

EFFECT OF VARIATION IN FORM ON THE COST OF TERRESTRIAL LOCOMOTION

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Accepted 30 January 1990

Summary

The mass-specific minimum cost of terrestrial locomotion (C_{\min}) decreases with an increase in body mass. This generalization spans nearly eight orders of magnitude in body mass and includes two phyla. The general relationship between metabolic cost and mass is striking. However, a significant amount of unexplained interspecific variation in C_{\min} exists at any given body mass. To determine how variation in morphology and physiology affects metabolic energy cost, we measured the oxygen consumption of three comparably sized insects running on a miniature treadmill; the American cockroach *Periplaneta americana*, the caterpillar hunting beetle *Calosoma affine* and the Australian field cricket *Teleogryllus commodus*. Steady-state oxygen consumption ($\dot{V}_{O_{2ss}}$) increased linearly with speed. C_{\min} was similar for crickets and cockroaches (8.0 and 8.5 ml O₂ g⁻¹ km⁻¹, respectively), but was substantially lower for beetles (4.6 ml O₂ g⁻¹ km⁻¹). The predicted value of C_{\min} for all three insects was within the 95% confidence intervals of the C_{\min} versus body mass function. However, the 95% confidence intervals extend approximately 2.5-fold above and 40% below the regression line, making the variation at any given body mass nearly sixfold. Normalizing for the rate of muscle force production by determining the metabolic cost per stride failed to account for the interspecific variation in the cost of locomotion observed in the three insects. Ground contact costs (i.e. $\dot{V}_{O_{2ss}}$ multiplied by leg contact time during a stride) in insects were similar to those measured in mammals (1.5–3.1 J kg⁻¹) and were independent of speed, but did not explain the interspecific variation in the cost of locomotion. Muscles of the caterpillar hunting beetle may have a greater mechanical advantage than muscles of the Australian field cricket and American cockroach. Variation in musculo-skeletal arrangement, apart from variation in body mass, could translate into significant differences in the minimum cost of terrestrial locomotion.

Introduction

The mass-specific cost of terrestrial locomotion decreases with an increase in

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Key words: locomotion, energetics, muscle, arthropods.

body mass (Tucker, 1970; Schmidt-Nielsen, 1982; Taylor *et al.* 1970). This generalization spans nearly eight orders of magnitude in body mass and includes two phyla that are separated by more than 500 million years of evolution (Full, 1989; Herreid, 1981). Body mass accounts for nearly 85 % of the variation among animals that differ in leg architecture, leg number, skeletal type and body temperature (Full, 1989). Ants (Jensen and Holm-Jensen, 1980; Lighton *et al.* 1987), cockroaches (Herreid and Full, 1984; Herreid *et al.* 1981*a,b*), beetles (Bartholomew *et al.* 1985; Lighton, 1985), crabs (Full, 1987; Full and Herreid, 1983, 1984), centipedes (Full, 1989), salamanders (Full, 1986; Full *et al.* 1988), lizards (John-Alder *et al.* 1986), birds and mammals (Taylor *et al.* 1982; Fedak and Seeherman, 1979) all follow the same function relating body mass and metabolic cost (Full, 1989; Herreid, 1981).

The general relationship between metabolic cost and body mass for over 150 species is striking. However, variation in the cost of locomotion at a given mass appears to be equally impressive. Yet the effect of variation in form or phylogeny on metabolic cost has received little attention relative to allometric studies. Several investigators have reported cases in which the cost of locomotion varies considerably from predicted allometric functions. Hopping kangaroos use less energy than expected due to elastic savings (Dawson and Taylor, 1973). Snakes may require less energy to crawl, since repeated oscillations of the center of mass against gravity are absent (Chodrow and Taylor, 1973). Lions and polar bears expend more energy than expected, possibly because of thermoregulation (Chassin *et al.* 1976; Hurst *et al.* 1982). Crawling slugs require 10 times more energy than predicted from their body mass (Denny, 1980). This elevated energy cost has also been found in other gastropods (Houlihan and Innes, 1982). Waddling penguins use twice the energy of animals the same size (Pinshow *et al.* 1977). This larger than predicted energy utilization on land may indicate a compromise between terrestrial locomotion and adaptations for swimming. Fedak and Seeherman (1979) have suggested that 'cursorial, fast or graceful animals seem to fall near the lower end of the distribution for their size... while animals we think of as awkward tend to fall high in the distribution'.

