7

The concepts of efficiency and economy in land locomotion

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7.1 INTRODUCTION

Is the concept of efficiency in terrestrial locomotion useful when applied at the level of the whole animal? Can measures of efficiency aid in revealing the consequences of variation in morphology and physiology that relate to locomotion on land? Can these measures quantify the effect of variation in leg number (two in humans to over 600 in a millipede), leg length and orientation, stepping pattern (metachronal waves gaits, trotting versus hopping), muscle type, musculo-skeletal arrangement (exo- versus endoskeletons), body shape (long in centipedes and millipedes versus round in some crabs), and locomotor style (forwards versus sideways travel in crabs)? Can measures of efficiency provide useful information about the mechanistic, ecological and evolutionary bases of how animals of diverse body form move? Most lay people, as well as researchers, would probably answer yes to each question. Many functional morphologists, physiologists and biomechanists believe they can recognize efficient terrestrial locomotion. Unfortunately, when our hypotheses are tested, the results are often ambiguous. Whether or not our hypotheses are based on sound principles of physics or physiology seems to make little difference. Awkward marathon runners win gold medals; athletes ranked as inefficient expend less energy than more graceful runners (Cavagna and Kram, 1985); some mammals with large limbs use no more energy than those that evolved more 'efficient' tapered limbs (Taylor *et al.*, 1974); and animals, such as a centipede, that 'waste' motion as they laterally undulate actually require somewhat less energy to travel a given distance than other animals of the same mass (Full, 1989).

7.2 WHAT IS THE DEFINITION OF EFFICIENCY ?

How can we resolve this apparent mismatch between reasonable hypotheses and evidence? There are at least two reasons for the mismatch. One has its origins in the definition and use of the term efficiency, whereas the other results from the complexity of the systems used in locomotion. What is the definition of the term efficiency and how do we apply it to comparative terrestrial locomotion? Efficiency has at least two definitions and is most often used in two ways. Efficiency, in the context of mechanics, is defined as:

(n.) 1. the ratio of work or energy (E) output to input
(mechanical efficiency = E_{output}/E_{input}).

This definition most often refers to animals performing straight-ahead, constant-speed locomotion. Measurements of both input and output have been conducted on surprisingly few species (Alexander and Vernon, 1975; Cavagna *et al.*, 1977; Dawson and Taylor, 1973; Blickhan and Full, 1987; Heglund *et al.*, 1982b; Herreid and Full, 1984; Full, 1987; Full and Tu, 1989). Mechanical efficiency simply relates one measure of performance, metabolic energy input, to one possible explanation of its variation, mechanical energy output.

A second definition of efficiency is:

(n.) 2. effectiveness or competency in performance.

It is often this second notion of effective performance that best describes the common use of the term efficiency. This definition has considerable utility in addressing mechanistic, ecological and evolutionary questions.

7.3 WHAT IS THE 'EVENT' AND HOW DO YOU MEASURE PERFORMANCE?

When we make a statement concerning an animal's efficiency, two questions must be answered. First, exactly what task or 'event' is the animal performing? Second, what is the measure of performance? In many cases, our hypotheses concerning the efficiency of one animal compared to another would probably be supported, but we simply may not be conducting the appropriate test, staging the appropriate 'event' to measure performance. For example, an animal may be very inefficient at steady-state, constant-speed locomotion, but may be highly effective at maneuvering around or over obstacles. Likewise, animals that are very effective sprinters may be inefficient steady-state runners when migrating long distances. Selecting the 'event' to study for comparison is crucial and cannot be ignored. To best study the consequences of variation in locomotor structure and function (such as leg number, leg position, skeletal type), it is obvious that efficiency or effectiveness indices must include not only steady-state locomotion, but also intermittent activity, obstacle negotiation (e.g. climbing, leaping and maneuvering) and burst locomotion.

Selecting the relevant measures of performance may be equally as important as selecting the appropriate event. Inappropriate measures of performance could result in a mismatch between data and our hypotheses of efficiency. What are the criteria used to evaluate locomotion? If we compare the performance of animals moving over a comparable distance, does the efficient animal use the least energy, travel the distance in the shortest time, or recover the fastest for the next bout of activity? Energy utilization is not the only measure of effective performance. Obviously, we demand other performance measures when purchasing wheeled vehicles, such as automobiles, motorcycles and trucks. Performance measures other than energy utilization are receiving more attention in legged locomotion for a variety of species. Some of these include: (1) endurance or fatigue resistance, (2) distance travelled, (3) acceleration and maximum speed, (4) durability and strength, and (5) maneuverability and stability.

7.4 QUESTIONS ADDRESSED BY COMPARING PERFORMANCE

Variation in locomotor performance within and among species has and will continue to reveal clues to the mechanistic bases of muscular, skeletal and nervous systems. Considering multiple events and performance measures is likely to reveal interesting functional and structural compromises, since few complexes are optimized for a single event. For example, Biewener and Blickhan (1988) found that, for their mass, kangaroo rats have proportionately large hind limb muscle, tendons and bones to withstand the large forces associated with rapid acceleration during predator avoidance. These relatively large structures, however, limit their ability to store and recover elastic strain energy during steady-state locomotion. Using the concept of efficiency as effective performance cannot only address mechanistic questions, but also permits the formulation of evolutionary and ecological hypotheses. Recent attempts have been made to explain variation in locomotor performance in terms of ecology and evolution (Huey, 1987; Huey and Bennett, 1986). The evolution or origin of morphological and physiological characters is studied by mapping variation in performance onto independently established phylogenies. For example, evolutionary change in relative hind limb length of Anolis lizards can explain much of the variation measured in sprinting and jumping performance (Losos, unpublished). Maintenance and selection of locomotor characters is addressed in an ecological context by measuring variation in performance within populations (Arnold, 1983).

7.5 METABOLIC ENERGY INPUT - THE ECONOMY OF LOCOMOTION

The economy of locomotion is one performance measure that has been used frequently to evaluate efficiency in both senses of the word, effectiveness and mechanical efficiency. The economy of locomotion, metabolic energy input, is the denominator in the mechanical efficiency equation. It is commonly represented by the submaximal, steady-state oxygen consumption (V_{O2ss}) per unit time (time-specific economy) or per unit distance (distance-specific economy) of an animal running at a constant speed on a treadmill. Animals considered to be economical have lower values of submaximal, steady-state oxygen consumption per unit time or distance. Can the economy of locomotion, as a measure of efficiency, aid in revealing the consequences of variation in morphology and physiology? The answer depends upon whether: (1) we can obtain comparable measures of economy in diverse species, (2) significant variation in economy exists, and (3) variation in economy can be related to variation in morphology and physiology.

7.5.1 A. What is the common currency?- Is oxygen consumption the appropriate measure?

For most legged runners, steady-state oxygen consumption (V_{O2ss}) during constant-speed treadmill exercise is a reasonable indicator of the energy used. Non-aerobic contributions appear to be negligible at V_{O_2} rates below 80% of maximum. The oxygen transport systems of birds and mammals (Seeherman *et al.*, 1981), lizards (Seeherman *et al.*, 1983), insects (Herreid and Full, 1984), centipedes and millipedes (Full and Herreid, 1986), some crustaceans (Full, 1987; Full and Herreid, 1983; Herreid and Full, 1985) and even a lungless salamander (Full, 1986) adequately delivery oxygen to aerobically functioning muscles. However, the assumption that V_{O2ss} is a reliable measure of metabolic power input must be checked, since it is violated in other species, such as some lungless salamanders, crabs and spiders, in which V_{O2} uptake kinetics are very slow (half time to steady-state is 4–6 min) and/or locomotion at even very slow speeds represents a large fraction of V_{O2max} (Full and Herreid, 1984; Full *et al.*, 1985; Herreid *et al.*, 1983; Anderson and Prestwich, 1985; Prestwich, 1983). In the future, more studies of anaerobic end-product (e.g. lactate) production and removal are needed to better quantify the contributions of accelerated glycolysis or other anaerobic pathways (Brooks *et al.*, 1984).

