

LOCOMOTION ENERGETICS OF THE GHOST CRAB II. MECHANICS OF THE CENTRE OF MASS DURING WALKING AND RUNNING

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SUMMARY

Terrestrial locomotion involving appendages has evolved independently in vertebrates and arthropods. Differences in the mechanical design of the locomotor apparatus could impose constraints on the energetics of locomotion. The mechanical energy fluctuations of the centre of mass of an arthropod, the ghost crab *Ocypode quadrata* (Fabricius), were examined by integrating the ground reaction forces exerted during sideways locomotion. Crabs used a pendulum-type energy exchange mechanism during walking, analogous to an egg rolling end over end, with the same effectiveness as birds and mammals. Moreover, ghost crabs were found to have two running gaits. A switch from a slow to a fast run occurred at the same speed and stride frequency predicted for the trot–gallop transition of a quadrupedal mammal of the same body mass. In addition, the mass-specific mechanical energy developed over a unit distance was independent of speed and was within the limits measured for birds and mammals. Despite the obvious differences in mechanical design between crabs and mammals, energy-conserving mechanisms and the efficiency of locomotion were remarkably similar. These similarities may result from the fact that the muscles that generate forces during terrestrial locomotion have relatively conservative mechanical and energetic properties.

INTRODUCTION

Metabolic measurements during treadmill locomotion, as in the first paper of this study (Full, 1987), suggest that the minimum cost of terrestrial locomotion in arthropods and vertebrates is a function of body mass, but may be relatively independent of locomotor design (Full & Herreid, 1983, 1984; Herreid & Full, 1984, 1985; Herreid, Full & Prawel, 1981). The reason behind this similarity is unknown.

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One possible explanation is that these animals perform similar amounts of mechanical work, despite having different locomotor designs. The present paper is the first attempt to describe the mechanics of an arthropod's centre of mass during terrestrial locomotion, including the locomotor style, force production, and the mechanical energy output.

A variety of birds and mammals produce similar force patterns and mass-specific mechanical energy changes during locomotion (Cavagna, Heglund & Taylor, 1977; Fedak, Heglund & Taylor, 1982; Heglund, Cavagna & Taylor, 1982a). Examination of these data indicates that two mechanisms are used by birds and mammals to minimize energy expenditures, and that both involve alternately storing and recovering energy. One is prevalent during walking and is analogous to a swinging pendulum or an egg rolling end over end (Cavagna *et al.* 1977; Cavagna, Thys & Zamboni, 1976; Heglund *et al.* 1982a). With this mechanism, kinetic energy and gravitational potential energy are exchanged, and not simply lost, as the animal's centre of mass rises and falls during a stride. The second mechanism, analogous to a spring or bouncing ball, is used for all running gaits, such as hopping, trotting or galloping. In large animals elastic elements, such as tendons, can alternately store and release energy within each stride (Cavagna, Saibene & Margaria, 1964; Heglund, Fedak, Taylor & Cavagna, 1982b). Not only do birds and mammals use common mechanisms during locomotion, but they also appear to perform similar amounts of mechanical work per unit of mass during locomotion (Heglund *et al.* 1982b). Estimates of total mechanical power output are directly proportional to body mass over a wide range of speeds.

It is not clear whether the design of arthropods imposes any limitations on their ability to use the same basic mechanisms during locomotion as are used by birds and mammals. Moreover, the magnitude of the mechanical power necessary to move the centre of mass is unknown. Investigations of the mechanisms of arthropod locomotion have been directed primarily towards an understanding of central and peripheral neural control (Clarac, 1981; Delcomyn, 1981). Single-leg forces produced during locomotion have been estimated for stick insects (Cruse, 1976), spiders (Blickhan & Barth, 1985) and two crustaceans (Klärner & Barnes, 1986; Clarac & Cruse, 1982), but primarily in an attempt to clarify the role of peripheral force inputs in the neural control of locomotion. Graham (1983) has suggested from neural data and force measurements that insects use a walking behaviour very different from that found in vertebrates. Legs are actively used to decelerate the body at regular intervals during walking, resulting in a type of 'lurching' locomotion. This behaviour could exclude the use of energy-saving mechanisms, such as a pendulum.

The present study of arthropod locomotion mechanics focuses on the sideways running ghost crab, *Ocypode*, because, as its generic name implies (swift of foot), this crab is adapted for terrestrial locomotion. Its exoskeleton is relatively thin and lightweight, its legs considerably longer than those of other crabs of the same mass, and its extensor muscles, which provide the main pushing thrust in the trailing legs, are large (Hafemann & Hubbard, 1969; Warner, 1977). Maximum sprinting speeds approaching 4 m s^{-1} have been reported (Cott, 1929; Hafeman & Hubbard, 1969).

At these fast speeds, the crab apparently has aerial phases during its stride with all eight legs off the ground (Burrows & Hoyle, 1973). The wide range of speeds, different possible gaits, and large size (which facilitates the measurement of ground reaction forces) make the ghost crab a choice arthropod for the study of locomotion mechanics.

MATERIALS AND METHODS

Animals

Ghost crabs, *Ocypode quadrata*, were collected from the beaches of Beaufort, North Carolina, near the Duke University Marine Laboratory. Only intermoult animals ranging in body mass (M_b) from 30 to 96 g (mean = 63.0 ± 3.1 g, S.E.) were used. The crabs were kept in individual containers filled with 50% sea water to a depth of 1 cm and fed fresh fish twice a week. Experiments began within 1 week of captivity.

Experimental approach

By measuring the horizontal and vertical components of the ground reaction forces, the potential, kinetic and total energy changes of the centre of mass can be calculated. The time course of these energy fluctuations can be used to examine basic mechanisms of locomotion, in addition to the mechanical energy of transport.

Force

Force measurements were obtained from a force platform (modified from that used by Heglund, 1979, 1981; Fig. 1). At approximately 1.5 m from the start of the tracks were four separate aluminium plates in series (covering a distance of 0.75 m). The outputs from each plate were summed to provide the total horizontal and vertical force produced by the crab as it travelled along the platform. Wiring the strain gauges in a full bridge configuration reduced the cross-talk between vertical and horizontal outputs to less than 3% and decreased drift resulting from changes in temperature. By balancing two arms of the Wheatstone bridge, the variation in force output at any particular site on the plate was reduced to less than 1% without affecting the temperature compensation. Signals from the force plates were filtered digitally (Butterworth, cut-off frequency 100 Hz, phase shift = 0°).

Speed

The crab's average speed was determined by placing two photocells 15 mm above the level of the track and perpendicular to the direction of motion. The distance between the photocells (0.50 m) was divided by the time the animal took to travel from the first beam of light to the second.