To determine how variation in morphology and physiology affects metabolic energy cost, we measured the oxygen consumption of three comparably sized insects running on a miniature treadmill. We chose the American cockroach *Periplaneta americana*, the caterpillar hunting beetle *Calosoma affine* and the Australian field cricket *Teleogryllus commodus*. *T. commodus* moves primarily by walking, but has hind limbs modified for jumping during escape and take-off. This limb architecture represents a potential functional compromise between jumping and walking. Graham (1983) suggested that crickets, locusts and stick insects use a 'lurching gait' during walking. This lurching motion is associated with braking and may significantly elevate the cost of locomotion. The American cockroach *Periplaneta americana* is well known for high-speed locomotion, reaching 40 body lengths per second (McConnell and Richards, 1955). At these speeds limb cycling frequency can equal wing beat frequency (i.e. 25 Hz; Delcomyn, 1971). By

contrast, the caterpillar hunting beetle *Calosoma affine* has a considerable capacity for sustained locomotion. Radar tracking has shown that the beetle can travel hundreds of meters in one night (H. Wallin, personal communication).

We attempted to answer two questions concerning the effect of variation in form or phylogeny on the cost of terrestrial locomotion. The first addressed the extent of variation in metabolic cost independent of body mass. How much variation in metabolic cost is necessary to conclude that a species is more or less economical than other similarly sized animals? To answer this question, we compared results from the present study with those for all other pedestrians. The second question dealt with the possibility that we can explain the variation in the interspecific cost of terrestrial locomotion at a given body mass by considering the time course of muscle force production. The rate of force development in mammals is highly correlated with the variation in metabolic cost resulting from differences in body mass (Heglund and Taylor, 1988). Taylor (1985) suggested that the cost of force generation in small mammals is higher than in large ones because small mammals must turn their muscles on and off at higher rates to generate force. When cost is multiplied by stride period, to normalize for the rate of force production, the mass-specific cost of locomotion per stride is remarkably constant in mammals for over four orders of magnitude in body mass (Heglund and Taylor, 1988).

Materials and methods

Animals

Adult male crickets *Teleogryllus commodus* (0.95 ± 0.07 g, s.d.) were obtained from the laboratory colony of Dr Werner Loher, Entomology Department, UC Berkeley. Each animal was housed in a glass jar with dog chow and lettuce *ad libitum*. Male *Periplaneta americana* (0.90 ± 0.11 g, s.d.) were obtained from Carolina Biological Supply Company. Cockroaches were housed in individual plastic containers and were given water and dog chow *ad libitum*. Male beetles *Calosoma affine* (0.62 ± 0.08 g, s.d.) were obtained from Dr Henrik Wallin from the Division of Biological Control, University of California at Berkeley. Beetles were housed in individual paper containers with water *ad libitum*, and fed grubs every 2 days. Animals were kept at ambient temperature ($24 \pm 2^\circ\text{C}$) on a local photoperiod.

Oxygen consumption

Animals were exercised on a miniature treadmill enclosed in an airtight Lucite respirometer. The respirometer was placed in an incubator (Lab-Line, Ambi-Hi-Lo Chamber) to control temperature at $23\text{--}24^\circ\text{C}$. Oxygen consumption (\dot{V}_{O_2}) was determined using open-flow respirometry (Herreid *et al.* 1981a). The air flow rate was 40 ml min^{-1} for crickets during rest and exercise, 90 ml min^{-1} for running cockroaches, and 60 ml min^{-1} for running beetles. To measure the \dot{V}_{O_2} of resting cockroaches and beetles, the flow rate was reduced to 20 and 50 ml min^{-1} , respectively, to provide detectable oxygen concentration differences. Air leaving

the chamber passed through a filter containing Drierite to remove water vapor. Oxygen concentration was measured continuously with an electrochemical oxygen analyzer (S-3A/II Ametek), interfaced with a chart recorder (Omega) or a computer (IBM/AT) *via* an analog to digital converter (Cyborg). Mass-specific \dot{V}_{O_2} was calculated as described by Herreid *et al.* (1981a,b). Oxygen consumption rates were corrected to STPD.

For each experiment an animal was weighed and given a 30 min rest period in the respirometer before exercise. The resting oxygen consumption ($\dot{V}_{O_{2rest}}$) of crickets was measured during this 30 min rest period, whereas the $\dot{V}_{O_{2rest}}$ rates for cockroaches and beetles were measured during experiments devoted only to $\dot{V}_{O_{2rest}}$ measurements. After the rest period, the treadmill was turned on to the desired speed. To measure the \dot{V}_{O_2} during locomotion, each animal was exercised for 10–20 min at a single speed. All animals attained steady-state oxygen consumption ($\dot{V}_{O_{2ss}}$, the rate at which \dot{V}_{O_2} varied by less than 15 % during exercise) in 3–5 min. The slowest speeds were chosen so that animals walked consistently without extraneous movements. The highest speeds represented rates at which animals could sustain $\dot{V}_{O_{2ss}}$ for 4–6 min, but fatigued within 10–15 min. $\dot{V}_{O_{2ss}}$ was calculated by averaging the \dot{V}_{O_2} for 5–10 min after a running animal had attained a steady state. Individuals were rested for at least one full day before the next trial.

