. ($N=42$; Fig. 3).

Stride frequency and stride length

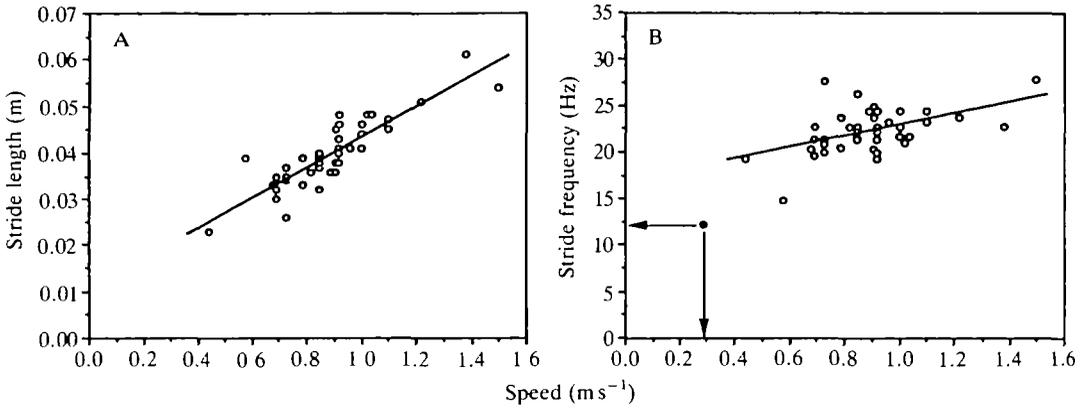Stride length (in units of m) increased as speed (v, m s^{-1}) increased: stride

Fig. 4. (A). Stride length as a function of speed for *Periplaneta americana*. Stride length increased as running speed increased. (B). Stride frequency as a function of speed. Increased running speed did not result in a large increase in stride frequency. The closed circle shows the speed and stride frequency predicted for a 1 g animal using the allometric equations from mammals for the trot–gallop transition (Heglund *et al.* 1974). The pattern of stride length and stride frequency for *P. americana* is characteristic of animals traveling at speeds above the trot–gallop transition.

length=$0.033\pm0.0029v$ (s.e.) $+0.011\pm0.003$ (s.e.) (Fig. 4A). Stride frequency (Hz) also increased significantly with speed: stride frequency=$6.3\pm1.6v$ (s.e.) $+16.6\pm1.5$ (s.e.) (Fig. 4B).

Mechanical energy of the center of mass

The mass-specific power used to lift and accelerate the center of mass ($\dot{E}_{cm}$, W kg^{-1}) increased with increasing speed (v, m s^{-1}): $\dot{E}_{cm}=1.47\pm0.29v$ (s.e.) -0.16 ± 0.27 (s.e.) (Fig. 5). Mechanical power generation due to fluctuations in horizontal kinetic energy increased as running speed increased and comprised the largest fraction of the total mechanical power output of the center of mass (Fig. 6). In contrast, fluctuations in the vertical and lateral kinetic and gravitational potential energies contributed a small percentage to $\dot{E}_{cm}$ and both remained constant or decreased in magnitude as running speed increased.