Data acquisition

Signals from the force plates and photocells were sent to an oscilloscope and a PDP11/23 computer. The oscilloscope provided an instantaneous recording of the

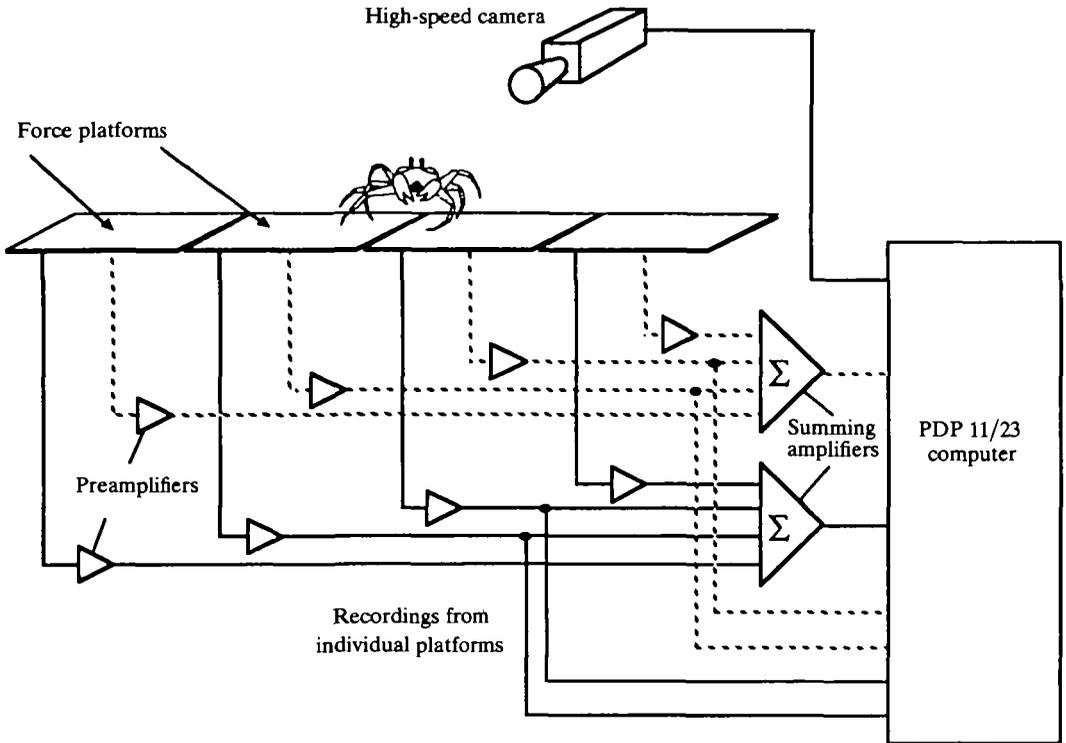


Fig. 1. Experimental apparatus. A crab ran sideways on a track consisting of 3–6 force platforms, each sensitive to the horizontal (----) and vertical (—) components of the ground reaction force. By summing the respective signals from all plates the total force acting on the centre of mass of the animal was measured. Simultaneous high-speed cinematography allowed determination of the stepping pattern. All data were collected on line and processed using a laboratory computer.

horizontal and vertical forces along with the time taken to travel between the photocells. These tracings were used to eliminate trials in which the crabs did not walk in the centre of the plates or bumped into the side walls. Three channels, horizontal force, vertical force and the photocell status (on or off), were read by the computer's 12-bit analogue/digital converter at a sampling rate ranging from 500 to 1000 samples s^{-1} (1–2 ms intervals).

Stride period and frequency

Stride period was determined from the force records by calculating the autocorrelation function. This function provides a measure for the similarity of a signal with a time-shift of itself. If the signal is shifted by its major period, the autocorrelation function reaches a local maximum. The position of the maximum represents the period, even when the signals are noisy. This analysis was performed on both the horizontal and vertical force records. The record showing the highest correlation (i.e. the most regular periodicity) was used to determine the stride frequency and stride period. Stride frequencies calculated by this method agreed with those determined by high-speed filming.

Velocity and displacement of the centre of mass

The horizontal and vertical velocities of the centre of mass were calculated by integrating the horizontal force recording, and the vertical force recording minus the body weight, respectively. The vertical displacement was obtained by integrating the vertical component of the velocity. Before the integration was attempted, any drift in the force recordings was corrected by comparing the signals before and after the crab was on the plates. The integration constant for the horizontal velocity of the centre of mass was taken to be the animal's average speed. The integration constant for the vertical component of velocity was assumed to be zero, as was the integration constant for vertical displacement. The crabs examined on film did not show any major shifts in the vertical position of their centre of mass from the beginning to the end of a stride, once the animal had raised its body into the walking or running position.

Overall accelerations and decelerations of the centre of mass (i.e. during one stride period) significantly alter the work done during this interval. For this reason, we restricted our analysis to trials where the average speed over a stride was constant, the sum of the increases and decreases in speed (horizontal and vertical) were within 50% of the periodic fluctuations in speed.

Force produced by leading and trailing legs

In order to distinguish which set of legs (trailing or leading) accelerates the crab forward, the forces (vertical and horizontal) produced by each set of legs were determined. Two plates were wired so that the forces from the first plate could be measured independently from those of the second (Fig. 1). In addition, the sum of the forces from both plates was recorded. Because crabs move sideways, the first forces recorded from the second plate in the series were produced by the leading legs, while the last forces seen on the first plate were produced by the trailing legs.

Stepping pattern

In a separate series of experiments crabs were filmed, as they travelled down the track, to aid in determining their stride period and to correlate their stepping patterns with the forces produced by their legs. A high-speed camera (Photo-sonics, 16 mm-IPL) was used at 200 frames s^{-1} with an exposure time of 1/1000 s. The crabs were filmed from the side and from the top by using a mirror placed at a 45° angle above the track. Horizontal and vertical forces were measured simultaneously with filming. Synchronization between the force output and the filming was provided by simultaneously recording a shutter correlation pulse.

Footfall patterns were obtained with the aid of a motion analyser (Vanguard Instrument Co., Melville, NY) from frame-by-frame analysis of the film records. The frames corresponding to the beginning of the power stroke and the beginning of the return stroke were noted for each leg. Footfall patterns were then constructed by combining the data from each leg for one or more complete strides.

Energy calculations

The kinetic energies of the centre of mass (E_k), horizontal and vertical, were calculated from their respective velocities (v) according to the equation: $E_k = 1/2M_b v^2$. The gravitational potential energy (E_p) of the centre of mass was determined by integrating the vertical velocity to obtain the vertical displacement of the centre of mass (Δh) and then multiplying this vertical displacement by body mass and the acceleration due to gravity ($E_p = M_b g \Delta h$).

The total energy of the centre of mass (E_{CM}) was calculated by summing the kinetic and gravitational potential energies at each time interval. The total rate of power required to lift and accelerate the centre of mass (\dot{E}_{CM}) was calculated by summing the positive increments of E_{CM} over one or more strides and dividing by the time interval required to complete those strides (i.e. a multiple of the stride period).

RESULTS

Walk

Crabs used eight legs (legs 2–5) during slow sideways locomotion, but in the manner similar to an inverted pendulum which characterizes a walk in bipeds and quadrupeds (Fig. 2). The stepping pattern used for walking can be described as an ‘alternating tetrapod’ gait (Barnes, 1975). Legs 3 and 5 on one side of the body tended to alternate with legs 2 and 4, while each leg on the trailing side was out of phase with its contralateral leg on the leading side. Because of the irregularity of the pattern, it is possible that in many cases a metachronal wave may better describe the leg movements during slow walking.