Kinematics

Insects were video taped with a high-speed camera (Video Logic CDR660) at 180–300 frames s^{-1} while running on the treadmill. Animals were filmed from the side at four speeds. The top of the head, the tip of the abdomen and the tarsus of the third leg were painted for better visibility. Video frames were grabbed and digitized using a motion analysis system (Peak Performance Tech. Inc.). Stride frequency and contact time (i.e. the length of time a leg is in contact with the ground during a stride) were calculated from the digitized data.

Values are \pm S.E., unless stated otherwise.

Results

Oxygen consumption

The average $\dot{V}_{O_{2rest}}$ was 0.99 ± 0.02 ml O_2 g^{-1} h^{-1} ($N=49$) for crickets, 0.18 ± 0.01 ml O_2 g^{-1} h^{-1} ($N=6$) for cockroaches and 0.21 ± 0.02 ml O_2 g^{-1} h^{-1} ($N=3$) for beetles.

The $\dot{V}_{O_{2rest}}$ for male crickets was approximately double that reported for other insects of similar body mass (Herreid and Full, 1984), and about three times higher than the rates found for *T. commodus* by Kavanagh (1987). We believe the $\dot{V}_{O_{2rest}}$ measured in the present study was elevated from the animal's actual resting metabolic rate. Crickets often 'rested' with their abdomens raised high off the ground. This posture fits the description of the 'standing high' threatening posture described by Loher and Rence (1978). The threatening posture may recruit more muscle, thus increasing $\dot{V}_{O_{2rest}}$. The mass-specific $\dot{V}_{O_{2rest}}$ rate found for

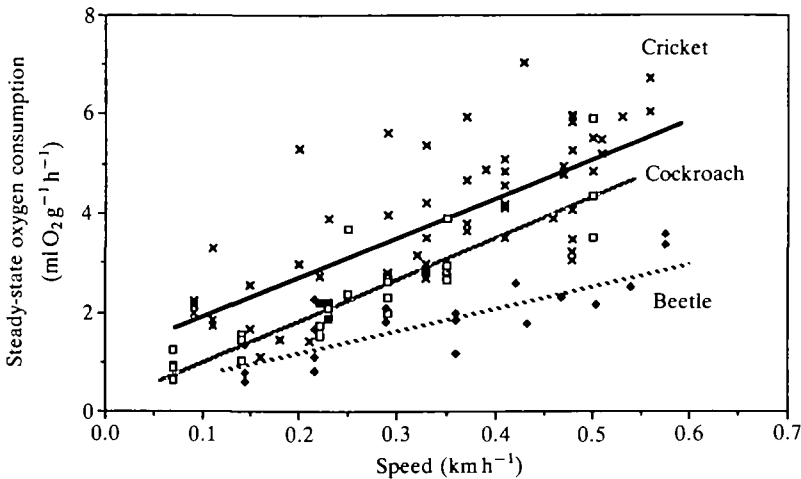


Fig. 1. Steady-state oxygen consumption ($\dot{V}_{O_{2ss}}$) during exercise for crickets (\times), cockroaches (\square) and beetles (\blacklozenge). The slopes of the lines relating $\dot{V}_{O_{2ss}}$ and speed (i.e. the minimum cost of transport, C_{\min}) were similar for crickets and cockroaches, but significantly lower for beetles.

P. americana was approximately threefold lower than that found by Herreid and Full (1984). The animals used in the present study were 26 % larger and exhibited less extraneous movement than those used by Herreid and Full (1984).

During exercise crickets, cockroaches and beetles rapidly attained $\dot{V}_{O_{2ss}}$. The time to reach half $\dot{V}_{O_{2ss}}$ was similar to that found for other cockroaches (Herreid and Full, 1984). $\dot{V}_{O_{2ss}}$ increased linearly with speed in each species (Fig. 1). A linear increase in $\dot{V}_{O_{2ss}}$ is typical for other insects and most other pedestrian species (Full, 1989; Taylor *et al.* 1982). The least-squares regression lines were $\dot{V}_{O_{2ss}} = 8.03 (\pm 1.92)v + 1.10$ ($N=60$; $r^2=0.54$) for crickets, $\dot{V}_{O_{2ss}} = 8.45 (\pm 1.43)v + 0.17$ ($N=30$; $r^2=0.84$) for cockroaches and $\dot{V}_{O_{2ss}} = 4.63 (\pm 0.72)v + 0.27$ ($N=17$; $r^2=0.71$) for beetles, where $\dot{V}_{O_{2ss}}$ is in $\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$, and v is velocity in km h^{-1} .