High-speed running by *P. americana* sometimes involved small net changes in the height of the center of mass over several strides in addition to the vertical oscillations associated with each step. Our calculation of the gravitational potential energy changes, therefore, included a contribution of energy due to net displacement of the center of mass. The change in energy due to these displacements was small relative to our estimates of $\dot{E}_{cm}$. Recalculation of the gravitational potential energy changes without the assumption of constant vertical position produced energy values that change $\dot{E}_{cm}$ by less than 10 %.
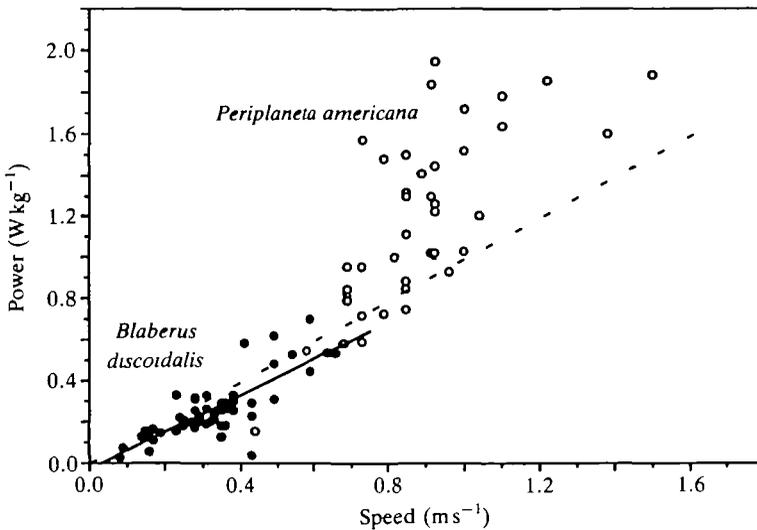
Fig. 5. Mechanical power ($\dot{E}_{cm}$) used to lift and accelerate the center of mass as a function of speed. Open circles represent data for *Periplaneta americana*. Filled circles and solid line represent data obtained previously for the cockroach *Blaberus discoidalis* (Full and Tu, 1990). The dashed line represents the predicted mechanical power output of the center of mass based on data for mammalian and arthropod runners (Full, 1989; see Fig. 7). For *P. americana*, $\dot{E}_{cm}$ appears to be a curvilinear function of speed. *P. americana* did not sustain locomotion at a constant horizontal speed in the range $0-0.4\,\text{m s}^{-1}$.

Discussion

Gait, ground reaction forces and energy fluctuations of the center of mass

Stepping patterns of the American cockroach have been well studied because *P. americana* has served as an important model of neural control for 20 years (Delcomyn, 1971, 1981, 1985, 1989). At speeds of $0.05-0.80\,\text{m s}^{-1}$ the American cockroach uses an alternating tripod gait that has been referred to as a walk (Delcomyn, 1971). Results of the present study confirm the use of the tripod gait at speeds less than $1.0\,\text{m s}^{-1}$. However, at all except the slowest speeds ($<0.40\,\text{m s}^{-1}$) we suggest the gait be called a run.

Walking gaits can be defined by the time course of the mechanical energy changes of the center of mass. In walking gaits, the kinetic and gravitational potential energy fluctuations of the center of mass occur out of phase, and energy can be transferred in a manner analogous to energy exchange in a pendulum (Cavagna *et al.* 1977). The gait used by *P. americana* did not result in effective energy conservation by pendulum-like exchange. Kinetic and potential energy changes of the center of mass were nearly in phase at all speeds (Fig. 1G,H), and energy recovery averaged 6.7 % (Fig. 3). Pendulum-like energy exchange is also low in the slower cockroach *Blaberus discoidalis* (15.7 %, Full and Tu, 1990). Neither of these insects appears to utilize a pendulum-like walking gait at speeds
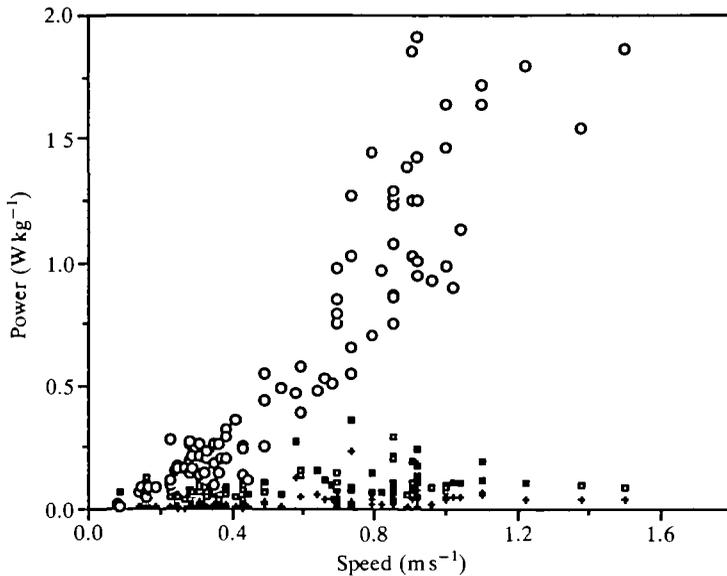
Fig. 6. Three components of the total mechanical power ($\dot{E}_{cm}$) of the center of mass as a function of speed. $\dot{E}_{cm}$ was obtained by summing the positive increments of the kinetic and potential energy fluctuations. Fluctuations in the horizontal kinetic energy (○) represent the greatest fraction of the power used to lift and accelerate the center of mass. Vertical kinetic energy changes (+) and gravitational potential energy changes (□) were relatively small and decreased in magnitude at high speeds.