During walking, the crab’s body oscillated considerably (Fig. 3, tracing 5), which resulted in fluctuations of gravitational potential energy (Fig. 3, tracing 8). Changes in potential energy tended to be out of phase with the fluctuations of horizontal kinetic energy (Fig. 3, tracing 7). This phase relationship results in an exchange between potential and kinetic energy (Cavagna, 1975). Potential energy is converted to kinetic energy as the animal’s body falls forward over stiffened legs. This increase in kinetic energy can be recovered during the next portion of the stride as gravitational potential energy when the body rises. The magnitude of energy recovery can be determined by comparing the energy necessary to maintain a constant walking speed, if there were no exchange, with the amount actually expended. This comparison can be expressed by the following equation:

$$\% \text{ recovery} = \frac{\Sigma \Delta E_k + \Sigma \Delta E_p - \Sigma \Delta E_{CM}}{\Sigma \Delta E_k + \Sigma \Delta E_p} \times 100,$$

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 centre of mass, respectively. If complete exchange were to occur, as in an ideal pendulum, then the total energy would not fluctuate ($\Sigma \Delta E_{CM} = 0$) and the recovery would be 100%. Fig. 3 shows that the total energy (tracing 9) does fluctuate in the ghost crab during walking. Exchange or recovery is not 100%, however: the fluctuations in total energy are less than those of

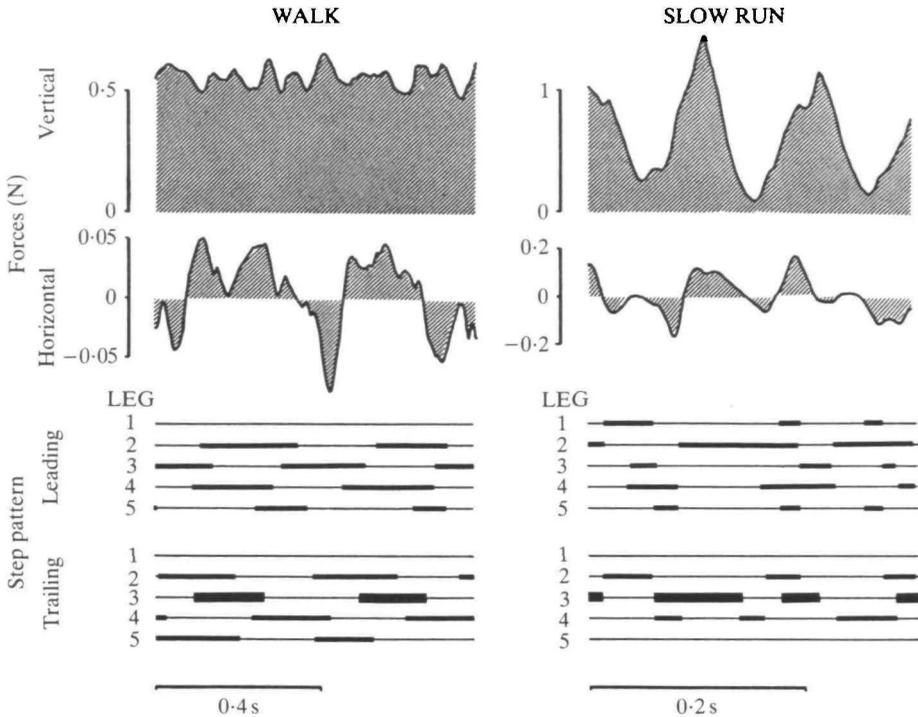


Fig. 2. Force and stepping pattern for a walk (0.09 m s^{-1}) and a slow run (0.42 m s^{-1} ; bars mark the time of ground contact for the respective leg). During a walk the time course of the vertical forces shows small, almost random fluctuations around the animal's weight. However, the periodicity seen in the horizontal force component is in agreement with cinematographic data. The vertical force measured during a slow run displays a time course typical for running mammals. The power stroke of the third trailing leg (emphasized by bold line) is correlated with acceleration (positive horizontal force changes). The chelae (leg 1) were not used for propulsion during walking or slow running even though at times they made contact with the substrate.

gravitational potential energy. The amount of recovery in crabs was a function of speed (Fig. 4). At low walking speeds, recovery ranged from 15 to 55%, with a maximal mean recovery of 31% at 0.25 m s^{-1} .

Both accelerating and decelerating forces were produced by trailing legs and leading legs during walking (Fig. 5). The average force during walking ($0.15\text{--}0.23 \text{ m s}^{-1}$, $N = 4$) for the time interval when leading legs were on one plate and trailing legs were on the other, was of similar magnitude, but opposite in direction. Leading legs tended to decelerate the body ($-0.28 \pm 0.18 \text{ N kg}^{-1}$, s.e.), while trailing legs pushed it forward ($0.27 \pm 0.13 \text{ N kg}^{-1}$, s.e.). In one case, the leading legs were clearly accelerating the body, while the trailing legs produced a deceleration.

Slow run

The majority of crabs used a bouncing gait during locomotion at speeds greater than 0.4 m s^{-1} . The stepping pattern still resembles an alternating tetrapod (Fig. 2),

but the vertical component of the ground reaction force showed large fluctuations with two distinct maxima during each stride. Fluctuations in kinetic and gravitational potential energy tended to be in phase, so little exchange was possible