Cost of locomotion

For crickets, cockroaches and beetles the total cost of locomotion, defined as the amount of O_2 used per gram to travel 1 kilometer, decreased with increasing speed and approached a minimum at high speeds (Fig. 2). The minimum cost of locomotion (C_{\min}) is equivalent to the slope of the line relating $\dot{V}_{O_{2ss}}$ and speed (Taylor *et al.* 1970). C_{\min} was 8.03, 8.45 and 4.63 $\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$ for crickets, cockroaches and beetles, respectively. C_{\min} values for crickets and cockroaches were not significantly different (ANCOVA: $F_{(1,88)}=0.083$; $P=0.8$). C_{\min} for beetles was significantly different from that of cockroaches and crickets (ANCOVA: $P<0.05$ for both). The C_{\min} of *P. americana* was not significantly different from that measured by Herreid and Full (1984).

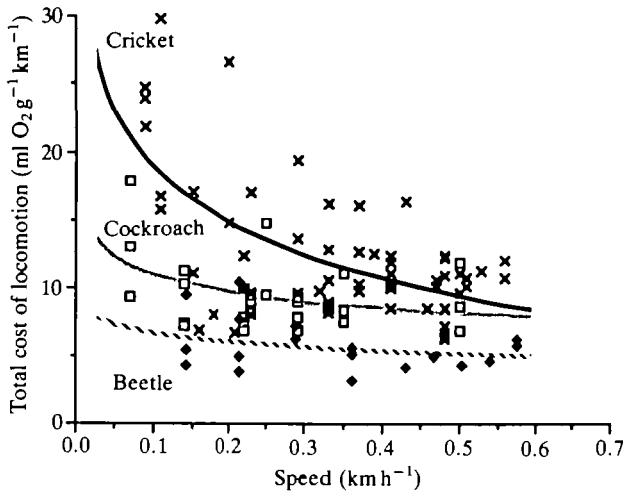


Fig. 2. Total cost of locomotion (C_{tot} , obtained by dividing $\dot{V}_{\text{O}_{2\text{ss}}}$ by the speed of travel) as a function of speed for crickets (\times), cockroaches (\square) and beetles (\blacklozenge). At high speeds, C_{tot} decreases to a minimum (C_{min}), represented by the slope of the $\dot{V}_{\text{O}_{2\text{ss}}}$ vs speed function.

Kinematics

Stride frequency (f) increased linearly with speed in each species (Fig. 3A). The least-squares regression lines were: $f=9.1v+1.74$ ($N=34$; $r^2=0.65$) for crickets, $f=8.9v+0.88$ ($N=31$; $r^2=0.87$) for cockroaches and $f=9.2v+1.6$ ($N=20$; $r^2=0.81$) for beetles, where f is in Hz, and v is velocity in km h^{-1} . The slopes of the regression lines were not significantly different (homogeneity of slopes, $P>0.05$), but the y -intercept was significantly higher in crickets and beetles compared to cockroaches (ANCOVA, $P<0.05$).

Contact time (C_t) decreased curvilinearly with speed in each species (Fig. 3B). A second-order polynomial regression significantly improved the fit of the data compared to a linear function in two of the three species (in crickets and beetles; stepwise regression analysis, $P<0.05$). The second-order polynomial regressions were: $C_t=0.88v^2-0.92v+0.36$ ($N=34$; $r^2=0.61$) for crickets, $C_t=0.50v^2-0.73v+0.36$ ($N=31$; $r^2=0.83$) for cockroaches and $C_t=1.05v^2-1.09v+0.39$ ($N=20$; $r^2=0.88$) for beetles, where C_t is in seconds, and v is velocity in km h^{-1} . The slopes of log-transformed data were not significantly different (homogeneity of slopes, $P>0.05$), but the y -intercept was significantly higher in cockroaches than in crickets and beetles (ANCOVA, $P<0.05$).

Cost per stride and ground contact cost

The cost per stride was determined by dividing $\dot{V}_{\text{O}_{2\text{ss}}}$ by stride frequency. The cost per stride was independent of speed in each species (Fig. 4A). The least squares regression lines were: cost per stride $= -0.43v+4.6$ ($N=45$; $r^2=0.001$) for