7.5.2 B. Where is metabolic energy used during locomotion?

Certainly, most of the metabolic energy used during locomotion is required by contracting locomotor muscles (Fig. 7.1). Yet, other tissues and organs must be maintained. Some may demand less energy during activity, such as digestive and excretory processes (Stainsby *et al.*, 1980). On the other hand, hormone release during exercise can elevate tissue respiration during and after exercise (Cain, 1971). An increased energy demand may result from a Q_{10} effect on tissues as body temperature rises or additional energy may be required for thermoregulation (Hurst *et al.*, 1982). The cost of operating respiratory and circulatory systems at higher rates during exercise may vary among species (see Milsom in Chapter 8). Are circulatory costs lower or higher in open versus closed systems? Is the metabolic cost of gill ventilation in crabs substantial and does it increase with speed? How does this cost compare to the cost of lung ventilation in lizards or tracheal ventilation in insects as a function of speed? Do lungless salamanders save energy during exercise by having no ventilatory costs? One important issue that must be addressed is whether or not whole animal measures of oxygen consumption can allow partitioning of these different sources demanding energy.

7.5.3 C. Gross, net and incremental economy - which to use for efficiency?

In the majority of animals tested thus far, including, birds and mammals (Taylor *et al.*, 1970; Seeherman *et al.*, 1981), lizards (Bennett,

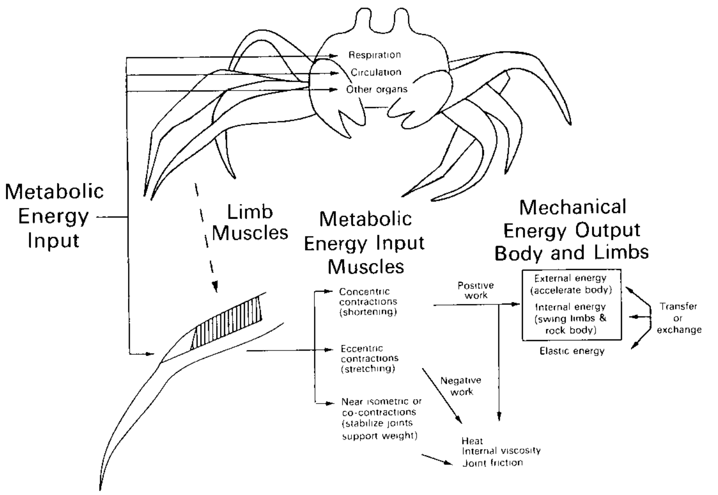


Fig. 7.1. Metabolic energy input and output in land locomotion. Metabolic energy is used by both locomotor muscles and non-locomotor sources. Limb muscles require energy when they shorten (concentric contraction), are stretched (eccentric contraction), or used to stabilize joints and support an animal's weight. Metabolic energy is dissipated due to friction and lost as heat. Concentric contractions generate increases in mechanical energy to move the body (external energy) and limbs and trunk relative to the body (internal energy). Eccentric contractions are associated with decreases in mechanical energy. Mechanical energy can be transferred from one source to another and between segments, as well as within a segment.

1982; Seeherman *et al.*, 1983), insects (Herreid *et al.*, 1981), centipedes and millipedes (Full and Herreid, 1986), some crustaceans (Full, 1987; Full and Herreid, 1983; Herreid and Full, 1985), and lungless salamanders (Full, 1986), V_{O2ss} or, better, the gross rate of oxygen consumption ($V_{O2gross}$) increases linearly with speed below the maximum oxygen consumption. Ponies forced to walk or trot at higher or lower than normal speeds (Hoyt and Taylor, 1981), walking humans (Margaria *et al.*, 1963), and running polar bears(Hurst *et al.*, 1982), squirrels (Hoyt and Kenagy, 1988), and minks (Williams, 1983) are exceptions, showing curvilinear or discontinuous functions. Hopping kangaroos decrease $V_{O2gross}$ with speed (Dawson and Taylor, 1973).

Traditionally, the linear $V_{O2gross}$ vs. speed function has been partitioned into three components, maintenance (V_{O2mat}), offset ($V_{O2offset}$) and incremental oxygen consumption (V_{O2inc}; Fig. 7.2) where:

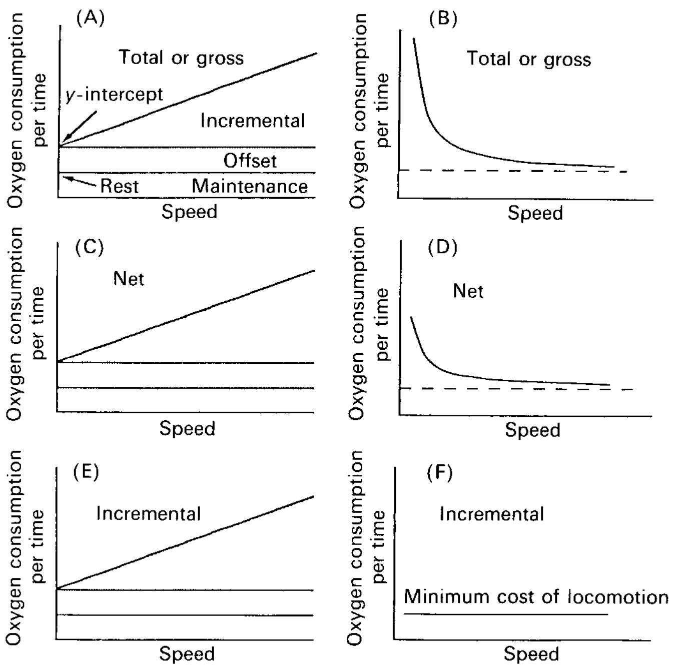


Fig. 7.2. Metabolic cost of locomotion per unit time and distance as a function of speed. (A) Metabolic energy per time (rate of oxygen consumption) increases linearly with speed. Total or gross metabolic cost (shaded area) is the sum of three components; rest, offset and incremental. (B) Total metabolic cost per distance. Dashed line represents the minimum cost of locomotion. (C) Net metabolic cost per time (shaded area) includes offset and incremental costs. (D) Net metabolic cost per distance. Dashed line represents the minimum cost of locomotion. (E) Incremental or work metabolic cost per time. (F) Incremental metabolic cost per distance or the minimum cost of locomotion which equals the slope of the metabolic cost versus speed function.

$$V_{O2ss} = V_{O2gross} = V_{O2mat} + V_{O2offset} + V_{O2inc} \qquad (7.1)$$

This partitioning of steady-state oxygen consumption has lead to at least three different economy values, gross ($V_{O2gross}$), net (V_{O2net}) and incremental (V_{O2inc}). These values have been used extensively in human and animal exercise physiology. Disagreement exists over which value is the most appropriate measurement of economy (Donovan and Brooks, 1977; Stainsby *et al.*, 1980).

(1) **Gross or total metabolic cost** is the sum of all three compo-

nents of the V_{O_2} vs. speed function, $V_{O2offset}$, V_{O2mat} and V_{O2inc} (Fig. 7.2A). Time-specific, gross metabolic cost increases with speed, whereas distance-specific, gross metabolic cost decreases with speed (Fig.2B). (2) **Net metabolic cost** equals the gross metabolic cost minus resting oxygen consumption (V_{O2rest}) and assumes that V_{O2rest} equals V_{O2mat} at all speeds (Fig. 7.2C). Time-specific, net metabolic cost increases with speed, whereas distance-specific, net metabolic cost decreases with speed (Fig. 7.2D). Net metabolic cost includes $V_{O2offset}$. (3) **Delta, incremental or instantaneous metabolic cost** equals the gross metabolic cost minus V_{O2mat} and $V_{O2offset}$ (Fig. 7.2E). Time-specific, incremental metabolic cost increases with speed, whereas distance-specific, net metabolic cost is independent of speed (Fig. 7.2F). Variation in incremental metabolic cost can result if $V_{O2offset}$ or V_{O2mat} are not baselines that remain constant as a function of speed.

7.5.4 D. Maintenance and 'offset' costs during locomotion - What are the bases of baselines and are they lines?

(1) Maintenance costs Variation in V_{O2mat} can significantly affect metabolic cost if $V_{O2gross}$ is used. Direct measures of V_{O2mat} are difficult and few estimates have been attempted. In most cases a constant baseline, approximated by V_{O2rest}, is the standard assumption (Fig. 7.2A; Stainsby *et al.*, 1980). This assumption needs further testing, especially if maintenance components are large fractions of the total or gross $V_{O2gross}$ and increase or decrease as a function of speed.

Several variables such as body mass, temperature and species affect V_{O2rest}.

Body mass. Much of the variation in V_{O2mat} can be attributed simply to body mass. Mass-specific V_{O2rest} decreases with increasing body mass in nearly all animals; however scaling exponents show considerable variation (Fig. 7.3; Hemmingsen, 1960).

Temperature. In most ectotherms, changes in temperature will add to this variation. V_{O2rest} approximately doubles with a 10°C increase in temperature, but Q_{10} values also vary.