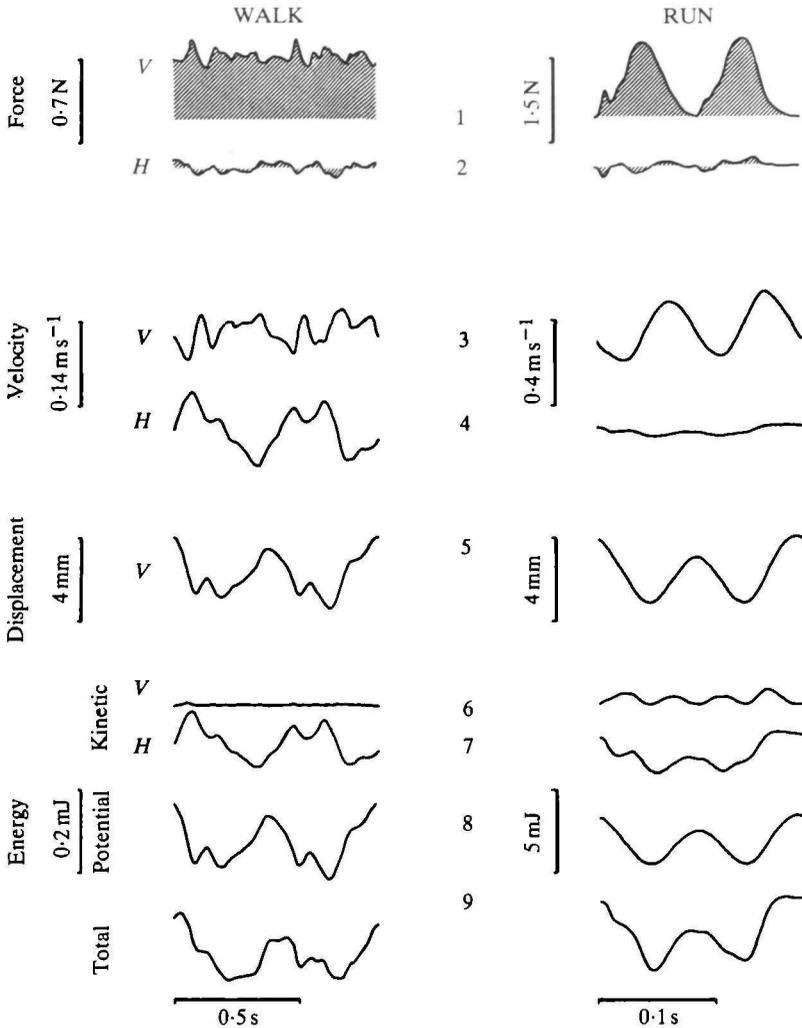


Fig. 3. Force, velocity, displacement and energy changes of the centre of mass during one stride (i.e. one complete cycle of a leg) for a crab (0.5 N) walking (0.25 m s^{-1}) and running (0.76 m s^{-1}). The traces represent the following: (1) vertical (V) and (2) horizontal (H) forces obtained from the force platform, (3) vertical and (4) horizontal velocity changes calculated by integration of the force recordings, (5) vertical displacement of the centre of mass calculated by integration of the vertical velocity, (6) vertical and (7) horizontal kinetic energy changes of the centre of mass, (8) fluctuations in the gravitational potential energy, and (9) the total energy changes of the centre of mass. During walking the vertical and horizontal energy changes are out of phase, indicating a pendulum-like energy-conserving mechanism. During running, the respective energy components are in phase, indicating a bouncing gait. The vertical and horizontal force attain zero levels simultaneously, indicating aerial phases (i.e. no legs touching the ground).

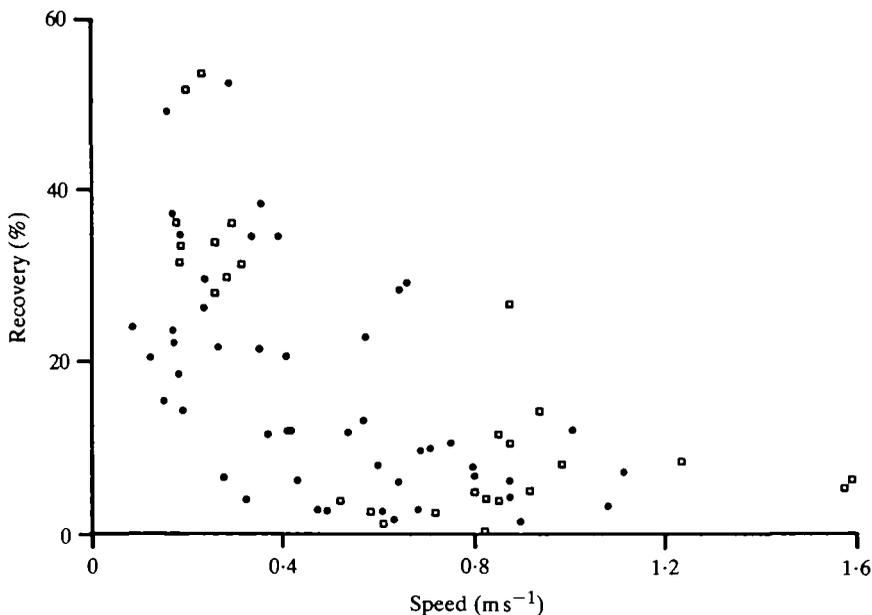


Fig. 4. Energy recovery as a function of speed. A value of 100% would indicate complete transfer between kinetic and gravitational potential energy, as in an ideal pendulum. Ghost crabs recover the maximum amount of energy (55%) at 0.2 m s^{-1} . Open squares represent 30-g crabs, whereas closed circles represent larger crabs.

(Fig. 3, traces 7, 8). This is supported by the recovery values, which were low compared to those for walking (average 9%, Fig. 4).

Stride frequency (f) within the gait increased linearly with speed as in the walk ($f = 5.27v + 1.56$; $r^2 = 0.77$; Fig. 6). A roughly linear increase in stride frequency with speed appears to be typical for arthropods moving at higher speeds (Chasserat & Clarac, 1983). For the ghost crab an increase in speed was partly achieved by an increase in stride length. Stride length increased by a factor of two in the speed range $0.1\text{--}0.9 \text{ m s}^{-1}$. This is in contrast to other crustaceans, such as the rock lobster, where stride length remains relatively constant as speed is increased (Chasserat & Clarac, 1983).

Fast run

At speeds above 0.9 m s^{-1} , the crabs again changed gait. Force recordings clearly revealed aerial phases at this transition speed. When all eight legs were off the ground, the vertical and horizontal force decreased to zero (Fig. 3, first trace). Energy recovery remained low (approx. 7%), indicating a bouncing gait (Fig. 4). Stride frequency remained constant ($6.3 \text{ strides s}^{-1}$). Speed was increased only by an increase in stride length (from 143 to 254 mm).

Trailing legs generated only accelerating forces ($3.12 \pm 0.26 \text{ N kg}^{-1}$, s.e.), while the leading legs produced a significantly lower decelerating force ($-0.86 \pm 0.14 \text{ N kg}^{-1}$, s.e.; t -test, $P < 0.02$; running speed: $0.83\text{--}1.0 \text{ m s}^{-1}$, $N = 6$; Fig. 5). The distance covered during the time from stepping on the leading plate and leaving the

trailing plate was only 60 mm for this speed range, compared to 120 mm for slow walks. Therefore, the leg tips of the leading and trailing legs must be positioned closer together during a fast run.

