

ENERGETICS OF ASCENT: INSECTS ON INCLINES

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Summary

Small animals use more metabolic energy per unit mass than large animals to run on a level surface. If the cost to lift one gram of mass one vertical meter is constant, small animals should require proportionally smaller increases in metabolic cost to run uphill. To test this hypothesis on very small animals possessing an exceptional capacity for ascending steep gradients, we measured the metabolic cost of locomotion in the cockroach, *Periplaneta americana*, running at angles of 0, 45 and 90° to the horizontal. Resting oxygen consumption ($\dot{V}_{O_{2\text{rest}}}$) was not affected by incline angle. Steady-state oxygen consumption ($\dot{V}_{O_{2\text{ss}}}$) increased linearly with speed at all angles of ascent. The minimum cost of locomotion (the slope of the $\dot{V}_{O_{2\text{ss}}}$ versus speed function) increased with increasing angle of ascent. The minimum cost of locomotion on 45 and 90° inclines was two and three times greater, respectively, than the cost during horizontal running. The cockroach's metabolic cost of ascent greatly exceeds that predicted from the hypothesis of a constant efficiency for vertical work. Variations in stride frequency and contact time cannot account for the high metabolic cost, because they were independent of incline angle. An increase in the metabolic cost or amount of force production may best explain the increase in metabolic cost. Small animals, such as *P. americana*, can easily scale vertical surfaces, but the energetic cost is considerable.

Introduction

Many small animals appear to scale rocks, stalks, tree trunks and other vertical surfaces effortlessly. One frequently quoted explanation (e.g. in Calder, 1984; Schmidt-Nielsen, 1983, 1984; Vogel, 1988) for this capacity is that increases in metabolic cost for small animals running on inclines are relatively insignificant (Taylor *et al.* 1972). When moving vertically, a body acquires potential energy equal to its weight times the vertical distance traveled. Lifting 1 kg of body mass 1 m vertically will increase potential energy by 9.8 J. If muscular efficiency is constant (Hill, 1950), the amount of energy required to lift a 1 kg body mass 1 vertical meter will be the same irrespective of animal size. In contrast, it is well established that small animals use more metabolic energy per unit mass than large

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animals to run on a level surface (Taylor *et al.* 1970, 1982; Full, 1989). Therefore, if the vertical cost for moving 1 kg of body mass uphill is nearly constant, then the relative increase in metabolism needed for running up inclines will be much less for small animals. The fact that the energy demand for climbing in small animals is minimal could have profound effects on morphological and physiological design, ecology (e.g. habitat selection and foraging strategy) and evolution.

One alternative to the constant-efficiency hypothesis is based on the metabolic cost of muscle force production. Taylor *et al.* (1980) have suggested that the metabolic cost of locomotion depends directly on force production. Greater or more rapid force production appears to increase the metabolic cost of locomotion (Taylor, 1985). If the metabolic cost of force production increases during climbing, then oxygen consumption could show a substantial increase, even in small animals.

To test these hypotheses for very small animals possessing an exceptional capacity for running up very steep slopes, we measured the oxygen consumption of the American cockroach, *Periplaneta americana*, running on a miniature treadmill oriented at 0, 45 and 90°. This cockroach is ideal for studying the effect of size on the energetics of incline running. They are very small (less than 1 g) and readily scale almost any vertical surface. If the constant vertical efficiency hypothesis is supported and small animals require very little additional metabolic energy to travel up inclines, then the minimum cost of transport (i.e. the energy required to transport 1 kg for 1 m, C) should be similar for incline and level running. Running animals at fast speeds on the steepest possible inclines should maximize any differences in metabolic cost (Wunder and Morrison, 1974; Taylor *et al.* 1972).