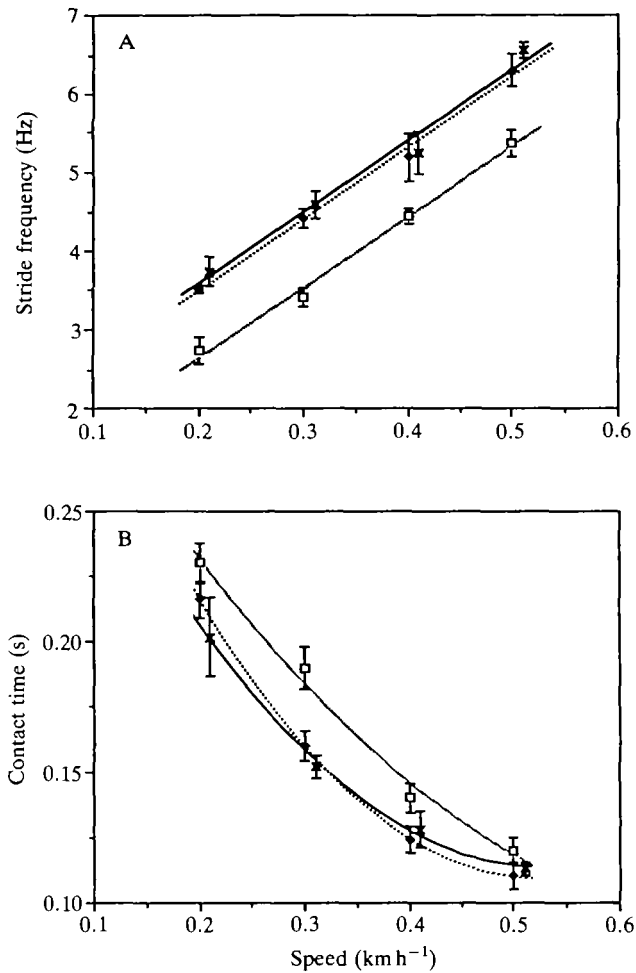


Fig. 3. Kinematics of steady-state locomotion determined from the hind leg of crickets (\times), cockroaches (\square) and beetles (\blacklozenge). (A) Stride frequency increased linearly with speed. (B) Contact time (i.e. the length of time the leg is in contact with the substratum during one stride) decreased as speed increased. A second-order polynomial fitted the data best. Bars represent ± 1 s.e.

crickets, cost per stride = $2.8v + 3.3$ ($N=22$; $r^2=0.11$) for cockroaches and cost per stride = $-1.45v + 2.6$ ($N=11$; $r^2=0.06$) for beetles, where cost per stride is in J kg^{-1} (assuming $1 \text{ ml O}_2 = 20.1 \text{ J}$) and v is velocity in km h^{-1} . Cost per stride was significantly lower in beetles ($2.1 \pm 0.18 \text{ J kg}^{-1}$) compared to crickets ($4.4 \pm 0.19 \text{ J kg}^{-1}$) or cockroaches ($4.2 \pm 0.18 \text{ J kg}^{-1}$; ANOVA, $F_{(2,80)}=21$, $P=0.0001$ and Scheffe F -test).

The ground contact cost was determined by dividing $\dot{V}_{\text{O}_2\text{ss}}$ by stride frequency and multiplying by the fraction of the stride period the leg was in contact with the ground (i.e. duty factor). This calculation is equivalent to multiplying $\dot{V}_{\text{O}_2\text{ss}}$ by

contact time. The ground contact cost was independent of speed in each species (Fig. 4B). The least-squares regression lines were: ground contact cost = $-0.68v + 3.4$ ($N=45$; $r^2=0.005$) for crickets, ground contact cost = $1.7v + 2.2$ ($N=22$; $r^2=0.10$) for cockroaches and ground contact cost = $-1.67v + 2.0$ ($N=11$; $r^2=0.13$) for beetles, where ground contact cost is in J kg^{-1} (assuming $1 \text{ ml O}_2 = 20.1 \text{ J}$) and v is velocity in km h^{-1} . Ground contact cost was significantly lower in beetles ($1.5 \pm 0.14 \text{ J kg}^{-1}$) than in crickets ($3.1 \pm 0.13 \text{ J kg}^{-1}$) or cockroaches ($2.7 \pm 0.12 \text{ J kg}^{-1}$; ANOVA, $F_{(2,80)} = 21.1$, $P = 0.001$ and Scheffe F -test).