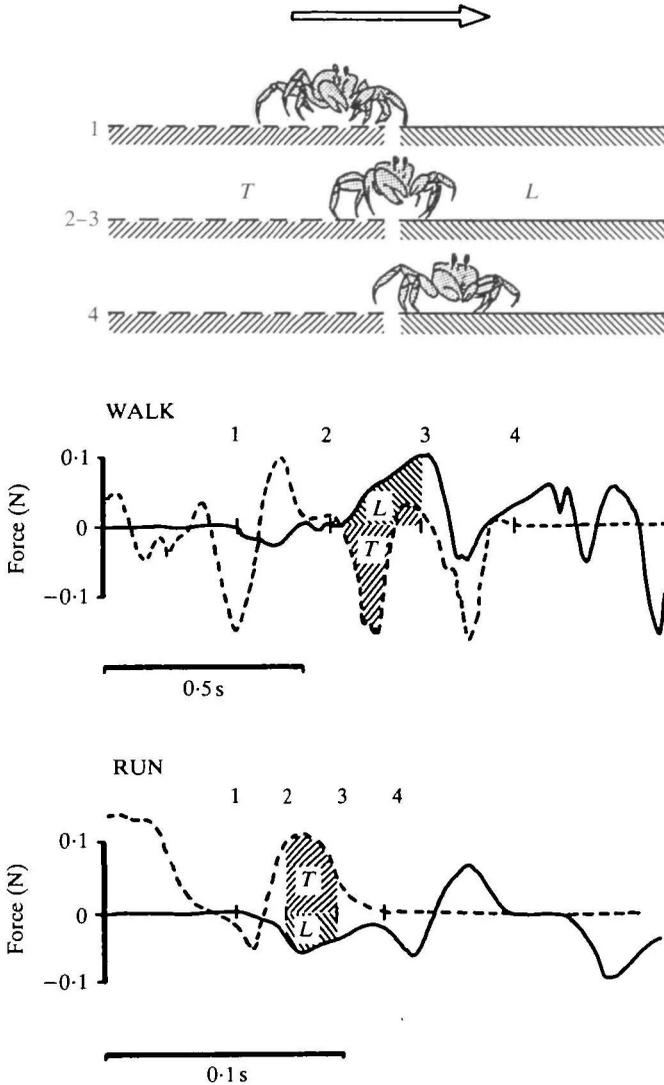


Fig. 5. Horizontal forces measured on two consecutive plates (leading plate —, trailing plate - - -) for a walk (0.18 ms^{-1}) and for a run (1.0 ms^{-1}). The numbers correspond to the crab's position as it moved from the trailing plate to the leading plate. (1) Time when the first leg touched the leading plate. (2-3, hatched area) Animal had approximately half of its body weight on each plate. The average horizontal force in this segment was used as a measure for deceleration or acceleration for both the leading and trailing legs. (4) The animal left the trailing plate with its last leg. The selected example shows that for a slow walk the trailing side (*T*) can be decelerating (negative force) and the leading side (*L*) accelerating (positive force) during a walk (i.e. the crab pulled itself along with its leading legs). Trailing legs only provided acceleration during running.

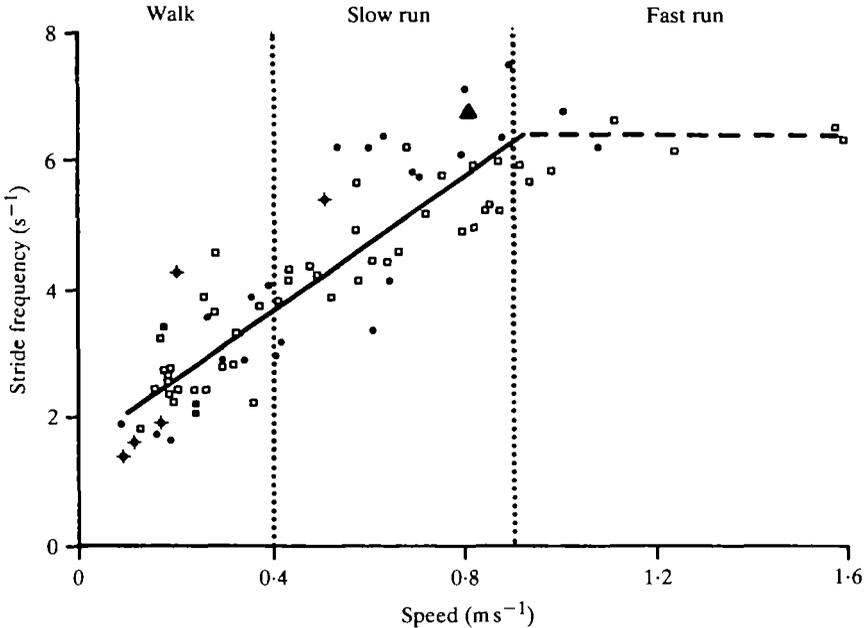


Fig. 6. Stride frequency (f) as a function of speed (v) for intermediate (filled circles: 30 g) and large (open squares: 50 g) crabs. Stippled lines represent postulated gait changes from a walk to a slow run and from a slow run to a fast run. The transition from a slow run to a fast run occurs at nearly the same speed and frequency as the trot-gallop transition in quadrupeds (large filled triangle). (Filled circles with cross: stride frequencies obtained from high-speed cinematography.)

Mechanical energetics of the centre of mass

The mass-specific rate of mechanical power required to lift and accelerate the centre of mass (\dot{E}_{CM}/M_b) increased linearly with speed ($\dot{E}_{CM}/M_b = 0.95v + 0.03$, $r^2 = 0.71$; $N = 76$; Fig. 7). This is the mass-specific power that must be generated by muscles and elastic structures for locomotion. No significant difference was found when the regression line of all animals ($M_b = 64.6$ g; $N = 63$) was compared to that of only the smallest animal ($M_b = 30.0$ g; $N = 13$; t -test for bivariate samples, Clarke, 1980; $P > 0.05$). Mass-specific power appeared to be independent of the animal's body mass.

Speed distribution

Fig. 8A shows the speed distribution for the 21 crabs that were tested on the track. Crabs chose to walk at a low speed (< 0.1 ms^{-1}) in only 3% of the trials. The preferred speed range was 0.1 – 0.3 ms^{-1} ; nearly 50% of the 400 trials fell within this range. Speeds 3–10 times as fast were observed, but much less frequently. The maximum speed attained by any crab was 1.6 ms^{-1} .

Large crabs (70–90 g) never selected speeds greater than 0.5 ms^{-1} (Fig. 8B). Their tendency when prodded was to remain in place and adopt an aggressive posture. Smaller animals (30–50 g) consistently attained the fastest speeds.

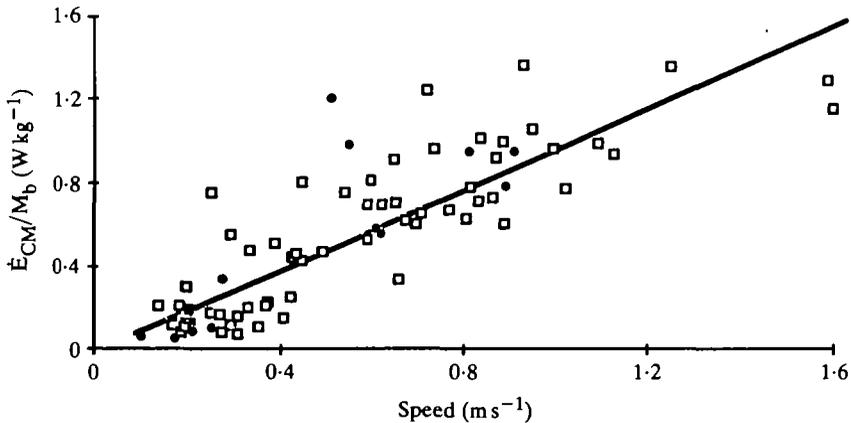


Fig. 7. Sum of the positive increments of the energy of the centre of mass (\dot{E}_{CM}) as a function of speed (v). \dot{E}_{CM} was calculated on the basis of a stride period and is shown per kilogram body mass (M_b). Open squares represent 50-g crabs, whereas closed circles represent 30-g crabs.