that they sustain for more than a few strides. In contrast, birds, mammals and ghost crabs adopt walking gaits during which pendulum-like energy exchange reduces the energy used to maintain a constant speed by 31–70 % (Cavagna *et al.* 1977; Heglund *et al.* 1982*a*; Blickhan and Full, 1987).

P. *americana*, running on six legs, as well as four or two, produced patterns of ground reaction force that were not qualitatively different from those produced by the cockroach *B. discoidalis* (Full and Tu, 1990), the ghost crab (Blickhan and Full, 1987), and running and trotting mammals (Fig. 1A,B; Cavagna *et al.* 1964, 1977). Two-, four-, six- and eight-legged runners can all use alternating sets of propulsers during regular symmetrical gaits (Full, 1989). The resulting ground reaction forces consist of two maxima in both the vertical and horizontal ground reaction forces during each stride. The vertical force pattern can be described by a shape factor (q) calculated from a Fourier series (Alexander and Jayes, 1978). The shape factor for P. *americana* ($q=-0.01$) and the duty factor (i.e. the fraction of a stride duration for which a foot is on the ground, $\beta=0.5$) correspond to a trot when compared with bipedal and quadrupedal mammals. Results of this analysis for the American cockroach are similar to those found for *B. discoidalis* (Full and Tu, 1990) and are consistent with the contention that insects use a running gait.

Running or bouncing gaits can be defined by the timing of the mechanical energy fluctuations of the center of mass. During running and trotting gaits,

horizontal kinetic and gravitational potential energy fluctuations of the center of mass occur in phase (Cavagna, 1975; Cavagna *et al.* 1976, 1977). In a typical running gait, fluctuations in the kinetic and gravitational potential energies occur in phase when the maximum vertical force precedes the maximum horizontal force by one-quarter of the step period. Patterns of energy fluctuation show that *P. americana* used a running gait (Fig. 1G,H), similar to the bouncing gaits of two- and four-legged vertebrates (Cavagna *et al.* 1977; Heglund *et al.* 1982a) and eight-legged crabs (Blickhan and Full, 1987). The vertical force maxima for *P. americana* always preceded the nearest maxima in horizontal force by a time period equal to or less than one-quarter of the step period. In no case did a maximum in vertical force occur after the nearest maximum in horizontal force, as would be expected in a walking gait. In many trials the horizontal accelerating force attained a maximum more nearly in phase with the vertical force maxima (Fig. 1A,B). Preliminary studies on single leg forces in cockroaches suggest that this phase relationship would result if the forces produced by the first leg were significantly reduced (R. J. Full, R. Blickhan and L. Ting, in preparation; Ting *et al.* 1989).