Materials and methods

Animals

Periplaneta americana (0.78 ± 0.09 g, \pm s.d.) were obtained from Carolina Biological Supply Company and from Dr Rody Pipa at the University of California at Berkeley. Cockroaches were housed in individual plastic containers with a layer of cedar shavings. Animals were given water and puppy chow *ad libitum*. All cockroaches were kept on a local photoperiod at ambient temperatures (24 ± 2 °C). All experiments were conducted during the daylight hours under ambient light.

Oxygen consumption

Cockroaches were exercised on a treadmill enclosed in an airtight Lucite respirometer. The tread belt consisted of fine wire mesh that prevented slippage. The respirometer was mounted on a vice which could be oriented at angles from 0 to 90°. The respirometer and vice were placed in an incubator (Lab-Line, Ambi-Hi-Lo Chamber) to control ambient temperature at 23°C. Oxygen consumption (\dot{V}_{O_2}) was determined using open-flow respirometry (Herreid *et al.* 1981). We used

a flow rate of 90 ml min^{-1} to measure oxygen consumption during exercise. To provide a detectable oxygen concentration difference, we used a lower flow rate of $35\text{--}50 \text{ ml min}^{-1}$ to measure resting oxygen consumption ($\dot{V}_{\text{O}_2\text{rest}}$). Air leaving the chamber passed through filters containing Drierite to remove water vapor. The oxygen concentration of air exiting the chamber was measured using an electrochemical oxygen analyzer (S-3A/II, Ametek), interfaced with a computer (IBM/AT) via an analog to digital converter (Cyborg).

To measure $\dot{V}_{\text{O}_2\text{rest}}$, an animal was placed in the respirometer oriented at 0, 45 or 90° and monitored for more than 1 h. $\dot{V}_{\text{O}_2\text{rest}}$ was attained in approximately 15 min if the animal was not active (i.e. wandering around the chamber). All resting values were calculated from the second or third hour of the rest period. Resting rates for individual animals were calculated by averaging the \dot{V}_{O_2} over a 5–10 min period during which the animal remained motionless. If the animal would not rest for at least 10 min, the results were discarded.

For each experiment measuring \dot{V}_{O_2} during exercise, cockroaches were weighed and given a 20 min rest period within the chamber prior to exercise. Following rest, animals were exercised for 10 min at four different speeds, and given a 10 min rest period between successive speeds. The multiple-speed protocol did not yield significantly different results from single-speed experiments in which animals were exercised at one speed daily. Animals attained steady-state oxygen consumption ($\dot{V}_{\text{O}_2\text{ss}}$, the rate at which \dot{V}_{O_2} varied by less than 5% during exercise) in approximately 3 min. The experimental speeds were 0.07, 0.14, 0.22 and 0.29 km h^{-1} . The slowest speed was chosen so that animals walked consistently without extraneous movements. The highest speed represented the rate at which animals could sustain $\dot{V}_{\text{O}_2\text{ss}}$ during vertical running for 4–5 min, but fatigued within 10–15 min. Experiments were terminated if an animal could not sustain a certain speed or would not run consistently. Animals would occasionally cling to the sides of the chamber before climbing back onto the tread belt to resume exercise. Periods off the tread belt lasted less than 2 s. If there were more than five of these instances in one 10 min exercise bout, the results were discarded. $\dot{V}_{\text{O}_2\text{ss}}$ was calculated by averaging the \dot{V}_{O_2} for 4–6 min after an exercising animal had attained a steady state. Horizontal, 45° and vertical exercise bouts followed the same protocol, and individuals were tested only once a day. All \dot{V}_{O_2} values were corrected to STPD (Herreid *et al.* 1981).

Kinematic analysis

Cockroaches were video-taped with a high-speed camera (Video Logic CDR660) at 180 or $300 \text{ frames s}^{-1}$ while running on a treadmill. Three animals were taped at four speeds (0.2, 0.3, 0.4 and 0.5 km h^{-1}) for each of the three angles (0, 45 and 90°). Video frames were grabbed and digitized using a motion-analysis system (Peak Performance Tech. Inc.). Stride frequency and contact time (i.e. the duration of a stride a leg is in contact with the ground) were calculated from the digitized data.