DISCUSSION

Walking

The limits imposed by the architecture of the arthropod locomotor design do not restrict the ability of these travellers to use energy-conserving mechanisms. In birds and mammals, a walk is characterized by a pendulum-like exchange between potential and kinetic energy (Cavagna *et al.* 1977; Heglund *et al.* 1982a). Vaulting over stiffened legs results in up to a 70% conservation in energy that would otherwise have to be provided by muscles and tendons. Energy recovery in *O. quadrata* approached 55% (Fig. 4), a value typical for walking birds and mammals (Cavagna *et al.* 1977; Heglund *et al.* 1982a). This magnitude of recovery in an eight-legged sideways walking crab strongly suggests that the pendulum-like, energy-conserving mechanism is very general and does not depend on the type of skeleton (exoskeleton *vs* endoskeleton), the number of legs, or the positioning of the legs with respect to the trunk (sprawled *vs* upright).

The crab skeleton allows pivoting around one or more of its joints positioned laterally to the animal's centre of gravity located within the body (Fig. 9). The effective 'hip' height (l) of this arrangement can be determined from the maximum speed (v_{max}) if the body moves on an arc of radius l . At this transition speed, the gravitational force equals the centrifugal force ($g = v_{max}^2/l$). At a higher speed the centrifugal force would drive the animal off the ground, making walking impossible. Given a maximum walking speed of $v_{max} = 0.4 \text{ m s}^{-1}$ (Fig. 3), the effective 'hip' height equals approximately 1.6 cm. This suggests that the crabs were mainly pivoting around the propodite-dactylopodite joint. They operated effective pendulums with their legs positioned laterally and did so without losing the advantage of a low centre of mass and a wide base of support, i.e. high stability.

It is remarkable that, despite the variability in stepping pattern, the resulting changes in the velocity and energy of the centre of mass were similar to those of

vertebrates, and that a pendulum-like energy-conserving mechanism was operating. Maximum energy recovery during walking in crabs should occur if all eight 'inverted pendulums' were operating in a tightly coupled alternating tetrapod. Yet irregular stepping patterns were used by the ghost crab during normal sideways walking (Fig. 2). This indicates that the summed forces from all legs provides a rather consistent lift and acceleration of the body, even though the forces produced by individual legs may vary. Irregular stepping patterns appear to be the rule among free-walking crustaceans, rather than the exception (Klärner & Barnes, 1986;

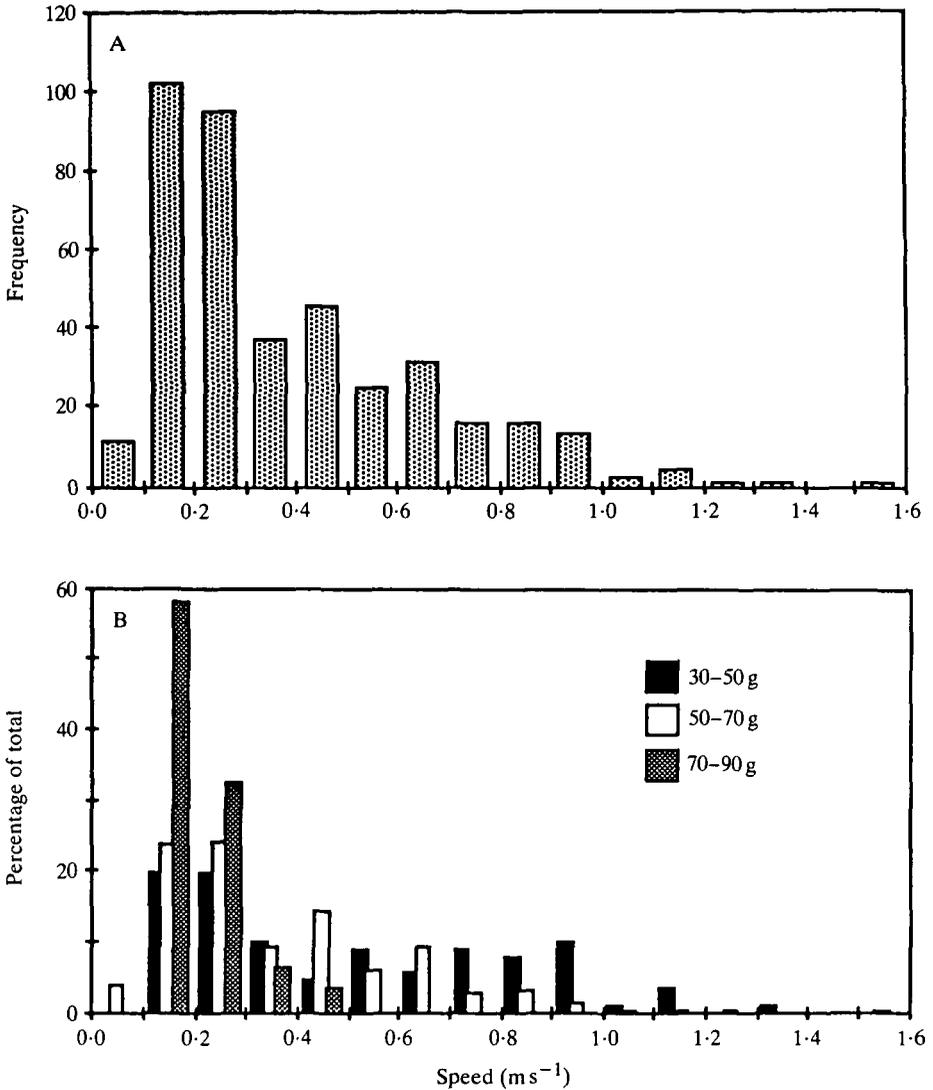


Fig. 8. Frequency of preferred speed obtained on the force track. (A) The preferred speed distribution for all crabs showed a maximum at 0.1–0.3 ms⁻¹. (B) The preferred speed with respect to body mass showed that large crabs seldom selected running gaits.