Body form - species differences. Considerable variation in maintenance cost is present for different species or taxa of the same body mass measured at the same temperature. Surprisingly, ectotherms require about only one-quarter the V_{O2rest} of an endotherm, even when both are operating at comparable body temperatures (Bennett, 1982). Considerable variation also exists among ectotherms. For example, sala-

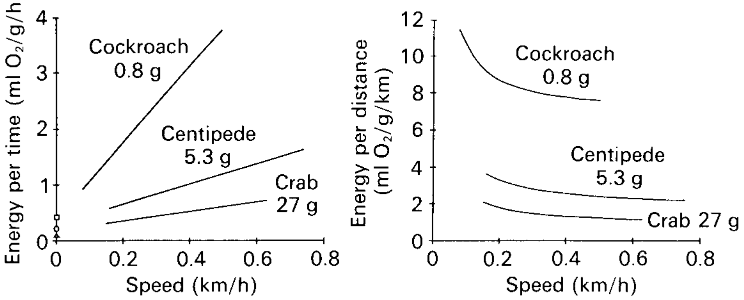


Fig. 7.3. Mass-specific oxygen consumption per time and distance as a function of speed for animals that differ in body mass and form. (A) Despite variation in form mass-specific maintenance, offset and incremental oxygen consumption all increase with a decrease in body mass. Resting oxygen consumption is shown for the cockroach (square), centipede (circle), and crab (triangle). (B) Smaller animals require more metabolic energy to move a gram of mass one meter. Data on ghost crabs from Full (1987). Cockroach and centipede from Full unpublished.

manders have an unusually low V_{O2rest} compared to other ectotherms at the same temperature (Fig. 7.4; Full *et al.*, 1988; Walton, unpublished).

(2) 'Offset' cost Animals may differ in gross or net cost of locomotion because of changes in 'offset' costs. $V_{O2offset}$ is energy used in addition to maintenance requirements at near zero speed. It results from the fact that the V_{O2ss} vs. speed function extrapolates above resting oxygen consumption V_{O2rest} at zero speed. It is calculated by subtracting V_{O2rest} from the y-intercept. Just as for maintenance costs, a constant baseline with an increase in speed is also the standard assumption for offset costs (Fig. 7.2B). Postural costs, stress, and an elevated body temperature have all been proposed as explanations of $V_{O2offset}$, including the possibility that it is an artifact resulting from the lack of data at very low speeds (Herreid, 1981; Herreid and Full, 1988; Schmidt-Nielsen, 1972). Surprisingly, hermit crabs without their shells do not show a $V_{O2offset}$ component; the V_{O2ss} vs. speed relationship extrapolates to V_{O2rest} (Herreid and Full, 1985). Locomotion at even the slowest speeds requires additional energy $V_{O2offset}$ to carry a shell that is about equal in weight to their own body. Perhaps $V_{O2offset}$ does correspond to the energy cost initially required to lift the center of mass. At present $V_{O2offset}$ has no identifiable physiological basis.

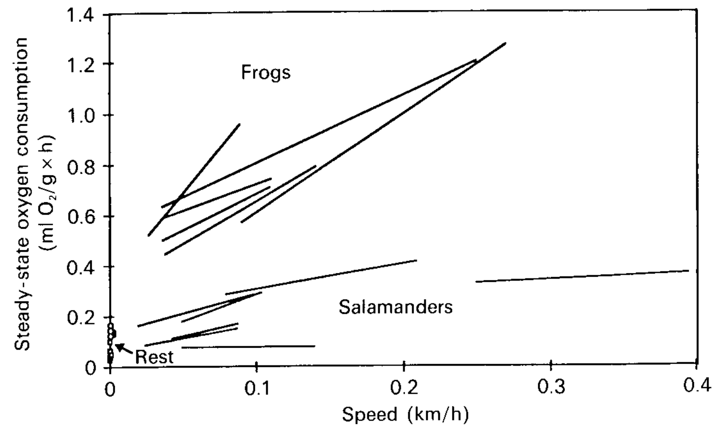


Fig. 7.4. Mass-specific oxygen consumption for frogs and salamanders of similar mass measured at comparable temperatures. Walking salamanders have significantly lower resting, offset and incremental metabolic costs. (Gatton, Miller and Full, in press). Resting oxygen consumption is shown by circles for frogs and squares for salamanders.

As with V_{O2mat}, $V_{O2offset}$ can be affected by body mass, temperature and species differences.

Body mass. $V_{O2offset}$ ranges from 30 to 190% of V_{O2rest} in birds and mammals, but averages approximately 70% of V_{O2rest} (Palidino and King, 1979). Mass-specific $V_{O2offset}$ decreases with increasing body mass in birds and mammals (Palidino and King, 1979, Taylor *et al.*, 1982). A similar relationship with body mass is likely in other animals, such arthropods (Fig. 7.3) and lizards. However, the y-intercept is more variable in these groups, because few animals have actually been measured at comparable temperatures.

Temperature. Increased temperature elevates $V_{O2offset}$ in ectotherms, but does not affect incremental cost (Herreid *et al.*, 1981). Some cockroaches and lizards double $V_{O2offset}$ with a 10°C increase in temperature, whereas others shower smaller Q_{10} effects (Herreid *et al.*, 1981; John-Alder and Bennett, 1981).

Body form - species differences. 'Offset' costs have been shown to vary considerably among species when the effects of body mass are removed. Salamanders have a low $V_{O2offset}$ compared to frogs even when measured at comparable temperatures (Fig. 7.4; Full *et al.*, 1988; Walton, unpublished). The y-intercept of running minks is 56% higher than predicted and cannot be accounted for by an elevated V_{O2rest} (Williams, 1983). Intraspecific variation is also apparent in $V_{O2offset}$. The mass-specific $V_{O2offset}$ of ghost crabs does not decrease with an increase in body mass (Full, 1987). At low speeds larger crabs actually require more energy on a per gram basis to locomote due to a high $V_{O2offset}$.

(3) Incremental or delta costs - the minimum cost of transport At least at high speeds, incremental or delta economy probably best represents locomotor muscle costs, because V_{O2mat} and $V_{O2offset}$ are likely to become small percentages of the gross cost (Fig. 7.2E). Margaria (1938) used this reasoning in calculating the distance-specific, incremental economy for the cost of human walking and running. In 1950, Gabrielli and Von Karman used a similar analysis to evaluate the efficiency of a variety of vehicles that differed in mass. Tucker (1970) and Schmidt-Nielsen (1972) used this efficiency index to compare runners, fliers and swimmers. Taylor *et al.* (1970) applied this calculation to locomoting mammals and found that distance-specific, incremental economy attains a minimum at high speeds (Fig. 7.2F). Taylor *et al.*, (1970) termed this index the minimum cost of transport (C_{min}). C_{min} represents the minimum metabolic cost required by an animal to travel a given distance. Mathematically, it equals the slope of the V_{O2ss} versus speed relationship (Fig. 7.2E).

Body mass and form affect C_{min}, but temperature appears to have little effect.

Body mass. Surprisingly, differences in body mass can account for much of the variation in C_{min} (Fig. 7.5A; Full, 1989; Herreid, 1981). When comparing over 150 species of animals that vary in leg number or position, body shape, and skeletal type, it is striking that larger animals of nearly all forms require less metabolic energy on a per gram basis to travel a given distance than do smaller animals. Birds and mammals (Taylor *et al.*, 1970; Fedak and Seeherman, 1979; Taylor *et al.*, 1982), lizards (John-Alder *et al.*, 1986), salamanders (Full *et al.*, 1988), crustaceans (Herreid and Full, 1988), insects (Herreid and Full, 1984; Herreid *et al.*, 1981; Jensen & Holm-Jensen, 1980; Lighton, 1985; Lighton *et al.*, 1987), and myriapods (Full and Herreid, 1986) follow a similar relationship. Moreover, studies on ghost crabs differing in body mass (2–70 g)

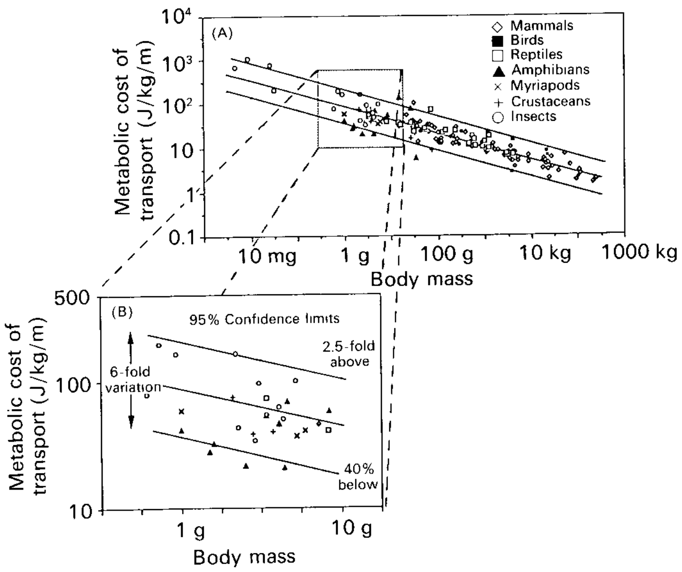


Fig. 7.5. Log mass-specific minimum cost of locomotion as a function of body mass. (A) Despite variation in body form the mass specific minimum cost of locomotion decreases with an increase in body mass over seven orders of magnitude in body mass. (B) Inset. Significant variation in the minimum cost of locomotion exists at an given body mass. Lines represent 95% confidence intervals. Data from various sources (see Full, 1989).

suggest that this same relationship may apply intraspecifically as well (Full, 1987).