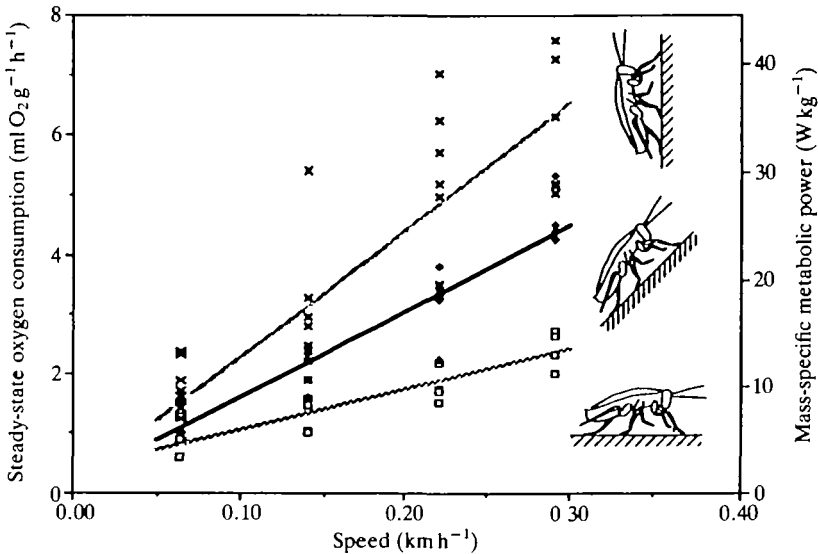


Fig. 1. Steady-state oxygen consumption as a function of speed for three angles of incline, 0° (□), 45° (◆) and 90° (×). Steady-state oxygen consumption increased linearly with speed at each angle. Mass-specific metabolic power is represented on the right-hand ordinate and was calculated assuming 1 ml O₂=20.1 J.

Results

Oxygen consumption during rest

Cockroaches were generally active for the first 1 h during $\dot{V}_{O_{2rest}}$ measurements in the horizontal position, but became more quiescent in the second hour. Animals usually began resting within 20 min at 45° and 5 min at 90°. Three out of five animals at 45°, and five out of seven at 90°, oriented themselves with their heads pointing downwards. Body orientation did not affect $\dot{V}_{O_{2rest}}$. $\dot{V}_{O_{2rest}}$ was not statistically different for cockroaches resting horizontally, vertically or at 45° (Table 1; ANCOVA; $F_{(2,12)}=1.55$; $P=0.2$).

Oxygen consumption during exercise

Steady-state oxygen consumption ($\dot{V}_{O_{2ss}}$) increased with speed during horizontal and incline running (Fig. 1; Table 1). Step-wise polynomial regression analysis showed that the next higher-order coefficient did not explain significantly more variation than that explained by a linear function ($P<0.05$). The linear regression equation relating speed and $\dot{V}_{O_{2ss}}$ for horizontal locomotion obtained in the present study (Table 1) was not different from that found by Herreid and Full (1983). Moreover, the slope of the $\dot{V}_{O_{2ss}}$ versus speed function for horizontal locomotion (C_{hor} , the minimum cost of horizontal transport) was well within the

Table 1. Aerobic metabolism of *Periplaneta americana* at rest and during exercise as a function of angle of incline

Angle of incline	$\dot{V}_{O_2\text{rest}}$ (ml O ₂ g ⁻¹ h ⁻¹)	$\dot{V}_{O_2\text{ss}}$ (ml O ₂ g ⁻¹ h ⁻¹) vs speed (v , km h ⁻¹)	Energy cost of running uphill (J kg ⁻¹ m ⁻¹)	Efficiency (%)
0°	0.22±0.01 (<i>N</i> =6)	$\dot{V}_{O_2\text{ss}}=6.77\pm0.84v+0.38$ (<i>N</i> =16; $r^2=0.82$)	—	—
45°	0.25±0.03 (<i>N</i> =5)	$\dot{V}_{O_2\text{ss}}=14.6\pm1.32v+0.15$ (<i>N</i> =18; $r^2=0.89$)	223	4.4
90°	0.25±0.01 (<i>N</i> =7)	$\dot{V}_{O_2\text{ss}}=21.4\pm2.30v+0.12$ (<i>N</i> =31; $r^2=0.75$)	290	3.4