In previous studies of arthropod locomotion, ground reaction force patterns, energy conservation and the timing of mechanical energy changes were used to define walking and running gaits (Blickhan and Full, 1987; Full and Tu, 1990). By all of these criteria, *P. americana* employed a running gait over the entire speed range we observed. It is important to emphasize that the presence of an aerial phase is not necessary for a gait to be classified as a run. The aerial phase of human runners can be reduced to zero by increasing the compliance of the legs (McMahon, 1985; McMahon *et al.* 1987). *Blaberus discoidalis* does not attain an aerial phase, yet force patterns, energy transfer and energy fluctuations of the center of mass indicate that the gait used by these insects is also a run (Full and Tu, 1990). The existence of aerial phases during rapid running in the American cockroach conclusively rejects the hypotheses that insects are confined to statically stable walking gaits.

Stride frequency and equivalent speeds

Running speed can be increased by an increase in stride frequency or stride length. Maximum stride length will be determined by leg length and the angle through which the limb swings. At fast speeds (i.e. $>1.0 \, \text{m s}^{-1}$), *P. americana* ran with its body raised well off the ground and its anterior end elevated relative to the posterior (Fig. 2). In this posture, the body was propelled primarily by the long hind legs. With the hind legs functioning as the primary propulsive units, *P. americana* may be able to overcome the limitations to stride length imposed by shorter limbs by lifting both front and middle legs off the ground. Increasing the angle of attack of the body may also allow a greater range of movement through which the hind legs can swing. The maximum theoretical stride length (i.e. two times limb length) for the hind limbs of *P. americana* is approximately 6 cm. This value is nearly the same as the maximum observed stride length (Fig. 4A). Since

the hind limbs are attached to a thorax which is elevated above the ground, maximum stride length is actually less than 6 cm. Highest speeds were attained by incorporating an aerial phase into each step during bipedal running (Fig. 2). Remarkably similar adjustments have been described for bipedal lizards (Synder, 1962). Speed also increases with bipedalism in lizards. As in *P. americana*, lizards tilt their head end upwards and increase stride length by using long hind legs.

Quadrupedal mammals typically switch from a trot to a gallop as they increase speed. A maximum sustainable stride frequency is attained at the trot–gallop transition speed. Greater speeds are attained by increasing stride length. Small animals generally switch from a trot to a gallop at lower speeds and higher stride frequencies than do larger animals. The speed at the trot–gallop transition has been referred to as an equivalent speed among animals that differ in size and body form. Bone strain and muscle force in mammals attain peak values during a fast trot and are reduced during a gallop (Biewener and Taylor, 1986; Taylor, 1985). Bone strain levels are similar among quadrupedal mammals at the trot–gallop transition despite large differences in speed and body mass (Biewener and Taylor, 1986). Among quadrupedal mammals, the speed and stride frequency at the trot–gallop transition varies predictably with body mass (Heglund *et al.* 1974; Heglund and Taylor, 1988). Surprisingly, our previous studies of ghost crab and cockroach locomotion indicate that the scaling of maximum sustainable stride frequency and the speed at which it is attained may also be a general feature of arthropod locomotion (Blickhan and Full, 1987; Full, 1989; Full and Tu, 1990). Ghost crabs and the cockroach *B. discoidalis* attain a maximum stride frequency at the speed and stride frequency predicted for the trot–gallop transition of a quadruped of the same mass.

The observed speeds for *P. americana* were well above the trot–gallop transition speed of $0.28 \, \mathrm{m \, s^{-1}}$ predicted from allometry on quadrupeds (Fig. 4B). The pattern of stride frequency and stride length for the American cockroach was similar to that of a quadrupedal mammal operating at speeds above the trot–gallop transition. Stride frequency increased by 30 % over the entire speed range, whereas increases in speed were attained by tripling stride length (Fig. 4). Although the relationship of stride frequency and speed was similar, the maximum sustainable stride frequency predicted for *P. americana* on the basis of data from quadrupedal mammals (Heglund *et al.* 1974) is only 12 Hz. *P. americana* running with maximal stride length at the predicted maximum sustainable stride frequency could only attain speeds approaching $0.8 \, \mathrm{m \, s^{-1}}$. This speed is half the highest speed actually observed. *P. americana* attained stride frequencies of more than twice the predicted value. High-speed running by the American cockroach at speeds of 50 body lengths per second was correlated with an exceptional capacity for cycling its legs. In contrast to galloping quadrupeds, the American cockroach attained very high stride frequencies, as well as long stride lengths, as speed increased.