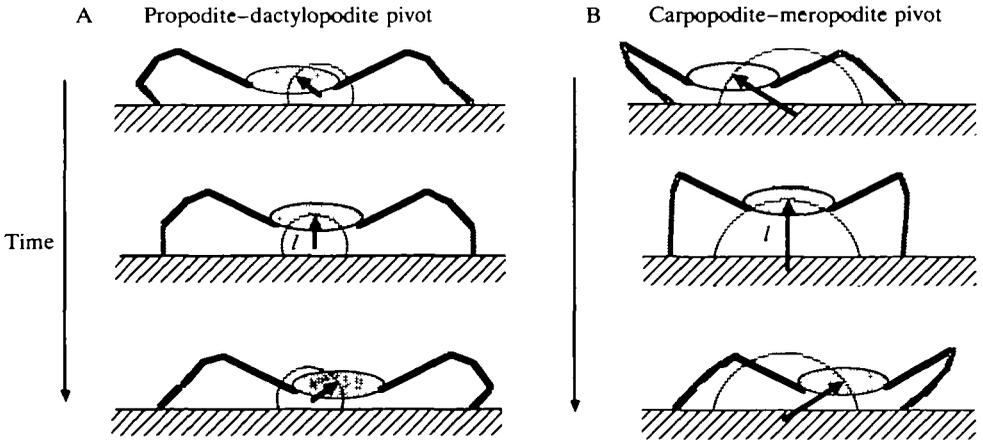


Fig. 9. Simplified model of a crab using an inverted pendulum mechanism during walking by pivoting over different joints. (A) Crabs appeared to pivot primarily around the propodite-dactylopodite joint (dactylopodite stippled). The effective 'hip height' (l = length of arrow) is determined by the radius of curvature followed by the centre of mass. (B) Using the carpopodite-meropodite joint results in a higher effective 'hip height' and maximum walking speed can be increased (carpo-, pro- and dactylopodite stippled). The proposed mechanism is simplified in the figure for clarity. Effective 'hip height' also depends on the change in angle of the leg with respect to the body (i.e. coxa-basi-ischium joint).

Chasserat & Clarac, 1983; Clarac & Chasserat, 1983; Clarac, 1981; Evoy & Fournier, 1973). Even motor output during treadmill locomotion is not constant from one cycle to the next (Barnes, Spirito & Evoy, 1972; Clarac & Chasserat, 1983). The resulting gait of a sideways-walking crab, such as *Uca pugnax*, has been best described as an 'approximate' alternating tetrapod, with tendencies for metachronal waves (Barnes, 1975). The variability of the stepping pattern during walking at low speeds could, in part, be explained by specialization of leg function. The stepping patterns of the leading *vs* trailing legs can differ (Barnes, 1975). During walking in *O. quadrata*, the trailing legs dominated by exerting pushing forces, while the leading legs at times generated pulling forces (Fig. 5). Many animals tend to use slow walking during exploratory behaviour. In arthropods, the leading legs are frequently used like feelers, as if seeking points of contact (Blickhan & Barth, 1985; Clarac & Coulmance, 1971; Cruse, 1976). Slow walking may employ greater sensory input for the modulation of individual leg movements. Because of the higher number of legs supporting the body, a more irregular stepping pattern would not jeopardize stability.

In crabs, both physiological and mechanical constraints favour the preferred gait for sustained locomotion – walking. The maximum recovery of mechanical energy for *O. quadrata* was found at $0.1\text{--}0.4\text{ m s}^{-1}$ (Fig. 4). This corresponds to the range of speeds that crabs preferred when allowed to move on a track (Fig. 8). Nearly 50% of the crabs tested chose to walk in this range of speeds. Large crabs (70–90 g) never selected speeds greater than 0.5 m s^{-1} , whereas crabs of intermediate mass (30–50 g) attained the fastest speeds. These findings are consistent with data on endurance

and metabolic energy demand (Full, 1987). Maximum oxygen consumption was attained at speeds ranging from 0.16 to 0.18 m s^{-1} ; above these speeds, whole body lactate content is significantly elevated. Moreover, endurance decreased to less than 10 min at speeds greater than 0.2 m s^{-1} . The largest crabs (71 g) showed poorer endurance than animals of intermediate size (27 g). Larger crabs attained maximum oxygen consumption at relatively low speeds.

Slow running

Walking gaits are constrained to a certain range of speeds. Above these speeds birds and mammals adopt running or bouncing gaits. A bouncing gait is characterized by the time course of the mechanical energy; kinetic and gravitational potential energy changes of the centre of mass are in phase. The absence of an aerial phase is not a sufficient condition to exclude a gait from being a run or a trot (McMahon, 1985).

Stepping patterns have been used to define gaits in arthropods. However, this may not be appropriate because of the irregularity of the patterns. Stepping patterns often become more regular at high speeds and this could be interpreted as a gait change. Ghost crabs were clearly limited to using a pendulum-like energy exchange mechanism at speeds of less than 0.4 m s^{-1} , yet no obvious change in stepping pattern was observed. Above these speeds, crabs used the same mode of oscillation of the whole skeletal mass as found in quadrupedal mammals. Fluctuations of the gravitational potential energy and the horizontal kinetic energy were largely in phase. The symmetrical footfall pattern (alternating tetrapod), the linear increase in stride frequency with speed, as well as the time course of the ground reaction force, match the pattern typical of trotting quadrupeds. Crabs obviously can change to a running or bouncing gait, even though no aerial phases are present.

High recovery values of about 30% were estimated for a few trials in the speed range of 0.4 – 0.9 m s^{-1} (Fig. 4). Two different mechanisms could account for these deviations from the general trend. (1) During walking, the crab's body is suspended in a low position between the legs (Fig. 9). Some leg joints are positioned well above the crab's centre of gravity. Pivoting around these joints would allow the crab to walk effectively at speeds approaching 0.8 m s^{-1} . This leg arrangement, which is typical in arthropods, could allow high walking speeds without losing the advantage of high stability that results from the low position of the centre of mass. The arthropod design could enable a crab to walk at speeds where mammals are forced to run. (2) During slow galloping gaits (e.g. canter) recovery values can reach up to 30% in quadrupeds (Cavagna *et al.* 1977). Such a gait probably includes pivoting, as well as bouncing, phases and could also be used by crabs.

Fast running

The 'fast' running gait of the ghost crab was remarkably similar to a mammalian gallop. The change in gait from a slow to a fast run occurred at almost the identical speed and stride frequency predicted for the trot–gallop transition in a mammal

of the same mass, i.e. 0.8 ms^{-1} and 6.6 Hz , respectively (Heglund, Taylor & McMahon, 1974). As in galloping mammals, faster speeds were attained by increasing stride length, whereas stride frequency remained constant (Fig. 6). Furthermore, leg movement and force production resembled that of galloping mammals. Measurements of zero vertical force during a portion of the stride clearly showed that all the crab's eight legs were off the ground (Fig. 3).

Aerial phases have also been discovered in another ghost crab, *O. ceratophthalma*, during rapid running. Burrows & Hoyle (1973) reported that at these running speeds *O. ceratophthalma* became bipedal, using only the alternating push of legs 2 and 3 on the trailing side to power successive leaps. Electromyographic recordings of the leading leg muscles show a relatively maintained tonus. Force measurements in the present study support these findings, since the force required for forward locomotion at high speeds was developed by the trailing legs, while the leading legs produced only decelerations (Fig. 5). Once again the remarkable similarity between small bouncing mammals and ghost crabs is apparent.

Similarities between crabs and mammals suggest that common constraints for terrestrial locomotion may apply to different morphological designs. Perhaps crabs, like mammals, switch from a slow to a fast run in order to minimize the metabolic energy cost at a particular speed. Hoyt & Taylor (1981) have shown that trotting at high speeds for horses entails a higher metabolic cost than galloping. This prediction is difficult to test in crabs, because these animals can only sustain these speeds for a few minutes and anaerobic metabolism is required (Full, 1987). Gait transitions may also occur when an animal has attained a high peak muscle stress (Taylor, 1985). A change in gait could allow a redistribution of muscle force over time, so that speed can be increased. No information is available on muscle stresses in crabs. However, the fact that a change in gait occurred at almost the identical speed and stride frequency predicted for mammals suggests a comparable whole body stiffness. A similarity in whole body stiffness could be based on the similarity in muscle and connective tissue properties. Both animals could be functioning as mechanical spring systems possessing similar spring-like characteristics (McMahon, 1985).