All values are ±1 s.e.
 $\dot{V}_{O_2\text{rest}}$, oxygen consumption of inactive animals during at least 5 min of rest.
 $\dot{V}_{O_2\text{ss}}$, steady-state oxygen consumption determined during at least 4 min of consistent running.
 1 ml O₂=20.1 J.
 Efficiency=cost of vertical metabolic work/mechanical work×100; mechanical work=9.8 J to lift 1 kg for 1 m.

95 % confidence limits for insects and other pedestrians (Full, 1989). The slopes of the regressions relating speed and $\dot{V}_{O_2\text{ss}}$ were statistically different for cockroaches running horizontally, at 45° and vertically (homogeneity of slopes: $F_{(2,59)}=12.9$; $P<0.001$).

Comparison with predictions based on a constant-efficiency hypothesis

To test if results from the present study on incline running support the hypothesis based on constant vertical efficiency, we compared the observed oxygen consumption rates of *P. americana* with predicted rates. We based our predictions on the equation:

$$(C_{\text{in}} - C_{\text{hor}})/\sin\beta = 15.5 \text{ J kg}^{-1}\text{m}^{-1} \quad (1)$$

(Taylor *et al.* 1972), where C_{hor} is the measured value of the minimum cost of locomotion (i.e. the slope of the $\dot{V}_{O_2\text{ss}}$ vs speed function) for horizontal running in J kg⁻¹ m⁻¹, C_{in} is the minimum cost of locomotion for incline running in J kg⁻¹ m⁻¹, β is the angle of incline in degrees, and 15.5 J kg⁻¹ m⁻¹ is the constant for the additional amount of energy required to lift 1 kg for 1 vertical meter found empirically by Taylor *et al.* (1972). $\sin\beta$ is the fraction of a meter climbed vertically per meter of run. For β we used 45 and 90°. Observed costs for cockroaches running on 45 and 90° inclines fall well above those predicted using the constant vertical efficiency hypothesis. When running at 0.15–0.30 km h⁻¹ on inclines of 45 and 90°, $\dot{V}_{O_2\text{ss}}$ values for *P. americana* were 60–120 % greater than those predicted if vertical efficiency were constant.