Temperature. In contrast to gross and net economy, temperature appears to have little affect on incremental economy or C_{min}. For example, Madagascar hissing cockroaches, as well as two other cockroach species require the same minimum amount of metabolic energy to move a given distance at 15, 25 or 35°C (Herreid *et al.*, 1981). Temperature independence of C_{min} has also been demonstrated in several species of lizards (John-Alder and Bennett, 1981; Taylor, 1977). An explanation for this temperature independence is not yet available.

Body form - species differences. Considerable interspecific variation in C_{min} does exist at a given body mass (Full *et al.*, 1989). For example, two insects of the same body mass measured at the same temperature can differ in C_{min} by two-fold (Full *et al.*, 1990). Fedak and Seeherman (1979) have noted that cursorial mammals tend to have a low C_{min} relative to other mammals. Penguins clearly require more energy when waddling than other walking birds (Pinshow *et al.*, 1977). Red kangaroos require less energy to hop than comparably sized animals (Dawson and Taylor, 1973). Gila monsters have a relatively lower C_{min} than other lizards of the same body mass (John-Alder *et al.*, 1982). Variation in morphology and physiology can result in a six-fold variation in the minimum cost of locomotion at any given body mass (Fig. 7.5B). Costs 2.5–fold above and 40% below the predicted rate for a given body mass fall within the confidence limits.

7.5.5 E. Conclusions - economy

Comparable measures of economy can be obtained on diverse species. However, more effort must be made at quantifying the determinants of energy expenditure and less effort should be directed toward refining baselines which have no physiological bases. Much of the variation in economy can be explained by body mass and temperature. Striking general trends in economy are apparent over eight orders of magnitude in body mass. Yet, significant variation still exists among species when the effects of body mass and temperature are removed.

7.6 MECHANICAL ENERGY OUTPUT

Comparing a broader notion of efficiency (i.e. effectiveness) with the more limited definition of mechanical efficiency is one reason for the mismatch between what we hypothesize as efficient and what has been measured. It is not the only reason. A mismatch may still occur even when we are referring to mechanical efficiency. The major reason for the mismatch is related to the complexity involved in locomotion. It is this complexity which makes the determination of the link between mechanical energy output and metabolic energy input extremely difficult to identify. The behavior of the whole system cannot be predicted easily from the sum of the parts studied in isolation. Muscles, nerves, skeletal and support elements, all must act in concert to allow movement.

What can measures of mechanical energy output reveal about the consequences of variation in morphology and physiology for legged runners? Whole animal mechanical energy output will be most useful if: (1) we can obtain comparable measures in diverse species, (2) significant variation in mechanical energy output exists, and (3) differences in metabolic energy input are produced by variations in mechanical energy output.

7.6.1 A. What is the mechanical energy output?

An animal moving at a constant speed on the level can be said to do no mechanical work (i.e. positive increases and negative decreases in energy fluctuations cancel). A zero mechanical efficiency for steady-state, terrestrial locomotion is misleading. If animals moved like rolling wheels at a constant speed, then little mechanical energy would be necessary to move, since drag appears to be small in comparison to swimming and flying. However, during locomotion on land, both the body and limbs undergo repeated accelerations and decelerations during each cycle. Only the average speed of the whole animal is constant when determined over several strides. The mechanical energy (i.e. potential and kinetic) used to accelerate the body or center of mass is referred to as external energy (E_{ext}; Fig. 7.1; Fenn, 1930; Cavagna, 1975). Internal energy (i.e. E_{int}) represents the energy used to rock the trunk and swing the limbs relative to the body's motion.

7.6.2 B. Increases in mechanical energy - counting energy more than once?

(1) Energy transfer - Is what you see what you pay for? Movements corresponding to external and internal energy changes are what we observe during locomotion. We usually assume that the energy generated to produce these movements is supplied by locomotor muscles during each step. Increases in mechanical energy originate from concentric contractions during which muscles shorten. Muscles which shorten in the direction of the applied force have accomplished positive mechanical work (Fig. 7.1). Increases in mechanical energy resulting from concentric contractions require metabolic energy. Unfortunately, summing the positive or absolute increases in kinetic, potential and rotational energy for each segment of the body and limbs will greatly overestimate the energy that must be supplied repeatedly by muscles and is aptly termed 'pseudowork' (Pierrynowski *et al.*, 1980; Williams, 1985). One source of the overestimate results from energy conservation and its transfer both within and between segments (Fig. 7.1). In humans one-third of the positive energy changes measured could be the result of exchanges within segments and one-third could result from exchanges between adjacent

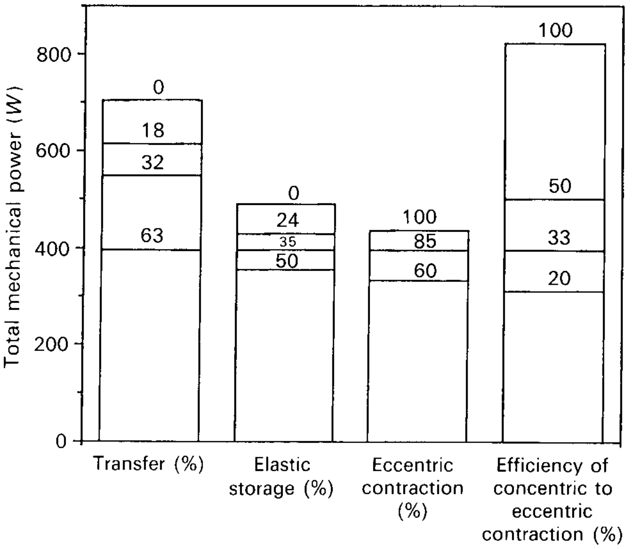


Fig. 7.6. The effect of various assumptions on the total mechanical power during running in humans. The percent energy transfer, elastic storage, eccentric contraction, and efficiency of concentric to eccentric contraction all significantly affect mechanical power output estimates. Total mechanical power = [(1 - %transfer/100)(1 - % elastic storage/100)* E_{pos}] + [% eccentric contraction * E_{neg}/% efficiency of contraction type] where E_{pos} equals the sum of the increase in mechanical energy and E_{neg} equals the sum of the decreases. Adopted from Williams and Cavanagh (1983).

segments (Pierrynowski *et al.*, 1980). The situation is analogous to determining the energy in a whip delineated into many segments. Energy, input from your hand, travels down the rope and causes each segment to move. If each segment had the capability of generating its own movement (i.e. had muscles that were active), then we might calculate the energy in the whip by summing the energy involved in moving each segment separately. Actually, each segment can be moved by the transfer of energy from the previous segment. Additional energy is not required for the movement of each segment. If energy transfer is complete, then the total energy can be determined from only one segment. Fig. 7.6 shows that mechanical power output estimates in humans can vary by 75% depending on the degree of transfer (Williams and Cavanagh, 1983).

During walking, many birds and mammals (Cavagna *et al.*, 1977; Heglund *et al.*, 1982a), as well as eight-legged crabs (Blickhan and Full, 1987), can transfer forward kinetic energy to gravitational potential and vice versa, much like an egg rolling end over end. As the body oscillates up and down, energy transfer or recovery can be as large as 50–70%. Summing the increases in forward kinetic and gravitational potential energy separately for a rolling egg would assume no transfer and lead to an obvious overestimate in the energy input for each cycle of rolling.