Mechanical energy of the center of mass

The mechanical power generated by *P. americana* to lift and accelerate its center

of mass ($\dot{E}_{cm}$) increased with speed (Fig. 5). The cockroach *B. discoidalis*, the ghost crab and birds and mammals show a linear increase in $\dot{E}_{cm}$ with speed (Blickhan and Full, 1987; Cavagna *et al.* 1977; Heglund *et al.* 1982*a*). The increase in $\dot{E}_{cm}$ with speed in *P. americana* is better described by a curvilinear function. At high speeds $\dot{E}_{cm}$ was greater than predicted for a 1 g animal (Full, 1989). The additional power output generated at high speeds was almost exclusively in the horizontal direction (Fig. 6). The elevated rates of mechanical energy generation at high speeds along with the changes in body angle suggest that drag forces may play a significant role in these small runners. We are currently investigating this possibility by testing cockroaches in wind tunnels (Full and Koehl, 1989). Bartholomew *et al.* (1985) have suggested that lift and possibly drag affect the desert beetle *Onymacris plana*, which can run at high speeds ($1.0 \, \mathrm{m \, s^{-1}}$) and is similar in mass to the American cockroach.

Even with the elevated power output of the center of mass at high speeds, the amount of mechanical energy used by *P. americana* to move a 1 kg mass for 1 m (1.5 J) was remarkably similar to values reported for animals that span nearly five orders of magnitude in body mass and vary greatly in morphology (Fig. 7). It is
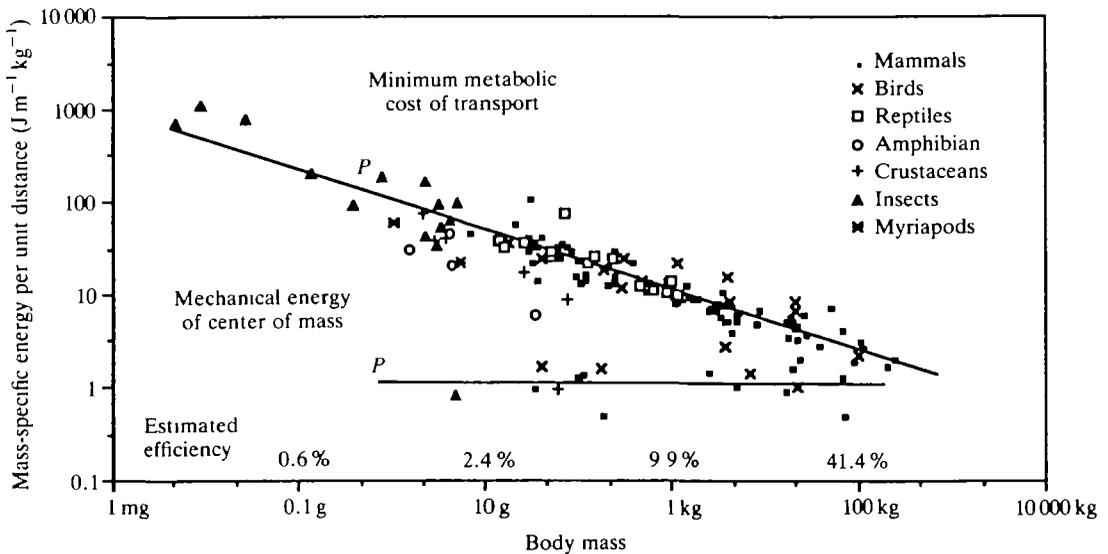