To test the generality of the constant-efficiency hypothesis, we plotted the

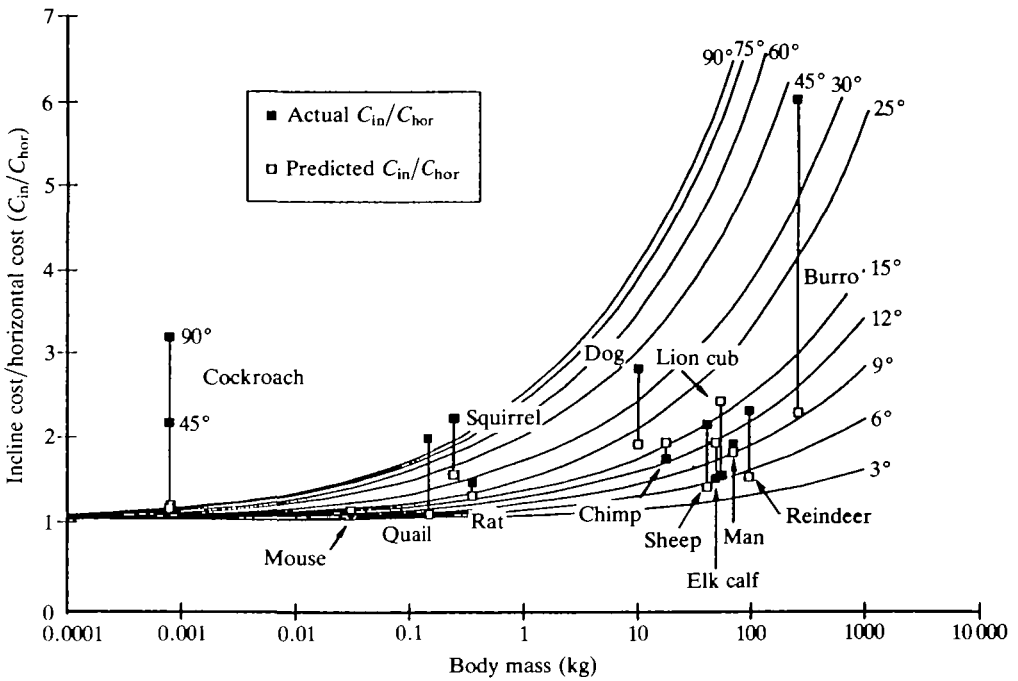


Fig. 2. Factorial increase in metabolic cost of incline running, relative to running on the horizontal, as a function of ascent angle and body mass on logarithmic coordinates for several species. The ratio of the metabolic cost of locomotion during incline running (C_{in} , the slope of the $\dot{V}_{O_{2ss}}$ vs speed function for a given angle of ascent) to the metabolic cost of locomotion during horizontal running (C_{hor} , the slope of the $\dot{V}_{O_{2ss}}$ vs speed function at a zero angle of ascent) is shown for values predicted on the basis of a constant efficiency of vertical work (vertical work = $15.5 \text{ J kg}^{-1} \text{ m}^{-1}$). Curved lines represent these predicted C_{in}/C_{hor} ratios as isopleths of a constant incline angle. Predicted C_{in}/C_{hor} ratios (open squares) for individual species are plotted with respect to body mass and their actual angle of ascent. Actual ratios, obtained from literature values of C_{hor} and C_{in} (closed squares), are plotted with respect to body mass (rat, Armstrong *et al.* 1983; elk calf, Cohen *et al.* 1978; dog, Raab *et al.* 1976; mouse and chimpanzee, Taylor *et al.* 1972; quail, Warncke *et al.* 1988; squirrel, Wunder and Morrison, 1974; lion cub, sheep, elk calf, man, reindeer and burro, see Cohen *et al.* 1978 for references).

relationship of C_{in}/C_{hor} and body mass on logarithmic coordinates for a variety of animals running on inclines ranging from 3 to 90°. The ratio of C_{in}/C_{hor} represents the factorial increase in energy cost during incline running. For comparison with actual factorial increases in energy cost, we generated a family of curves (i.e. isopleths) that represent the predicted ratios of C_{in}/C_{hor} for a given body mass and angle, based on the assumption that mass-specific vertical work is nearly constant (Fig. 2). To predict values of C_{hor} , we used the equation:

$$C_{hor} = 10.8 m^{-0.304} \quad (2)$$

(Full, 1989) in which m represents body mass in kg. To generate predicted values of C_{in} , we used equations 1 and 2 and solved for C_{in} :

$$C_{in} = 15.5\sin\beta + 10.8 m^{-0.304} . \quad (3)$$

The ratio can be calculated as follows:

$$C_{in}/C_{hor} = [(15.5\sin\beta)/(10.8 m^{-0.304})] + 1 . \quad (4)$$

By varying β and m in equation 4, we obtained predicted values for factorial increases in metabolic cost of animals running on inclines ranging from 3 to 90° and varying in body mass by seven orders of magnitude. Fig. 2 shows the results of this analysis. Each isopleth in this figure represents a different angle of ascent. Superimposed on this graph are both predicted and observed C_{in}/C_{hor} ratios for various animals running on different inclines. We used the animal's mass and angle of ascent to calculate predicted ratios based on a constant vertical efficiency (equation 4). For observed ratios, we used literature values for both C_{in} and C_{hor} . The length of the vertical bar for each species represents the difference between actual and predicted increases in metabolic cost. For example, the predicted increase in metabolic cost of a 250 kg burro running on a 9° incline is somewhat over twofold, whereas the actual increase in cost is over sixfold.