(2) Elastic strain energy During running, energy can be stored temporarily as elastic strain energy (E_e) in tendons and other musculoskeletal structures and later transferred to potential and kinetic energy of the body (Fig. 7.1; Alexander, 1984). When elastic strain energy is stored, muscles contract as tendons are stretched. Elastic strain energy is released when the same muscles then do work and shorten. Muscles and tendons operating in this mode are analogous to a spring of a pogo stick or a bouncing ball. If elastic strain energy were ignored and mechanical energy determined by summing the increases in kinetic and gravitational potential energy for each step or stride, it could greatly overestimate the energy that must be generated by the muscles. In humans, mechanical power output can vary by as much as 40% depending on the amount of elastic storage (Williams and Cavanagh, 1983; Fig. 7.6).

Variation in body mass and form can potentially affect the amount of strain energy that can be stored.

Body mass. The contribution of elastic storage and recovery (E_e) as a function of body mass remains unclear. However, large vertebrates must be able to store and recover considerable amounts of energy during locomotion, since whole body efficiencies greatly exceed estimates of peak isolated muscle efficiency (> 25%: Cavagna *et al.*, 1964, 1976, 1977; Heglund *et al.*, 1982b). The ability of small animals to store energy may be more limited. Kangaroo rats do not have the capacity to store as much elastic strain energy as kangaroos because they have relatively thicker tendons (Biewener *et al.*, 1981). It is not known whether small arthropods, such as cockroaches and crabs, are similarly limited in using their muscle, apodemes or other skeletal material as springs. Surprisingly, small cockroaches and eight-legged crabs have ground reaction force patterns and energy fluctuations that suggest the use of a bouncing or running gait comparable to that found in mammals (Fig. 7.7). Moreover, these animals attain a maximum sustainable stride frequency of the same magnitude and at the same speed predicted by scaling relationships of larger running mammals, despite the striking diversity

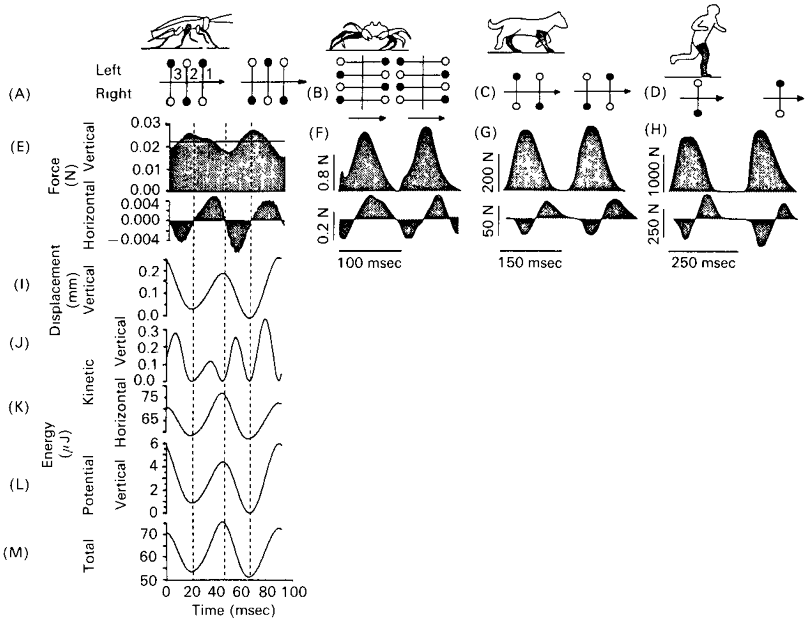


Fig. 7.7. Gait patterns of a cockroach (A), crab (B), dog (C) and human (D) during one stride. Filled circles represents a leg contacting the ground, whereas open circles represent legs moving in the air. Each animal can propel itself by two alternating sets of legs (i.e. 1–4 legs per set). Cockroaches use an alternating tripod gait. Left hind, right middle and left front alternate with the right hind, left middle and right front. Vertical and horizontal ground reaction forces for a running cockroach (E), ghost crab (F, Full, 1987), dog (G, Cavagna *et al.*, 1977) and human (H, Cavagna *et al.*, 1977). Segments represent one stride period. When vertical force equals zero the animal displays an aerial phase. Positive horizontal force represents braking, whereas negative values show acceleration of the center of mass forwards. Vertical displacement of the center of mass (I), vertical (J) and horizontal (K) kinetic energy, gravitational potential energy (L), and the sum of the three energies (M) for one stride of the cockroach.

in morphology and physiology (Full, 1989). Perhaps some storage can occur in these arthropods which operate their legs at high frequencies. Arthropods specialized for jumping, such as locusts and fleas, can store energy in apodemes and in resilin pads of joints (Bennett-Clark and Lucey, 1967; Bennett-Clark, 1975).

Body form - species differences. Since E_e is so difficult to quantify, it is not yet possible to know the extent of variation present for animals of similar size that vary in structure. In kangaroos metabolic energy actually decreases as speed increases (Dawson and Taylor, 1973).

As much as a 59% saving may result from elastic storage (Alexander, 1982; Alexander and Vernon, 1975; Cavagna *et al.*, 1977). Cavagna *et al.* (1964) estimate that running humans elastically conserve approximately 35% of the energy that must otherwise be supplied by muscles. Alexander (1984) suggested that in some galloping mammals the back might incorporate a spring that could store and return energy. Obviously, E_e requires further study, especially in small animals.

7.6.3 C. Decreases in mechanical energy

Surprisingly, decreases in mechanical energy can also require metabolic energy. Muscles that lengthen or are stretched while contracting are said to do negative mechanical work. Actually, muscles that undergo these eccentric contractions when lengthened are absorbing energy. Eccentric contractions require metabolic energy (Fig. 7.1). Since the metabolic costs of eccentric contractions are associated with decreases in energy, then perhaps mechanical energy output should be best estimated by summing the absolute value of positive and negative changes in mechanical energy. This approach has been used in the study of human locomotion (Pierrynowski *et al.*, 1980; Williams, 1985).

Summing the absolute value of the energy changes assumes that (1) all decreases in mechanical energy result in eccentric contractions and (2) the metabolic energy cost of negative and positive work is equal. Decreases in mechanical energy can also result from joint range limitations and muscle viscosity (Fig. 7.1). Mechanical power output in humans can vary by 20% if nearly all versus two-thirds of the decreases in mechanical power are associated with eccentric contractions (Fig. 7.6). In addition, several studies have shown that the metabolic costs of concentric contractions differ from eccentric contractions. Running uphill requires more positive work by muscles contracting concentrically, and more metabolic energy, than running downhill which demands more negative work by eccentrically contracting muscles. Eccentric contractions require one-third to as little as one-fifth of the metabolic energy of concentric contractions (Margaria, 1968; Williams and Cavanagh, 1983). Since the metabolic energy costs of negative and positive work are not equal, then perhaps mechanical energy output should be best estimated by weighting the negative changes in energy to reflect the lower cost. Williams and Cavanagh (1983) found a six-fold variation in the mechanical power output estimate depending on the relative cost selected for positive versus negative work (Fig. 7.6).

7.6.4 D. External energy - mechanical energy changes of the center of mass

External mechanical energy changes of the body or center of mass represent a major portion of the mechanical energy output of animals (Cavagna *et al.*, 1977; Heglund *et al.*, 1982a). Comparable estimates have been obtained in diverse species from measurements of the ground reaction forces. Surprisingly, vertical and horizontal ground reaction force patterns can be similar in two-, four-, six- and eight-legged runners (Fig. 7.7). Mechanical energy changes of the center of mass are derived from integration of the ground reaction forces. Most determinations of total mechanical energy change of the center of mass represent the instantaneous sum of the kinetic and potential energy fluctuations assuming complete transfer among energies. The external power of the center of mass (E_{ext}) has been calculated from the sum of the positive increases in the total energy assuming no eccentric contractions or ones of very low cost. Elastic storage has been assumed to be zero. In birds, mammals, crabs and cockroaches, E_{ext} increases linearly with speed and extrapolates to near zero at zero speed (Blickhan and Full, 1987; Cavagna *et al.*, 1977; Full and Tu, 1989; Heglund *et al.*, 1982a). Therefore, distance-specific E_{ext} is independent of speed and is analogous to distance-specific, incremental metabolic cost or the minimum cost of transport (Fig. 7.2F).