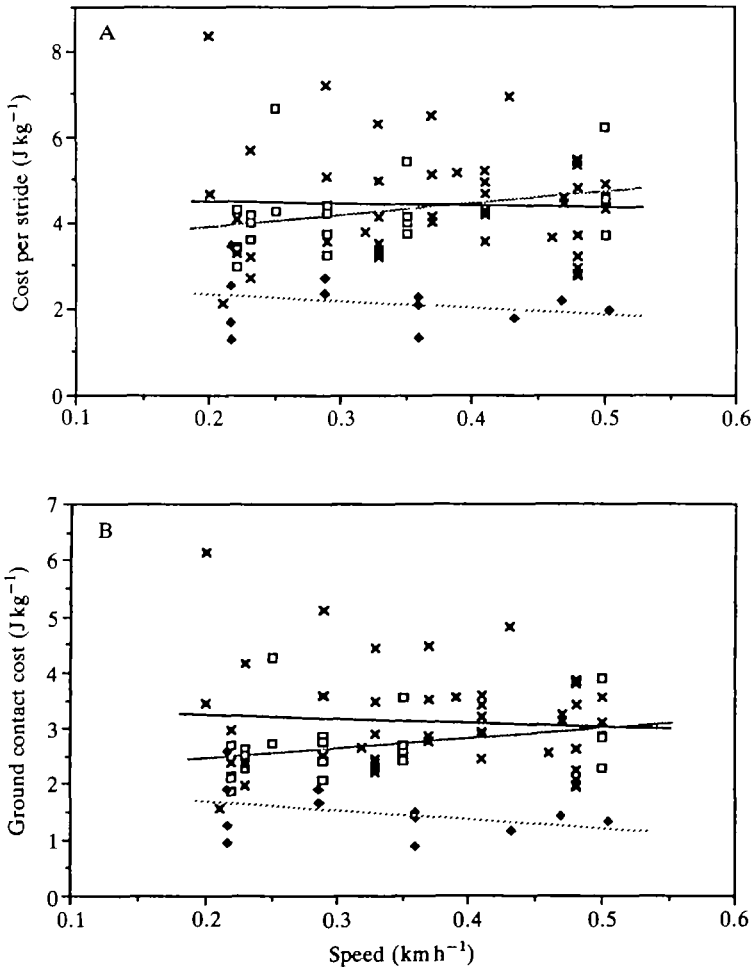


Fig. 4. Metabolic cost of locomotion normalized for the rate of force production in crickets (\times), cockroaches (\square) and beetles (\blacklozenge). (A) The metabolic cost of locomotion per stride was independent of speed. The metabolic cost of locomotion per stride was significantly lower in beetles 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. $1 \text{ ml O}_2 = 20.1 \text{ J}$.

Discussion

Variation in the minimum cost of locomotion

The metabolic cost of traveling a given distance (C_{tot} , obtained by dividing $\dot{V}_{\text{O}_2\text{SS}}$ by the speed) in crickets, cockroaches and beetles decreased with increasing speed to a minimum (the minimum cost of transport, C_{min} ; Fig. 2). This pattern is typical for nearly all other pedestrians (Herreid, 1981; Taylor *et al.* 1970). Hence, C_{min} has been a very useful value for comparing the metabolic costs of animals of different body mass, running at different speeds and with different rates of oxygen consumption at rest (Taylor *et al.* 1970; Tucker, 1970).

Body mass has been the single most important variable in predicting variation in C_{min} . Mass-specific C_{min} decreases with increasing body mass in mammals, birds and reptiles (Fedak and Seeherman, 1979; John-Alder *et al.* 1986; Taylor *et al.* 1970, 1982). Subsequent research on the metabolic cost of locomotion has found that animals of very different morphology and physiology, such as salamanders, insects, crustaceans and myriapods, also follow the same relationship (Full, 1989; Herreid, 1981). For the pedestrian species tested, mass-specific C_{min} decreases with body mass according to the function $C_{\text{min}} = 10.79M^{-0.31}$, where C_{min} is in $\text{J kg}^{-1} \text{m}^{-1}$ and M is in kg (Fig. 5A; Full, 1989).

The predicted value of C_{min} for all three insects in the present study was within the 95 % confidence interval of the C_{min} versus body mass function (Fig. 5A). Our measured values also fell within the 95 % confidence intervals determined for insects alone ($C_{\text{min}} = 7.23M^{-0.39}$; also see Lighton, 1985). With this analysis, we cannot conclude that variation in morphology or physiology of any of the three insects resulted in locomotor costs different from those of other pedestrians of the same mass.

One important question concerning C_{min} has yet to be adequately addressed. How much variation in metabolic cost is necessary to conclude that a species is more or less economical than other similarly sized animals? In the present study, C_{min} of the field cricket *T. commodus*, an animal with highly modified limb structure, was 67 % higher than predicted for its body mass, but was still well within the 95 % confidence limits. The C_{min} of the caterpillar hunting beetle *C. affine* was half that of the cricket or cockroach and was 20 % below the predicted C_{min} based on body mass. The 95 % confidence intervals of the log-transformed C_{min} versus body mass regression extend approximately 2.5-fold above and 40 % below the regression line, making the variation at any given body mass nearly sixfold (Fig. 5B). To examine whether the variation in C_{min} at a given body mass was determined primarily by one or two groups of animals, we calculated the standardized residuals of C_{min} for several major taxa (Fig. 6). Obviously, a significant amount of unexplained variability exists for all groups. At present, few trends are obvious, except perhaps the low costs measured in salamanders (Full *et al.* 1988) and possibly crustaceans.