Kinematics

Stride frequency increased with speed at all angles of ascent (ANOVA, $F_{(1,98)}=368$; $P<0.001$; Fig. 3A). Angle of ascent had no significant effect on stride frequency when the effect of speed was removed (ANCOVA, $F_{(2,98)}=2.7$; $P=0.07$). Contact time decreased with speed at all angles of ascent (ANOVA, $F_{(1,98)}=437$; $P<0.001$; Fig. 3B). Angle of ascent had no significant effect on contact time when the effect of speed was removed (ANCOVA, $F_{(2,98)}=2.6$; $P=0.08$).

Discussion

Resting oxygen consumption

Oxygen consumption was similar for *P. americana* resting at 0, 45 and 90° (Table 1). Yox *et al.* (1982) found that passive resting tension in the leg muscles of arthropods maintains limb position. This passive tension in the limbs of quiescent cockroaches could provide an energetically inexpensive mechanism for maintaining posture, regardless of the resting angle. Alternatively, it is possible that pretarsal claws along with other skeletal elements provide support on 45 and 90° inclines. Use of skeletal structures to maintain position would require no additional muscle force production, making any added gravitational effects energetically insignificant. More studies determining muscle activity need to be performed to give us a better understanding of posture.

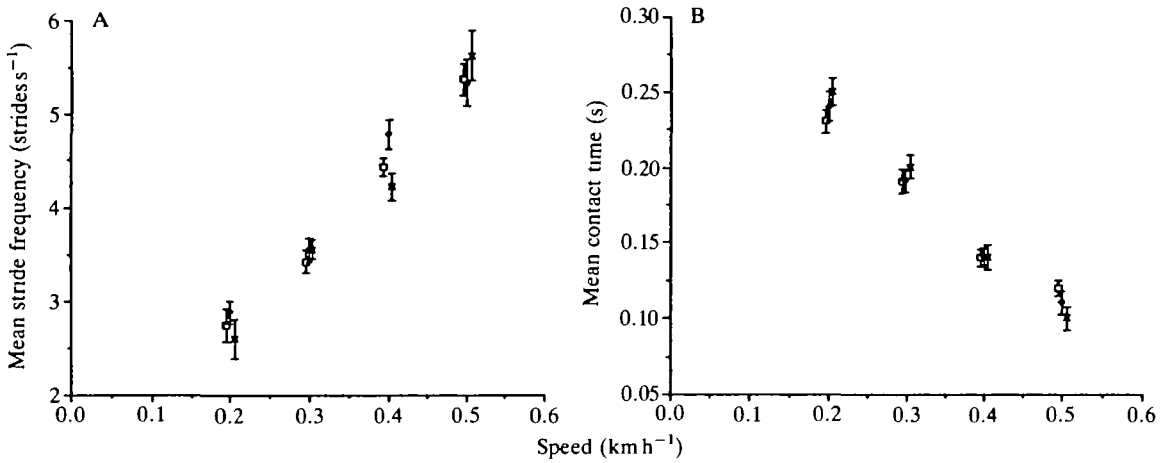


Fig. 3. Kinematics of locomotion as a function of speed and angle of ascent. (A) Mean stride frequency as a function of speed. Stride frequency increased with speed, but was not significantly different for angles of ascent of 0° (□), 45° (◆) and 90° (×). (B) Contact time (i.e. duration of a stride a leg was in contact with the ground) as a function of speed. Contact time decreased with speed, but was not significantly different for angles of ascent of 0° (□), 45° (◆) and 90° (×). Bars represent ± 1 s.e.