Mechanical energetics of the centre of mass

The external mechanical energy used to move the centre of mass of the ghost crab a given distance (M_{CM}) was not different from that used by a bird or mammal of the same mass (Fig. 10; revised after Heglund *et al.* 1982a; Cavagna *et al.* 1977). M_{CM} appears to be relatively independent of locomotor design. Moreover, M_{CM}/kg has been shown to be independent of body mass over a wide range of mass (i.e. four orders of magnitude; Heglund *et al.* 1982a). This is unexpected because animals of different size are using different gaits at the same speed. These similarities in mechanics hint at a general principle for legged terrestrial locomotion. The properties of a musculoskeletal system (i.e. endo- or exoskeleton) appear to allow movements only in a certain range of force, velocity and displacement.

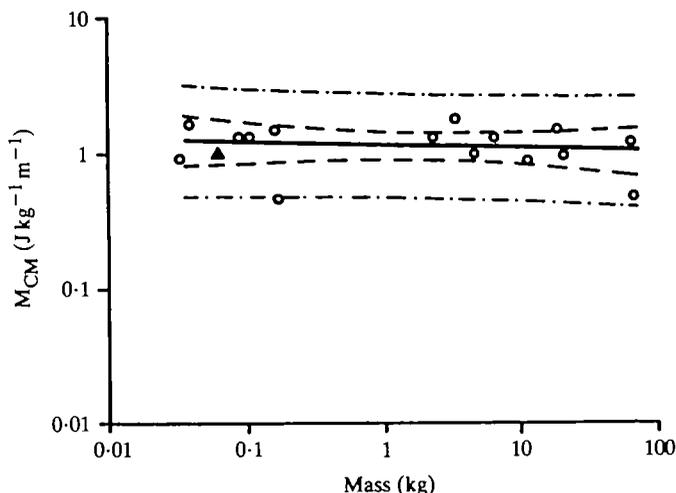


Fig. 10. Minimum mechanical energy per kg used to travel 1 m (M_{CM}) for birds and mammals (open circles) and the ghost crabs (filled triangles) as a function of body mass (revised after Heglund, Cavagna & Taylor, 1982a; Cavagna, Heglund & Taylor, 1977). Included are the 95% confidence interval of the regression (—) and the confidence interval predicting a single value from these data (---). M_{CM} appears to be relatively independent of body mass and was similar for mammals, birds and ghost crabs.

Comparison of mechanical and metabolic energy

The mechanical energy of the centre of mass (E_{CM}) represents a major portion of the total mechanical energy used during locomotion in small animals (67–93%; Heglund *et al.* 1982b). Yet this does not include the internal energy necessary to accelerate the limbs and the body relative to the centre of mass (E_I), the elastic strain energy of the system (E_E), or the transfer of energy that takes place between the different energies (Heglund *et al.* 1982b; Winter, 1979). The sum of these energies has not been estimated reliably for any animal. However, an assessment of these energies in the ghost crab based on previous research on vertebrates is possible, because the mechanical energetics of the centre of gravity as well as the metabolic energetics are similar.

\dot{E}_I , determined for bipedal and quadrupedal birds and mammals, increases curvilinearly with speed and is directly proportional to body mass (Fedak *et al.* 1982). Crabs undoubtedly expend energy internally to accelerate their limbs and body relative to their centre of mass, especially at fast speeds. If \dot{E}_I were of similar magnitude for a crab and a vertebrate of the same mass, then the total energy (\dot{E}_{tot}) would be better estimated by increasing the \dot{E}_{CM} estimate for the crab by approximately 7% at the lowest speeds and by as much as 39% at maximum speed. An estimate made by using high-speed film data for a running ghost crab showed an upper limit of 32% for \dot{E}_I at 0.72 m s^{-1} .

Mechanical energy can be transferred between segments if movement of a segment results in an acceleration of an adjacent segment (Winter, 1979). Heglund *et al.* (1982b) calculated an 8–32% decrease in \dot{E}_{tot} if complete transfer were

to have occurred between \dot{E}_I and \dot{E}_{CM} . If a similar degree of transfer occurred in the ghost crab, the estimate of \dot{E}_{tot} made from \dot{E}_{CM} should be decreased correspondingly.

Large vertebrates store and recover considerable amounts of energy during locomotion (Cavagna *et al.* 1977; Heglund *et al.* 1982*b*), since whole body efficiencies exceed estimates of muscular efficiency (>25%; Cavagna *et al.* 1964; Margaria, 1976). The ability of small animals to store energy may be limited (Biewener, Alexander & Heglund, 1982). However, arthropods specialized for jumping, such as locusts and fleas, can store energy in apodemes and in resilin pads of joints (Bennet-Clark, 1975; Bennet-Clark & Lucey, 1967). Ghost crabs may also possess the ability to store and recover elastic energy, especially during rapid running, but this requires further study. If this were the case, then energy stored elastically need not be repeatedly supplied by muscle at high metabolic costs. Therefore, estimates of \dot{E}_{tot} would be inflated when compared to the metabolic input from muscles.

With the above caveats in mind, let us examine the efficiency of locomotion (defined as the ratio of mechanical power output to metabolic power input) for the ghost crab. Assuming that \dot{E}_{CM} is the major contributor to the mechanical power required for locomotion and that the steady-state oxygen consumption determined during treadmill exercise is a reasonable measure of the total metabolic energy input, efficiencies ranging from 4 to 5% are found over the range of speeds where both metabolic and mechanical measurements are available (0.09–0.14 m s⁻¹). If the metabolic input is extrapolated to higher speeds, efficiencies increase, but not substantially (e.g. 5–9%). Large crabs (71 g) have somewhat greater efficiencies than ones of intermediate mass (27 g) because of the lower mass-specific metabolic cost of locomotion. These locomotor efficiency values are remarkably similar to those predicted for a bird or mammal in a similar mass range, 5–8% (Heglund *et al.* 1982*b*), when the differences in metabolic rate at zero speed (i.e. y-intercept including resting rates) have been removed.

The surprisingly low efficiencies in ghost crabs and small mammals raises the question of whether minimizing small changes in mechanical work output significantly alters the metabolic energy input. It is possible that the metabolic cost of maintaining muscle tension is more important than work production (Taylor, 1985). Muscles in crabs and small mammals may function more to stabilize joints and operate as springs (McMahon, 1985).

The similarities in efficiency, energy-conserving mechanisms, and gait changes are unexpected because ghost crabs and mammals differ radically in locomotor design. Yet both have jointed framework skeletons powered by a common tissue, muscle. Apparently, muscle can be arranged with both endoskeletons and exoskeletons so as to allow similar whole animal performance.

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