Cost per stride and ground contact cost

What can explain the variation in the interspecific cost of terrestrial locomotion

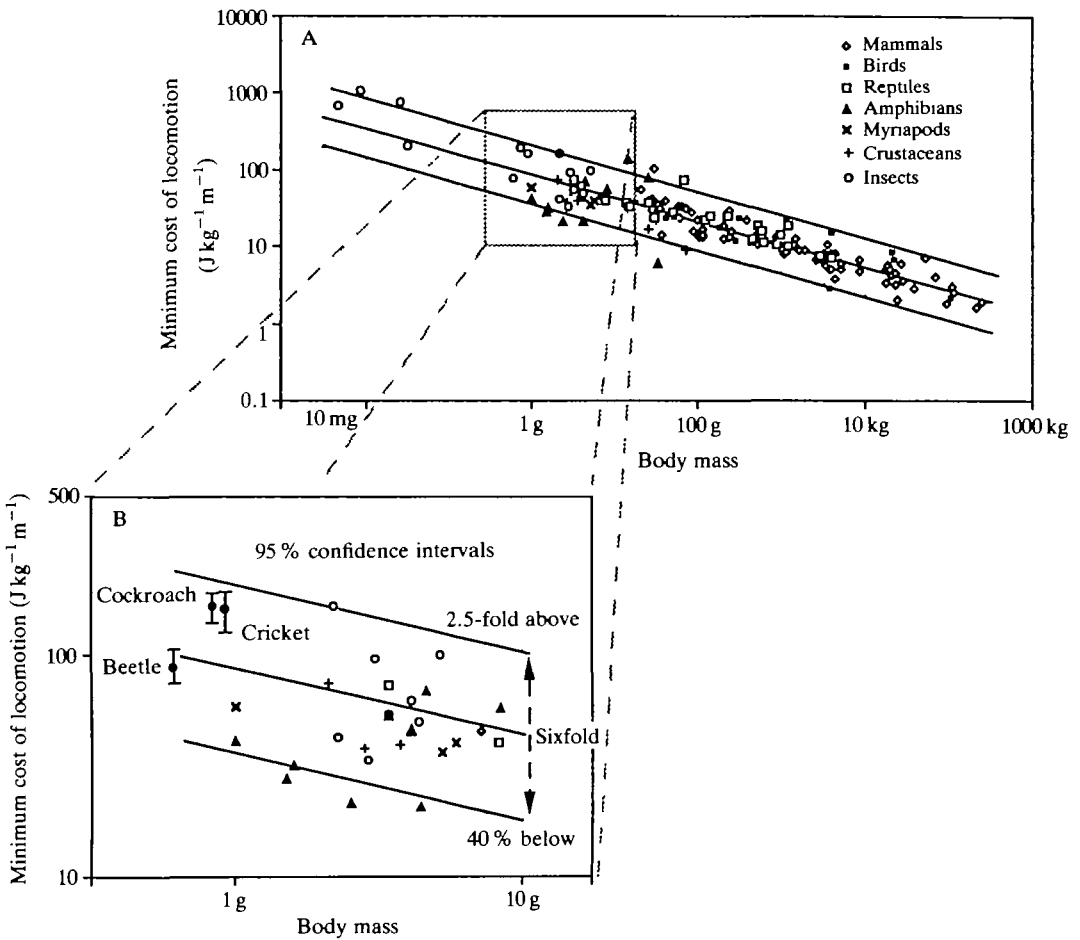


Fig. 5. (A) Double logarithmic plot of the mass-specific minimum cost of locomotion (C_{\min}) as a function of body mass for available data on pedestrians from various sources (see Full, 1989). $C_{\min} = 10.79M^{-0.31 \pm 0.02}$ ($N = 153$, $r^2 = 0.85$, where C_{\min} is in $\text{J kg}^{-1} \text{m}^{-1}$ and M in kg). Upper and lower lines represent the 95% confidence limits of an individual C_{\min} value calculated from log-transformed data. (B) Inset shows the variation in C_{\min} for body masses that include crickets, cockroaches and beetles. Error bars represent the 95% confidence limits of C_{\min} for insects of the present study.

resulting from differences in body form? Taylor (1980) suggested that the cost of muscle force production rather than the amount of mechanical work done by the muscle (Hill, 1950) 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 maintaining a running posture while supporting the body's weight. Taylor *et al.* (1980) tested this hypothesis on mammals by exploiting the 10-fold variation in C_{\min} related to body mass. Small and large animals were loaded with back-packs

