

# Energy Transformations in Cells and Organisms

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## Mechanics and Energetics of Terrestrial Locomotion: Bipeds to Polypeds

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### Introduction

Animals using legs for terrestrial locomotion show remarkable variation in form and function. Nevertheless, each variation must allow for the repeated generation of the necessary propulsive forces. Obviously, the properties of musculo-skeletal systems can only allow movement in a certain range of forces, velocities and displacements. Nearly all employ a jointed framework skeleton and striated muscle as levers to power movement.

Studies on humans, other mammals, birds and some lower vertebrates have addressed many critical questions concerning terrestrial locomotion (Alexander and Goldspink, 1977; Pedley, 1977; Heglund et al., 1982). The success of these studies has largely come from exploiting extremes in function that result from differences in body size, not body form. As a direct result of these and other studies, our understanding of vertebrate terrestrial locomotion has advanced considerably. Specific hypotheses have been generated concerning mechanical energy fluctuations (Cavagna et al., 1977; Fedak, et al., 1982; Heglund et al., 1982a,b), metabolic energy costs (Bennett, 1982; Taylor et al., 1982; Taylor et al., 1980), and stresses in muscle (Biewener et al., 1988; Taylor, 1985) and bone (Biewener, 1983). Moreover, useful mechanical models have been developed (see Blickhan, this volume; McMahon, 1985).

We have focused on variation in locomotor design to test whether or not legged locomotion is based on common design principles. Nowhere is there greater diversity in loco-

motor design than in the arthropods. Arthropods have evolved an extraordinary array of structures used to move on land (Herreid, 1981). They possess different numbers of walking legs (4 in a hermit crab to over 180 in a millipede), a variety of leg lengths and positions, numerous stepping patterns, different musculo-skeletal arrangements, a range of body shapes (long in millipedes and round in some crabs), different styles of locomotion (forwards versus sideways travel) and different oxygen transport systems (gills versus trachea).

Despite variations in structure, our past measurements of the metabolic cost of locomotion show a remarkable similarity among different arthropods and between arthropods and vertebrates, suggesting the possibility of underlying principles (Full, 1987; Full, and Herreid, 1983; Full and Herreid, 1984; Herreid, and Full, 1984; Herreid, and Full, 1985; Herreid et al., 1981). Our investigation of ghost crab locomotion examined locomotion mechanics as well as metabolic cost (Blickhan and Full, 1987; Full, 1987). This was the first complete study relating arthropod metabolic energetics to the mechanics of terrestrial locomotion. The results were surprising. Similarities in whole animal energetics and mechanics exist between crabs and vertebrates. Our most recent studies of cockroaches provide further evidence for common principles.

### Mechanics of Terrestrial Locomotion

*Walking:* Birds and mammals use an energy conserving mechanism during walking that

is analogous to an inverted swinging pendulum or an egg rolling end over end (Cavagna et al., 1977; Heglund et al., 1982a). By using this pendulum-like mechanism, kinetic energy and gravitational potential energy are exchanged, and not simply lost, as the animal's center of mass rises and falls during a stride. Vaulting over a relatively stiffened leg conserves up to 70% of the mechanical energy that must otherwise be provided by muscles and tendons. Moreover, using a stiff leg can reduce moments around joints and, thus, decrease the metabolic energy requirement (see Alexander, this volume).

A simple mathematical model can explain how crabs or other arthropods might use a pendulum-like energy exchange mechanism (Cavagna et al., 1977). The exoskeleton of crabs and most arthropods allows pivoting around one or more of its joints positioned laterally to the animal's center of gravity. The effective "hip" height ( $l$ ) of this arrangement can be determined from the maximum speed ( $v_{\max}$ ), assuming the body moves on a pathway or arc of radius  $l$ . At this speed the body has an acceleration towards the supporting foot equal to the centrifugal force,  $v_{\max}^2/l$ . Since an animal does not pull itself downward, its acceleration cannot exceed the acceleration due to gravity,  $g$ . Therefore,  $l \geq v_{\max}^2/g$ . Given the maximum walking speed, the effective "hip" height can be estimated. Calculations suggest that crabs and other arthropods could pivot around one or two joints, much as we do around our hip joint.