Fig. 7. Logarithmic plot of mass-specific mechanical energy of the center of mass and minimum metabolic energy used to move a 1 kg of animal 1 m in distance. Small animals, regardless of form, require relatively more metabolic energy to travel a distance than large animals, but do not produce relatively more mechanical energy to move their center of mass. In *Periplaneta americana* (*P*) the difference between metabolic and mechanical economy reaches 100-fold. No reassessment of mechanical energy changes can result in whole-body efficiencies of 25 %. Data for mammals and birds, lizards, amphibians, crustaceans, insects and myriapods are from various sources (see Full, 1989, for references). Minimum metabolic cost of transport (C_{min})$=10.8m^{-0.32}$ ($r^2=0.87$) and E_{cm}/distance$=1.07m^{-0.01}$, where *m* is mass in kg.

important to note that E_{cm} is the largest fraction of the total mechanical energy generated during locomotion, but not the only component. Total mechanical energy includes elastic strain energy (E_e), which reduces the total, and the internal energy (E_i) used to accelerate the limbs and rock the trunk relative to the body, which increases the total (Heglund *et al.* 1982*b*). The magnitudes of E_i and E_e are unknown for any insect. For *P. americana* and other insects, however, E_i is likely to be small with respect to E_{cm} because of their relatively light-weight limbs (Full and Tu, 1990). Based our on estimations, maximum $\dot{E}_i$ for the American cockroach running at $1.0\,m\,s^{-1}$ does not exceed 3 % of $\dot{E}_{cm}$.

Measuring the power output used to move the center of mass in *P. americana*, the smallest runner tested to date, provides an important test of a hypothesis proposed from the scaling energetics of birds and mammals. Heglund *et al.* (1982*b*) concluded that metabolic power input cannot be predicted from mechanical power output assuming a constant muscular efficiency of 20–25 %. Small birds and mammals (i.e.<1 kg) have muscular efficiencies well below 25 %, whereas large animals have values as high as 70 % (Cavagna *et al.* 1977; Heglund *et al.* 1982*b*).

Unfortunately, several processes and components make estimation of total mechanical power output difficult. Transfer of energy within and between segments, elastic energy storage, eccentric muscle contraction and variation in E_i as speed increases can significantly affect the slope of the mechanical power output function shown in Fig. 7. This is especially true in larger animals (i.e. >1 kg) that exhibit less than a 10-fold difference between metabolic and mechanical power (Heglund *et al.* 1982*b*). Estimates of mechanical power output for *P. americana* show that this difference reaches 100-fold in small insects (Fig. 7). This large difference between metabolic and mechanical power cannot be completely explained by any reassessment of the mechanical power estimate. Maximum mechanical power output estimates for cockroaches would have to be increased by 20- to 30-fold to attain a whole-body efficiency that approaches frequently quoted estimates of muscle efficiency (i.e. 25 %; Full, 1990). Maximum mechanical power output estimates for small animals (1 g) combined with minimum mechanical power output estimates for large animals (100 kg) only increase the difference in mechanical power between large and small animals to sevenfold, not nearly the 50-fold necessary to make whole-body efficiency independent of animal size (i.e. parallel relationship between the functions relating the minimum metabolic cost and mechanical energy per distance).

Whole-body efficiencies for terrestrial locomotion in the 1 g American cockroach are low (1.2 %), as are efficiencies for incline running in cockroaches (4 %; Full and Tullis, 1990), bee flight (6–14 %; Casey and Ellington, 1989) and isolated locust flight muscle (6.4 %; Josephson and Stevenson, 1989). Muscles used by insects appear to be inefficient machines (i.e. power output/power input) compared to muscles in larger animals such as mammals. Yet, these inefficient machines may be just as effective as the muscles of larger animals in generating force (Full, 1990). Full *et al.* (1990) showed that the cost of force production

in three insect species is remarkably similar to that found in mammals when the rate of force production is considered. If insect muscle is operating at high stress or force compared to strain when producing maximal mechanical power output, then metabolic cost may be best correlated with force production. A recent study on isolated locust flight muscle supports this hypothesis. At maximal power output, strain is low and rate of oxygen consumption is similar to that measured during a maximal isometric contraction (Josephson and Stevenson, 1989, and personal communication).

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