Body mass. Differences in body mass can account for much of the variation in E_{ext}. Despite variation in body shape and skeletal type, E_{ext} is directly proportional to body mass over a wide range of speeds (Blickhan and Full, 1987; Cavagna *et al.*, 1977; Full and Tu, 1989; Heglund *et al.*, 1982a). Studies on ghost crabs suggest that a similar trend may be present for animals of the same species that differ in mass (Blickhan and Full, 1987). In contrast to mass-specific, V_{O_2gross} (Fig. 7.4), mass-specific E_{ext} follows a similar function of speed for animals that differ in body mass (Fig. 7.8). The E_{ext} generated to move an animal one meter is nearly directly proportional to body mass or independent of body mass when represented on a mass-specific basis.

Body form - species differences. The mechanical power used to accelerate an animal's center of mass upwards and forwards (E_{ext}) has only been measured in about 15 species (Blickhan and Full, 1987; Cavagna *et al.*, 1977; Full and Tu, 1989; Heglund *et al.*, 1982a). The energy generated to move a kilogram of mass one meter is approximately 1.1 J/kg/m and varies by 50% (i.e. upper and lower 95% confidence limits).

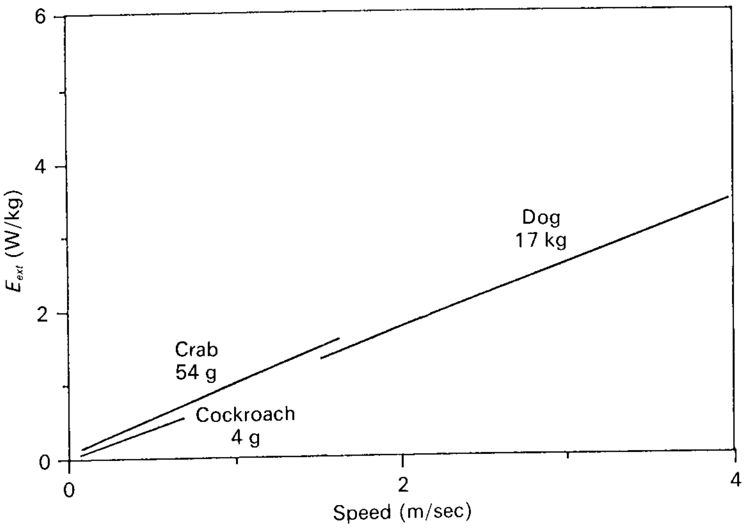


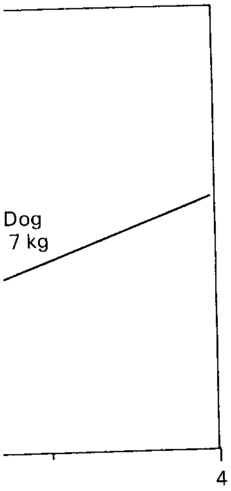
Fig. 7.8. Mass-specific mechanical energy of the center of mass (external energy) as a function of speed for cockroaches (4 g; Full and Tu, 1989); crabs (30–90 g; Blickhan and Full, 1987); and dogs (17 kg; Heglund *et al.*, 1982a).

This variation is much smaller than that measured for metabolic power. Surprisingly, animals with many legs due not appear to have smooth rides during which little acceleration and deceleration occur (Fig. 7.9; Blickhan and Full, 1987; Full and Tu, 1989).

7.6.5 E. Internal energy - limb and trunk motion relative to the center of mass

The internal energy necessary to accelerate the limbs and the body relative to the center of mass (E_{int}) increases curvilinearly with speed in birds and mammals (Fedak *et al.*, 1982). In most species, E_{int} becomes a greater portion of total mechanical energy as speed increases. Values will vary depending whether no transfer (0%), transfer between only adjacent segments (18%), transfer within segments (not between limbs; 32%), or maximum transfer (63%) is assumed (estimates on humans from Williams and Cavanagh, 1983; Fig. 7.6).

Body mass. Internal energy increases as a function of body mass in birds and mammals (Fedak *et al.*, 1982). Swinging larger limbs and



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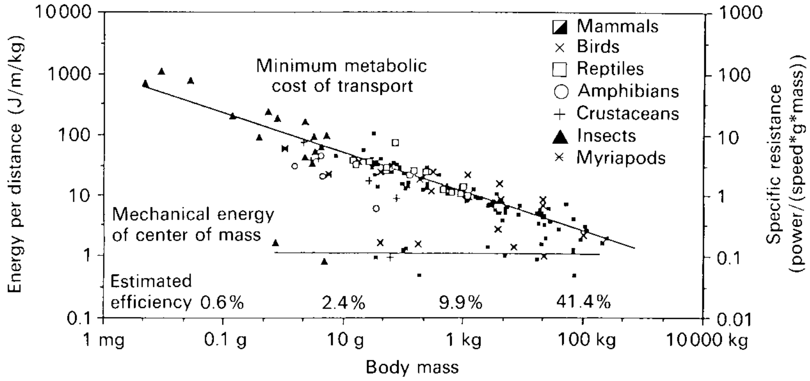

Fig. 7.9. Logarithmic plot of mass-specific external mechanical energy (E_{ext}) and minimum metabolic energy (C_{min}) used to move one kg of animal one meter in distance. Small animals, regardless of form, require relatively more metabolic energy to travel a distance than large animals, but do not produce relatively more mechanical energy to move their center of mass. Data for mammals and birds, lizards, amphibians, crustaceans, insects and myriapods are from various sources (see Full, 1989, for references). $C_{min} = 10.8\ M^{-0.32}$ (r2 = 0.87) and $E_{ext} = 1.07\ M^{-0.01}$.

trunks is associated with a greater E_{int} than swinging smaller limbs and rocking smaller bodies.

Body form - species differences. Variation in E_{int} among the few birds and mammals studied is significant. E_{int} ranged from 15% of the estimated total mechanical energy in a quail to 54% in a dog at the fastest speeds tested (Fedak *et al.*, 1982; Heglund *et al.*, 1982b). Mass-specific E_{int} does not show any regular function related to leg number or structure. Theory used to design walking machines predicts that an increase in leg number may actually reduce E_{int} (Hirose and Umetani, 1978). It also predicts that the 'knee above the hip' posture of most arthropods may decrease E_{int} compared to a four-legged animal with an upright stance (Kaneko *et al.*, 1987). Many-legged animals, such as crabs, undoubtedly generate considerable internal energy to accelerate their limbs and body relative to their center of mass, especially at fast speeds. Total mechanical energy would be better estimated in a 50 - g crab by increasing E_{ext} 7% at the lowest speeds and as much as 32% at maximum speed, just as it would for a mammal of the same body mass (Blickhan and Full, 1987; Cavagna *et al.*, 1977; Full and Tu, 1989; Heglund *et al.*, 1982a). Further and more rigorous estimates of E_{int}

are obviously necessary in many-legged animals, such as insects and myriapods.

7.6.6 F. Conclusions - mechanical energy output

Mechanical energy output will vary depending on: whether external and internal work are both determined; what assumptions are made concerning energy transfer within and between segments; the amount of elastic strain energy stored; the degree of eccentric contractions; and the relative efficiency of positive and negative work. Despite the potential for variation, the amount of energy per unit mass generated to move the center of mass one meter (E_{ext}) is remarkably similar for species that vary in size and form.

7.7 INSIGHTS FROM EFFICIENCY MEASURES - ALL EFFICIENCIES ARE NOT CREATED EQUAL

The mechanical efficiency of terrestrial locomotion can be calculated using one of at least four values for mechanical energy as the numerator and one of at least three values for metabolic energy input as the denominator. The number of different definitions for efficiency begins to rival those found in ecology. They include gross, net, incremental, instantaneous, work, apparent, muscle, muscular, pseudo, and center of mass efficiencies (Alexander, 1977; Donovan and Brooks, 1977; Gaesser and Brooks, 1975; Goldspink, 1977; Stainsby *et al.*, 1980; Taylor, 1980; Winter, 1979). The value selected for the numerator, mechanical energy output, will vary depending on: (1) whether external and internal work are both determined, (2) what assumptions are made concerning energy transfer within and between segments, (3) the amount of elastic strain energy stored, (4) the extent of eccentric contractions, and (5) efficiency of positive versus negative work. The value selected for the denominator, metabolic energy input, will vary depending on the assumptions made concerning the baseline energy during exercise (i.e. gross, net, incremental economy).