Ghost crabs, like birds and mammals, appear to use a pendulum-like energy conserving mechanism, despite differences in morphology, such as leg number and position (Blickhan and Full, 1987). Energy recovery approaches 55% at slow speeds. These slow speeds correspond to those crabs prefer when allowed to walk freely. By contrast, data collected on our newly-built, miniature force plate indicate that some cockroach

species may not use a pendulum-like mechanism (Full and Tu, unpublished). Energy recovery averages only 15% at all speeds.

Our initial studies of arthropod walking mechanics demand further investigation because the use of the pendulum-like mechanism may reveal an important feature in the design of arthropod legs. The M-like stance of arthropods may allow them to operate effective pendulums at higher speeds without forsaking the advantage of high stability due to a low center of mass. They essentially have extended hip heights. This would be analogous to the increase in walking speed that is possible when humans use crutches.

*Running:* Birds and mammals use a second energy conserving mechanism analogous to a spring or bouncing ball (Alexander, 1984). Walking gaits are constrained to a certain range of speeds. Above these speeds, birds and mammals adopt running or bouncing gaits (Blickhan, this volume). A bouncing gait is characterized by the time course of mechanical energy changes; kinetic and gravitational potential energy changes of the center of mass are in phase. At high speeds this mechanism allows humans and kangaroos to save more than half the metabolic energy required for locomotion.

Our study on ghost crabs noted that pendulum-like energy exchanges are limited to very low speeds. Above these speeds ghost crabs use the same mode of whole skeletal-mass oscillation found in running quadrupedal mammals (Blickhan and Full, 1987). At these high speeds, fluctuations of the gravitational potential energy and the horizontal kinetic energy are largely in phase. Thus, crabs also appear to change to a running or bouncing gait and perhaps store energy elastically, even though no aerial phases are present. In this case, whole animal force measurements reveal a shift in gait during locomotion that is not obvious in ordinary gait analysis. At very high speeds, ghost

crabs switch to a "fast" running gait that is remarkably similar to a mammalian gallop. The change in gait from a slow to a fast run occurs at almost the same speed and stride frequency as predicted for the trot-gallop transition of a mammal of comparable mass (Heglund et al., 1974). As in galloping mammals, faster speeds are attained by increasing stride length, while stride frequency remains constant. Furthermore, measurements of zero vertical force during a portion of the stride clearly show that all the crab's eight legs are off the ground.

Other arthropods may use bouncing gaits as well. However, studies on hopping mammals suggest that the capacity of small animals to store energy may be limited (Biewener et al., 1981). It is not known whether small arthropods, such as crabs, are similarly limited in using their muscle, apodemes or other skeletal material as springs. Arthropods specialized for jumping, such as locusts and fleas, can store energy in apodemes and in resilin pads of joints. The same is true of flying insects which operate at high wing-beat frequencies.

To further investigate the unexpected similarities among diverse locomotor designs, we recently studied the mechanics of a six-legged arthropod, the cockroach (Full and Tu, unpublished). At all speeds tested, cockroaches use an alternating tripod stepping pattern. The hind left, middle right and front left legs all move simultaneously, while each moves out of phase with its contralateral pair. This gait is similar to a quadrupedal trot, but with an additional pair of legs. Two-, four-, six- and eight-legged animals can all adopt gaits that result in propulsion by only two alternating sets of legs (i.e. 1-4 legs per set; Fig. 1A-D). Despite their hexapedal architecture, ground reaction force patterns are remarkably similar to those described for trotting octapedal crabs and quadrupedal dogs, and running bipedal humans. When the center of mass falls, vertical