Oxygen consumption during exercise

P. americana showed a linear increase in $\dot{V}_{O_{2SS}}$ with speed when running horizontally and on 45 and 90° inclines (Herreid and Full, 1983; Fig. 1). A linear increase in $\dot{V}_{O_{2SS}}$ with speed during incline running is also typical of mammals and birds (Taylor *et al.* 1972; Wunder and Morrison, 1974; Raab *et al.* 1976; Cohen *et al.* 1978; Armstrong *et al.* 1983; Warncke *et al.* 1988).

The minimum cost of transport (C , represented by the slope of the $\dot{V}_{O_{2SS}}$ versus speed function; C_{in} for the cost on an incline and C_{hor} for the cost on the horizontal) for cockroaches running on inclines increased with increasing angle of ascent. Cockroaches running at 45 and 90° had C_{in} values approximately two- and threefold higher, respectively, than C_{hor} for cockroaches moving at 0° (Fig. 1; Table 1). Most other animals show a substantial increase in C with increasing incline angle. For example, C for 250 g red squirrels increases 123% when running on a 37° incline relative to horizontal running (Wunder and Morrison, 1974). When running on a 24% slope, dogs (17.3 and 6.7 kg) had a 179% increase in C_{in} over C_{hor} (Raab *et al.* 1976). For 350 g rats running on a 16° incline, C_{in} increased 42% over C_{hor} (Armstrong *et al.* 1983).

There are, however, at least two exceptions to this trend. Taylor *et al.* (1972) found that 30 g mice did not show a significant increase in C when running up a 15° incline compared to running on the level. Herreid *et al.* (1981) found that the Madagascar hissing cockroach, *Gromphadorina portentosa*, did not use significantly more oxygen when running on 5, 15 and 25° inclines than when running on the level. One possible explanation for a lack of a significant increase in $\dot{V}_{O_{2SS}}$ i

that the variability in $\dot{V}_{O_{2ss}}$ prevents the resolution of any increases in cost when speeds are very slow and low angles of incline are used, as was the case for *G. portentosa*.

Cost of incline running

The hypothesis of a constant vertical efficiency for animals that vary in body mass offers one reason why small animals can easily run up inclines. Taylor *et al.* (1972) found that 30 g mice have the same C running on a 15° incline as they do running on the level. Chimpanzees (17.5 kg), however, show a twofold increase in C when running on a 15° incline. From their study, along with data on sheep and man, Taylor *et al.* (1972) suggested that the metabolic energy needed to lift 1 kg of body mass 1 vertical meter may be similar for animals that differ in body mass. They empirically derived an estimate of 15.5 J kg⁻¹ m⁻¹ for the metabolic energy needed to lift 1 kg of body mass 1 vertical meter. In contrast to vertical cost, mass-specific C_{hor} scales with body mass to the -0.30 power (equation 2; Full, 1989; Taylor *et al.* 1970). Compared to large animals, small animals have relatively high costs for horizontal running. Therefore, if the work required to lift 1 kg for 1 vertical meter is similar in animals that differ in mass, small animals running uphill should require proportionally smaller increases in energy over that used during horizontal running than would larger animals (Taylor *et al.* 1972).

Results from the present study on insects ascending steep angles do not support the hypothesis based on a constant efficiency for vertical work (Fig. 2). When running on 45 and 90° inclines, *P. americana*, an animal weighing less than 1 g, had approximately a two- and threefold elevation, respectively, in C_{in} over C_{hor} (Table 1). These increases correspond to values of 223 and 290 J kg⁻¹ m⁻¹, respectively, for the metabolic work needed to lift 1 kg of cockroach mass 1 vertical meter. These values yield efficiencies of only 3–4% (Table 1).