All efficiencies values represent whole body efficiency and are global measures. Insufficient evidence is available to claim that any ratio represents actual isolated muscle efficiency, although some values are undoubtedly better estimates than others. The inequality of whole body versus muscle efficiency has been pointed out several times in the past. In fact, this recognition has lead to terminology for whole body efficiency, such as muscular efficiency, as opposed to muscle efficiency (Stainsby *et al.*, 1980). This being the case, then what can whole body measures of efficiency tell us? Can these whole body measures reveal the consequences of variation in morphology and physiology that affect locomotion on land?

7.7.1 A. Does variation in mechanical energy output produce concomitant variation in metabolic energy input?

Do animals that have a lower mechanical power output consume less oxygen during exercise than those with a higher mechanical power output? If so, how much less? Muscles would be expected to use less metabolic energy if work was decreased by: effective storage of elastic strain energy and energy transfer among segments; reduced accelerations and decelerations of the center of mass in the horizontal, vertical and lateral directions; reduced limb moments of inertia produced by a decrease in limb mass or concentration of mass near the center of rotation.

Body mass. In birds and mammals variation in economy related to body mass cannot be completely explained by concomitant variation in mechanical energy output (Heglund *et al.*, 1982b). Larger animals use less metabolic energy to move a gram of body mass one meter than do small animals. Over orders of magnitude of five to seven in body mass, mass-specific metabolic cost (C_{min}) varies by more than two to three orders of magnitude, whereas the mass-specific, mechanical power (E_{ext}) generated to move a gram of animal one meter is relatively independent of body mass (Fig. 7.9). Therefore, whole body efficiency increases with body size. Large birds and mammals have efficiencies that exceed 30–50%. At least part of the reason for whole body efficiencies exceeding peak isolated muscle efficiency (i.e. 25–30%) is the inability to account for elastic storage and transfer in the mechanical energy estimate. Energy that is stored and transferred is instead calculated to be generated by muscles. If large animals store much more elastic strain energy, this may explain some, but not all, of the variation in whole body efficiency with body mass.

The different scaling of metabolic and mechanical power cannot be completely explained by any reassesment of the mechanical power estimate. Large animals (100 kg) exhibit approximately three to five-fold differences between metabolic and mechanical power (Fig. 7.9). Our recent estimates of mechanical power output show that this difference reaches 100-fold in small insects (0.07-4 g; Full and Tu, 1989, submitted; Fig.7.9). Maximum mechanical power output estimates for small animals (1 g; 0% transfer, 0% elastic storage; 85% eccentric contraction and 100% or equal efficiency of con- and eccentric contractions) would have to be increased by 20-30-fold to attain a whole body efficiency of 25%. Maximum mechanical power output estimates for small animals combined with minimum mechanical power output estimates for large animals (100 kg; 63% transfer; 60% elastic storage; 37% eccentric contractions and 20% efficiency of con- and eccentric contractions) only increases the difference in mechanical power between large and small animals to seven-fold, not nearly the 50-fold necessary to make efficiency independent of animal size (i.e. parallel relationship between the functions relating the minimum metabolic cost of transport and mechanical energy output to body mass; Fig 7.9).

Body form - species differences. Fewer efficiency data are available for animals of similar body mass. In kangaroos the low metabolic cost appears to result from a reduced mechanical power output (Dawson and Taylor, 1973). Kangaroos store significant amounts of elastic strain energy (Alexander and Vernon, 1975; Cavagna *et al.*, 1977). The elevated metabolic cost of waddling penguins and geese is most likely correlated with an increase in mechanical power, but actual output measurements are lacking (Pinshow *et al.*, 1977; Baudinettee and Gill, 1985). Williams and Cavanagh (1985) found that humans with a lower $V_{O2gross}$ were more effective at deriving power from energy transfer. Increased mechanical work due to loading the limbs is directly proportional to the increase in metabolic cost in humans (Martin, 1985; Myers and Steudel, 1985). When segments are loaded more distally, oxygen consumption increases as a function of the increase in mechanical power output.

More evidence is available that suggests a weak correlation between variation in economy or metabolic energy input and mechanical energy output. Cheetahs, gazelles and goats differ considerably in limb configuration, and presumably in the mechanical energy necessary to swing their limbs. Yet, Taylor *et al.* (1974) found no significant difference in oxygen consumption, at least at low speeds. Likewise, studies of animals running with loaded packs show a proportional increase in $V_{O2gross}$ with the load carried, a much greater metabolic cost than predicted if the metabolic cost of swinging the limbs was a very large fraction of the total cost (Taylor *et al.*, 1980). In humans, significant variation in economy of elite versus good distance runners does not correlate with mechanical parameters, except stride frequency (Cavanagh *et al.*, 1977; Pollack, 1977). In our laboratory we varied morphology and presumably mechanical energy output directly by producing quadrupedal cockroaches from six-legged animals (i.e. removed middle legs). Four-legged cockroaches wobble or roll considerably during locomotion. Surprisingly, four-legged runners do not show any significant difference in metabolic cost at high speeds when compared to six-legged runners (Full and Pham, unpublished).

If variation in metabolic energy input is produced primarily by variation in mechanical energy output, then animals with relatively low mechanical energy output should require less metabolic energy when the effects of body mass are removed for both energy values. My analysis of E_{ext} and C_{min} residuals does not show any correlation when the effects of body mass are removed. Animals with many legs or seemingly awkward running styles, such as crabs and cockroaches, do not show variation in mechanical power that is accompanied by a corresponding change in metabolic cost (Full, unpublished results). This may be in large part due to the inadequate sample size. Moreover, estimates of elastic strain energy and transfer are needed to determine if increases in the mechanical power used to accelerate an animal's center of mass upwards and forwards correlate with an elevated C_{min}.

7.7.2 B. What can explain the variation in economy or metabolic energy input in addition to mechanical energy output?

Metabolic cost can vary even when little difference in mechanical energy output is apparent. Why does such variation in whole animal efficiency exist? In 1980, Taylor suggested that the cost of muscle force production might determine the metabolic cost of locomotion. Many locomotor muscles function primarily as force generators and undergo near isometric contractions (i.e. average zero shortening velocity), especially when stabilizing joints and maintaining a running posture while supporting the body's weight. Moreover, muscles are active when they are stretched and absorb energy. Muscles functioning in these ways require metabolic energy without production of positive mechanical work (Fig. 7.1). The hypothesis that the cost of muscle force production determines locomotor cost is consistent with previous research on isolated muscle which has shown a good correlation between metabolic cost and the area under the muscle force versus time curve, the time-tension integral (Stainsby and Fales, 1973). Whole animal metabolic cost may best be explained by: (1) the rate of force production (Taylor, 1985); and (2) the total amount of force produced.

(1) Rate of force production **Body mass**. Taylor *et al.* (1980) used the 10–fold variation in C_{min} with body mass found in mammals to test the hypothesis that the metabolic cost of locomotion is determined by the cost of force production. They exercised animals loaded with back-packs on a treadmill. No change in acceleration of the center of mass was observed between loaded and unloaded animals. Therefore, muscle force increased in direct proportion to the load added. Oxygen consumption also rose in direct proportion to the added load for animals which ranged in mass from a rat to a horse. Since small animals have higher mass-specific metabolic costs for unloaded running (see Fig. 7.3), an equivalent increase in load or force produced a much greater increase in mass-specific metabolic cost in small animals compared to large. The development of each Newton of force by a small animal appears to require more metabolic energy than the development of the same amount of force by a large animal.

Small animals seem to require more metabolic energy to move a gram of body mass than larger ones because they must turn their muscles on and off more frequently per unit time or distance. The metabolic cost of force production varies with body mass in a similar manner to stride frequency (Fig. 7.10). Higher rates of contraction appear to result in additional cost due to more frequent activation (due to Ca^{++} movement; Rall, 1986) and the higher costs associated with the more rapid cycling of cross-bridges (Heglund and Cavagna, 1987). When the metabolic cost of locomotion is normalized for the rate of force production, the mass-specific metabolic cost of locomotion for one stride is remarkably independent of body mass (Heglund and Taylor, 1988). Therefore, the greater metabolic cost per unit mass of small animals to travel a given distance could be explained by the fact that small animals, with shorter legs than larger animals, must take more steps costing an equivalent amount of mass-specific metabolic energy to cover the same distance.