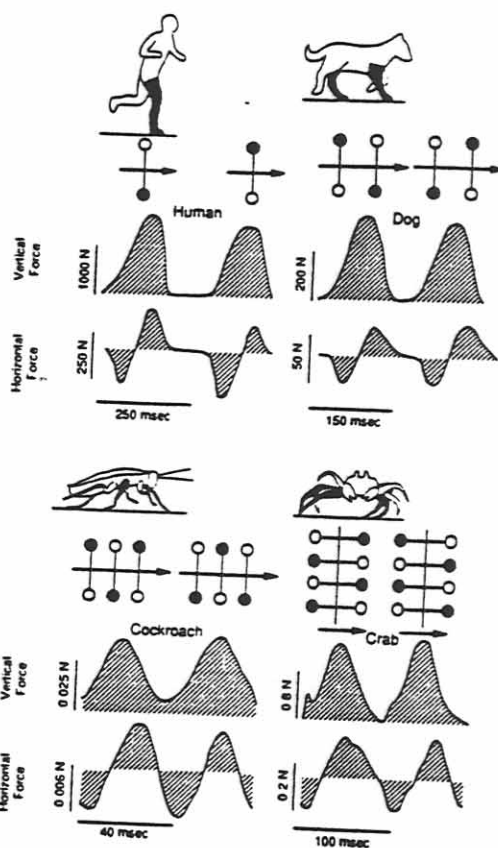


Fig. 1 Gait patterns and ground reaction force patterns of 2-legged (A), 4-legged (B), 6-legged (C) and 8-legged (D) runners during one stride. Filled circles represent a leg contacting the ground, whereas open circles represent legs moving in the air. Each animal can propel itself by two alternating sets of legs (i.e. 1-4 legs per set). When vertical force equals zero the animal displays an aerial phase. Negative horizontal force represents braking, whereas positive values show forward acceleration of the center of mass.

force increases and deceleration or braking produces a negative horizontal force. Peak vertical force is 1.5 times the body weight (1.5 G), similar to that produced by a slow trotting dog. Subsequent forward acceleration of the body produces a positive horizontal force. Vertical force decreases as the center of mass rises and an aerial phase is nearly