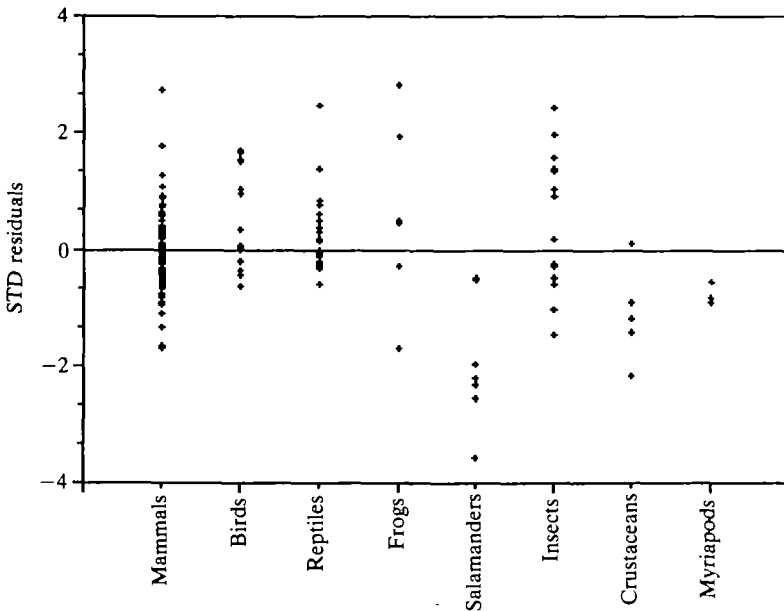


Fig. 6. Variation in the minimum cost of locomotion (C_{\min}) as a function of taxa with the effect of body mass removed. Shown are the standardized residuals of log-transformed C_{\min} . A value of +2 represents a 2.5-fold elevation above predicted values, whereas -2 represents a 40% reduction. Data are from Fig. 5A.

and run on a treadmill while oxygen consumption was measured. The results showed that 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. Taylor (1985) suggested that small animals require more metabolic energy to develop an equivalent amount of force than larger animals because they must turn their muscles on and off more frequently per unit of time or distance. Higher rates of contraction appear to result in additional cost due to more frequent activation (due to Ca^{2+} movement; Rall, 1986) and the higher costs associated with the more rapid cycling of cross-bridges (Heglund and Cavagna, 1987).

The hypothesis that the metabolic cost of force production in mammals determines the variation in C_{\min} related to body mass is supported by data on limb cycling rates or stride frequency (Heglund and Taylor, 1988). The metabolic cost of locomotion varies with body mass at equivalent speeds in a manner similar to stride frequency. When the metabolic cost of locomotion is normalized for the rate of force production by dividing the cost by stride frequency, the mass-specific metabolic cost of locomotion in mammals for one stride is nearly independent of body mass (Heglund and Taylor, 1988). Therefore, the greater metabolic cost per unit mass for 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 metabolic energy per gram to cover the same distance.

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 observed in the present study of three insects (Fig. 4A). The relatively low C_{\min} of the beetle was not accompanied by a low stride frequency, long stride period or an apparently low rate of muscle force production. The stride frequencies of the beetle and cricket were similar and significantly greater than rates measured in cockroaches (Fig. 3A). Surprisingly, the energetic cost of locomotion per stride for these insects ($2.1\text{--}4.3\text{ J kg}^{-1}$) is remarkably similar to the value found in mammals at their preferred trotting speed (5.0 J kg^{-1} ; Heglund and Taylor, 1988).

Perhaps normalizing for the rate of force production by using ground contact time is more appropriate than dividing by stride frequency, because muscles are developing most of their force when the legs are in contact with the ground and supporting the body's weight. In mammals Heglund and Taylor (1988) found that the metabolic cost per stride increased with speed. To explain the increase in cost, they hypothesized a decrease in mechanical advantage (i.e. higher muscle forces for the same ground reaction force) with an increase in speed. However, Biewener (1989) showed that effective mechanical advantage is independent of speed in horses, dogs and ground squirrels. Most importantly, the metabolic cost per stride does become independent of speed when normalized for the duration of time the foot is in contact with the ground and is actually developing force (Kram and Taylor, 1989). These findings are not consistent with a higher cost resulting from a decrease in mechanical advantage. They do support the hypothesis based on differences in the cost of force production.

Although the ground contact cost in insects ($1.5\text{--}3.1\text{ J kg}^{-1}$) was similar to that measured in mammals (2 J kg^{-1}) and was also independent of speed, it did not explain the interspecific variation in the cost of locomotion (Fig. 4B). The relatively low C_{\min} of the beetle was not accompanied by long contact times and low rates of muscle force production. The contact times of the beetle and cricket were similar and significantly shorter than the duration measured in cockroaches (Fig. 3B).

Several alternative explanations for the effect of variation in body form on C_{\min} exist and remain to be explored. For example, beetles could store significantly more elastic strain energy than either cockroaches or crickets. Second, muscles of these insects may be operating on different areas of the force-velocity and length-tension functions. The force that a given cross-sectional area of muscle may produce could vary. Third, the muscles of beetles may have a greater effective mechanical advantage than the muscles of crickets and cockroaches. Variation in the total amount of muscular force generated to produce the same ground reaction force can lead to variation in metabolic cost. In mammals the mechanical advantage of limbs decreases 10-fold with a 1000-fold decrease in body mass (Biewener, 1983, 1989). Small mammals have a more crouched posture which

requires relatively greater muscle force for support. 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 differences in the metabolic cost of locomotion related to body mass in mammals (Biewener, 1989).

We propose that variations in body form (i.e. musculo-skeletal arrangement), apart from variation in body mass, could translate into significant differences in force production per volume of active muscle and, therefore, in the interspecific minimum cost of terrestrial locomotion.

We thank Werner Loher for suggesting the use of his experimental animal. This work was supported by NSF grant DCB 8904586.

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