Body form - species differences. Full *et al.* (1990) found significant variation in C_{min} of one gram insects that differ in form (i.e. leg configuration). Caterpillar hunting beetles use only half the energy of field crickets and American cockroaches of the same mass. Normalizing for the rate of muscle force production by determining the metabolic cost per stride fails to account for the interspecific variation in the cost of locomotion in insects of the same mass as it does for mammals that differ in mass (Fig. 7.11). Kram and Taylor (1989) suggested that normalizing for the rate of force production by using ground contact time may be more appropriate than dividing by stride frequency, because

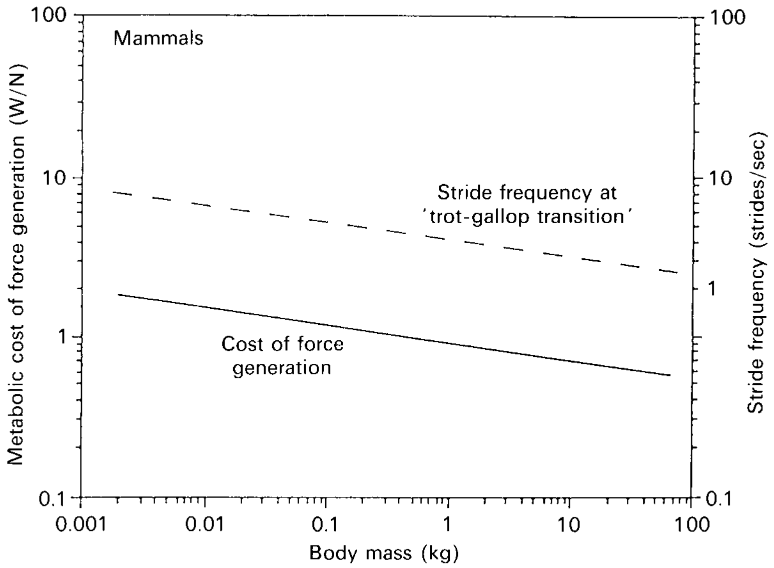

Fig. 7.10. Log body mass versus log stride frequency and the metabolic cost of force generation at equivalent speeds (e.g. trot-gallop transition for mammals; Heglund *et al.*, 1974). The metabolic cost of generating a Newton of force in a small animal is greater than in large animals and parallels the metabolic cost of locomotion (Fig. 7.9). The cost of force generation may be greater in small animals because of added costs due to more frequent activation (due to Ca^{++} movement) and the higher costs associated with the more rapid cycling of cross-bridges. Consistent with the idea that higher costs are associated with higher cycling rates are the data on stride frequency that parallel the cost of force generation (Taylor, 1985).

muscles are developing most of their force when the legs are in contact with the ground and are supporting the body's weight. Although the ground contact cost in insects (1.5–3.1 J kg^{-1}) was similar to that measured in mammals (2 J kg^{-1}), it also does not explain the interspecific variation in the cost of locomotion (Fig. 7.11).

(2) Amount of force production **Body size**. Variation in the total amount of muscular force generated to produce the same ground reaction force could lead to variation in metabolic cost. Biewener (1983, 1989) has found a 10-fold decrease in the effective mechanical advantage of mammalian limbs (i.e. due to variation in lever arms) with a decrease in body mass. Small mammals have a more crouched posture during locomotion than larger mammals which requires relatively greater mus-

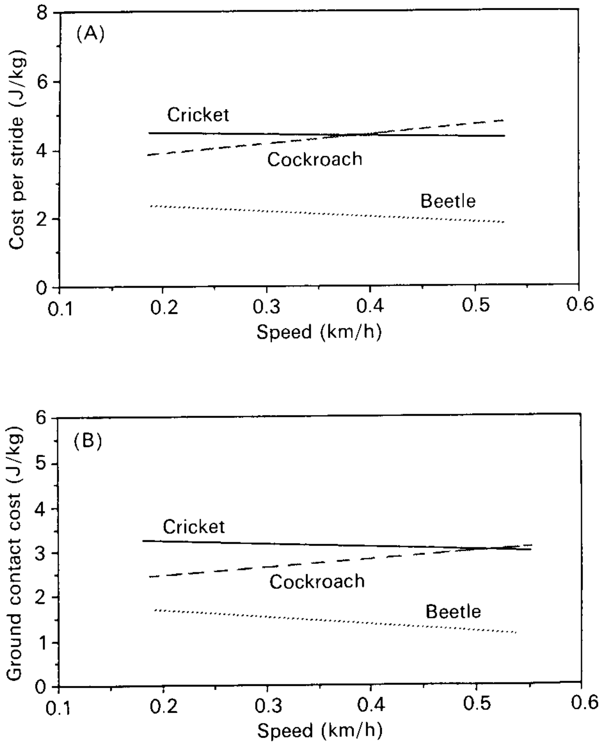

Fig. 7.11. Metabolic cost of locomotion normalized for the rate of force production in crickets, cockroaches and beetles of similar mass (1 g). (A). The metabolic cost of locomotion per stride was independent of speed, but was significantly lower in beetles than in crickets or cockroaches. (B). Ground contact cost was independent of speed and was significantly lower in beetles than in crickets or cockroaches. Ground contact cost was calculated by multiplying steady-state oxygen consumption by contact time (Full *et al.*, 1990). 1 ml O_2 = 20.1 J.

cle force production. Small mammals generate the additional force with a relatively greater cross sectional area of active muscle, keeping muscle stress relatively constant (Perry *et al.*, 1988). However, the larger force per volume of activated muscle in small mammals should result in metabolic costs which are relatively greater than in large mammals. Variation in mechanical advantage could also explain the variation in the metabolic cost of locomotion with body mass in mammals.

Body form - species differences. Variation in mechanical advantage could very well explain variation in the cost of locomotion in different species of the same body mass. Full *et al.* (1990) could not account for differences in metabolic cost of three similarly sized insects that differed in limb configuration by normalizing for variation in the rate or cost of force production (Fig. 7.11). Effective mechanical advantage and the amount of muscle force required to produce the same ground reaction force may explain the variation in the metabolic cost. The low cost of locomotion in the beetle may result from a greater effective mechanical advantage of leg muscles in the limbs compared to the cockroach and cricket. Preliminary estimates of locomotor muscle mass support this contention.

7.8 CONCLUSIONS

Efficiency, as applied to land locomotion, is used in two ways (1) mechanical efficiency, and (2) competency of performance. Unfortunately, both uses of the term represent many different numerical indices. One solution to this problem would be to stop using the general term 'efficiency' because of its ambiguity. This strategy is logical, but impractical. A better approach would be to state clearly its operational definition when using the term and to be skeptical when claims of efficiency are made without a precise definition.

(1) Whole animal efficiency used as a measure of effective performance is useful and can aid in our search for the mechanistic bases of how diverse animals move on land, as well as provide data for ecological and evolutionary studies. Steady-state, constant speed locomotion is only one of the 'events' that requires further study. Others include: intermittent activity, obstacle negotiation (e.g. climbing, leaping and maneuvering), and burst locomotion. Economy is only one measure of effective performance. Other performance measures which are receiving increasing attention include: endurance or fatigue resistance, distance travelled, acceleration and speed, durability and strength, and maneuverability and stability.

(2) The economy of locomotion is one performance measure that has been determined frequently. Variation in economy exists in resting, offset and incremental components. Functional explanations of these components are difficult because of our lack of data on the amount of energy required by non-locomotor sources during exercise. Less effort should be directed to refining baselines and more effort should be made at quantifying the determinants of energy expenditure. Much of the variation in

economy can be accounted for by variation in body mass and temperature. Yet, variation in body form is equally important. The minimum cost of locomotion at a given body mass or species differences can vary by as much as six–fold. This variation remains to be explained.

(3) Mechanical energy output provides only one source of variation in the economy of locomotion. It is only one link between performance and the structure and function of muscles and skeletal structures. Mechanical energy output will vary depending on: whether external and internal work are both determined, what assumptions are made concerning energy transfer within and between segments, the amount of elastic strain energy stored, the degree of eccentric contractions, and the relative efficiency of positive and negative work.

(4) Whole animal mechanical efficiency appears to be highly variable among animals that differ in body form and size and not simply equal to the efficiency of isolated muscle. Investigators comparing the mechanical efficiency among animals who propose hypotheses for reported differences must carefully consider the sources of variation in both mechanical energy output and metabolic energy input. The movements we observe are not necessarily paid for by the animal based on the assumption of a constant whole body mechanical efficiency. Mechanical energy can be stored and released, not requiring additional metabolic cost, or muscles may contract nearly isometrically and demand metabolic energy without producing detectable mechanical work.

(5) Variation in the economy of locomotion may be best explained by the differences in the cost of muscle force production and the total force produced.

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