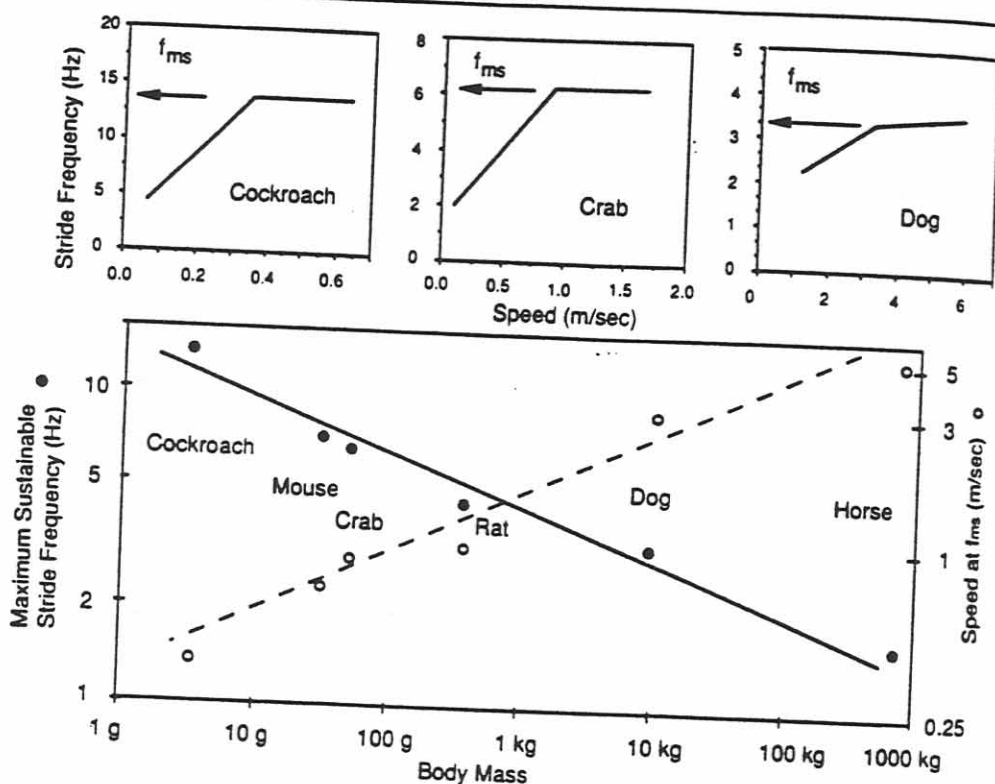


Fig. 2 (A) Stride frequency as function of speed for a six-legged cockroach (*B. discoidalis*; Full and Tu, unpublished), an eight-legged ghost crab (Blickhan and Full, 1987), and a four-legged dog (Heglund et al., 1974). This pattern is typical for quadrupedal mammals that change from a trot to a gallop at the maximum sustainable stride frequency ( $f_{ms}$ ). (B) Maximum sustainable stride frequency ( $f_{ms}$ ; closed circles and solid line) and the speed at the maximum sustainable stride frequency (open circles and dashed line) as a function of body mass on logarithmic coordinates.

attained. Just as in bouncing bipeds and quadrupeds, horizontal kinetic energy fluctuates in phase with gravitational potential energy.

At low speeds cockroaches increase speed by increasing stride frequency (Fig. 2A). At high speeds stride frequency attains a maximum. Faster speeds are achieved by longer strides. This pattern is typical of four-legged mammals and eight-legged crabs at the transition from a trot to a gallop or fast run. In mammals both the maximum sustainable stride frequency and the speed at which the maximum sustainable stride frequency is attained scale with body mass (Fig. 2B; He-

glund et al., 1974). A 30 g mouse changes from a trot to a gallop at a frequency twice that of a 9 kg dog, but at speeds 1/4 as fast. Surprisingly, small cockroaches and eight-legged crabs follow the same trend toward decreasing frequency with size, despite the striking diversity in morphology and physiology represented. For the first time, quantification of external forces produced and energy fluctuations may allow comparisons of "equivalent" gaits in very different morphological designs.

Similarities between crabs and mammals suggest that common constraints for terrestrial locomotion may apply to different

morphological designs. Perhaps arthropods, like mammals, switch gaits to minimize the metabolic energy cost at a particular speed. Horses incur a greater metabolic cost when forced to trot at speeds where they would naturally gallop (Hoyt and Taylor, 1981). Gait transitions may also occur when an animal attains a high peak muscle stress (Perry et al., 1988; Taylor, 1985). A change in gait could provide a redistribution of muscle force over time, thereby allowing greater speed increases. No information is available on muscle stresses in arthropods during locomotion. However, the fact that ghost crabs and cockroaches change gait at almost the identical speed and stride frequency predicted for mammals suggests that spring-like systems based on similar muscle and connective tissue properties are operating. Animals may very well operate as tuned mechanical spring systems possessing similar spring-like characteristics (see Blickhan, this volume; McMahon, 1985).

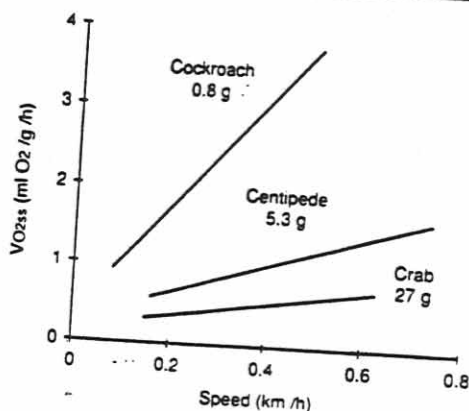


Fig. 3 Mass-specific, steady-state oxygen consumption ( $V_{O_{2ss}}$ ) as a function of speed in 6-, 8- and 40-legged runners (Full 1987; Full and Herreid, unpublished). Body mass, as opposed to variation in form, appears to correlate best with the cost of locomotion. Small animals on a per gram basis require more energy per time and per distance.

#### Energetics of Locomotion

Our studies of the metabolic cost of terrestrial locomotion for a variety of arthropods show remarkable similarities to data collected for birds, mammals and lizards. At the onset of activity, the rate of oxygen consumption in many arthropods increases rapidly from resting to a steady-state. Below the maximum rate of oxygen consumption, steady-state rates represent the energy required for locomotion since non-aerobic pathways appear to contribute little energy (Full, 1987). Steady-state oxygen consumption (energy per time) increases linearly with speed in two, four, six, eight and even 40-legged runners (Fig. 3). Differences in oxygen consumption become apparent when animals of different size are compared. A gram of a small animal uses more energy per unit time to travel at a given speed. More importantly, smaller runners demand more energy to increase speed. Likewise, they require more energy to travel a given distance. The

slope of the speed versus steady-state oxygen consumption represents the minimum energy requirement per unit distance, termed the minimum cost of locomotion.

The mass-specific minimum cost of locomotion in polypodal runners decreases with an increase in body mass (Fig. 4; Full, 1987; Full and Herreid, 1983; Full unpublished; Herreid and Full, 1984; Herreid and Full, 1985; Herreid and Full, 1988; Herreid et al., 1981; Jensen and Holm-Jensen, 1980; Lighton, 1985) and follows the same trend observed in two and four-legged runners (Full, 1986; Full et al., 1988; John-Alder et al., 1986; Taylor et al., 1982). To move a unit of mass one meter a three gram cockroach requires twice the energy of a 30 g crab or mouse and nine times that of a three kg dog. This suggests that variations in locomotor design are less important in determining metabolic cost than variations in body mass. Schmidt-Nielsen (1984) wondered as we did, "Is it a coincidence or an expression of a fundamental principle that (arthropods)

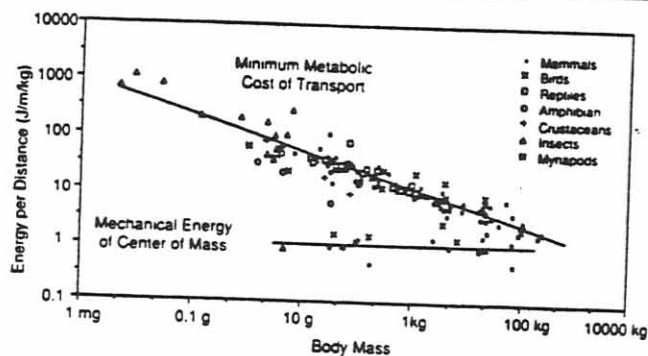


Fig. 4 Logarithmic plot of mass-specific external mechanical energy ( $E_{\text{mech}}$ ) and minimum metabolic energy ( $E_{\text{metab}}$ ) used to move a kg of animal 1 m in distance. Small animals, regardless of form, require relatively more metabolic energy to travel a distance than large animals, but do not produce relatively more mechanical energy to move their center of mass. Note that muscle efficiency (mechanical energy output / metabolic energy input) should not be determined by comparing these functions because external power does not necessarily equal total mechanical power. Data for mammals and birds (Taylor et al., 1982), lizards (John-Alder et al., 1986), amphibians (Full, 1986; Full et al., 1988), crustaceans, insects and myriapods (Full, 1987; Full and Herreid, 1983; Full unpublished; Herreid and Full, 1984; Herreid and Full, 1985; Herreid and Full, 1988; Herreid et al., 1981; Jensen and Holm-Jensen, 1980; Lighton, 1985) are from various sources.  $E_{\text{metab}} = 10.8 M^{-0.32}$  ( $r^2 = 0.87$ ) and  $E_{\text{mech}} = 1.07 M^{-0.01}$  where  $M$  is body mass in kg.

fall on an extension of the vertebrate regression line?" We attempted to test whether these findings were a result of radically different locomotor designs developing similar rates of mechanical work or whether similar-metabolic costs result despite differences in the mechanical power developed.

In our first attempt to examine these relationships, we selected the eight-legged ghost crab. The results were unexpected. The crab's minimum metabolic cost of locomotion was not significantly different from that of a similarly sized mammal (Full, 1987). Likewise, the external mechanical power developed was similar to that predicted for a bird or mammal of the same body mass (Blickhan and Full, 1987).

Our recent studies of cockroaches suggest that the rates of mechanical and metabolic energy production do scale predictably among legged runners. From the sum of kinetic and potential energy fluctuations of the cockroach, we calculated the external work done on the center of mass during one

stride (Cavagna, 1975). The rate of external work, or power, increased linearly with speed as in ghost crabs. Previously, Cavagna et al. (1977) and Heglund et al. (1982a) established that the rate of external work increased proportionally with speed in a variety of vertebrates including quail, dogs, humans and horses. To facilitate comparison of animals that run at different speeds, we calculated the amount of work done per distance rather than per unit time. Cockroaches produced 0.9 J of energy per kg to repeatedly accelerate their center of mass over 1 m (Fig. 4). Birds, mammals and an eight-legged crab generate about 1 J of energy per kg to move the same distance. When traveling similar distances, mass-specific, external mechanical energy appears to be relatively constant for animals of different morphology that vary in mass by more than three orders of magnitude. Similarities in metabolic cost and mechanics hint at general design constraints that may result from the relatively conservative mechanical and energetic properties of jointed-framework, musculo-skeletal systems.

These data on locomotion energetics show that mechanical power, as is presently estimated, cannot be used to predict the metabolic cost of locomotion (Taylor, 1985; Fig. 4). Metabolic cost varies by more than three orders of magnitude with changes in body mass, yet these differences are not reflected by parallel differences in mechanical energy. One possible reason for this apparent discrepancy is that all relevant mechanical variables that scale with size have not been included (e.g. elastic strain energy, internal energy, segmental energy transfer and limb geometry). A second reason relates to muscle function. Muscles do not produce only positive mechanical work during terrestrial locomotion. Metabolic energy is also required when a muscle is active, but doesn't change length and perform mechanical work. Furthermore, muscles are often active while work is being done on them (i.e. negative work) and they are stretched. Consequently, we might expect to find only a weak relationship between the mechanical power developed and the metabolic cost of locomotion (Williams, 1985). The cost of muscle force production may be a more appropriate indicator of total metabolic cost (Taylor, 1985).

### Conclusion

We support S.M. Manton's contention (1977) that, "In the absence of precise knowledge of the meaning of animal form, it has been safe to put forward many unsound comments on arthropod evolution" and on animal structure and function in general. Variation in form does not necessarily result in a similar variation of whole-animal function. Comparisons of equivalent speeds and gaits among taxa separated by millions of years of evolution is possible if force patterns, mechanical work and metabolic cost are quantified. Similarities in whole animal mechanics and metabolic cost are unexpected because cockroaches differ radically from crabs, birds and mammals in general

morphology and physiology. Nevertheless, each solution for legged locomotion must allow for the repeated generation of the necessary propulsive forces. All legged runners power a jointed framework skeleton by a common tissue, muscle. Muscles must be contracted and relaxed at a given frequency to produce a stepping pattern. Similar material properties and functional requirements of muscles and their connective tissues may be the basis for the common themes among many-legged runners.

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