When data on the energy required during running up slopes are viewed collectively, considerable variability is apparent (Fig. 2). Excluding results on cockroaches obtained in the present study, observed values of C_{in}/C_{hor} for birds and mammals range from 35.7% below (53.5 kg lion cub on a 17.7° incline) to 162% above (253.5 kg burro on a 9.6° incline) values predicted by Taylor *et al.* 1972. Cohen *et al.* 1978 found that the mean value representing the amount of metabolic energy used to lift a 1 kg mass 1 vertical meter is closer to 27 J kg⁻¹ m⁻¹. If the value for vertical work is increased from 15.5 J kg⁻¹ m⁻¹ (Taylor *et al.* 1972) to 27 J kg⁻¹ m⁻¹ (Cohen *et al.* 1978), observed C_{in} values for cockroaches running at 45 and 90° are still 80 and 146%, respectively, above predicted values. If a constant of 27 J kg⁻¹ m⁻¹ is used to predict the cost of incline running for other animals, predicted costs considerably underestimate some observed costs (e.g. by 55% in lion cubs, Chassin *et al.* 1976; and 31% in chimpanzees, Taylor *et al.* 1972) and substantially overestimate others (e.g. by 85% in burros, Cohen *et al.* 1978; and 65% in quails, Warncke *et al.* 1988).

The added cost of incline running appears to be highly variable and not a simple

function of angle and body mass. One alternative explanation to the constant-efficiency hypothesis is based on the metabolic cost of force production. Taylor *et al.* (1980) tested the hypothesis that the metabolic cost of force production determines the metabolic cost of locomotion by loading animals with back-packs while they ran on a treadmill. No change in acceleration of the center of mass was observed between loaded and unloaded animals. Thus, muscle force increased in direct proportion to the load added. Oxygen consumption also rose in direct proportion to the added load. Therefore, metabolic cost increased directly with muscle force production for animals ranging in mass from a rat to a horse. Taylor (1985) suggested that both greater force and a higher rate of force generation can increase metabolic cost. Larger forces will increase the volume of muscle active and result in a higher cost. Likewise, activation of the same volume of muscle, but at higher rates, can lead to a higher metabolic cost because faster fibers are recruited.

Loading studies on insects show an increase in \dot{V}_{O_2} proportional to the load carried (Nielsen *et al.* 1982; Lighton *et al.* 1987). As in mammals, the metabolic cost for insects may increase directly with muscle force production. Therefore, the greater metabolic cost of locomotion for incline running in *P. americana* may have resulted from a twofold increase in the cost of force production at 45° and a threefold increase at 90°. The lack of change in stride frequency and contact time with angle of ascent does not support the hypothesis that the cost of muscle force production is elevated because of higher rates of force development (Fig. 3). The greater metabolic cost of running on steeper inclines was not associated with higher stride frequencies or shorter contact times, which would have led to a higher cost of force production. However, changes in leg kinematics other than stride frequency and contact time, such as the orientation of the limb relative to the running surface, could result in an alteration of the mechanical advantage of the limb possibly affecting metabolic cost by increasing the amount of force production. Finally, an increased metabolic cost of force production could result from the substitution of less expensive eccentric contractions (i.e. contraction during muscle stretching) used in level running with more costly concentric contractions (i.e. contraction producing muscle shortening) necessary for climbing (Margaria, 1938).

Insects cannot easily walk up steep inclines simply because of a relatively low energy expenditure. Variables other than energy cost need to be considered, such as adaptations for grasping. Added work or force production during incline running for small animals does result in significant increases in metabolic cost. Although *P. americana* can scale vertical surfaces with remarkable ease, the energetic cost is considerable.

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References

- ARMSTRONG, R. B., LAUGHLIN, M. H., ROME, L. AND TAYLOR, C. R. (1983). Metabolism of rats running up and down an incline. *J. appl. Physiol.* **55**, 518–521.
- CALDER, W. A. (1984). *Size, Function and Life History*. Cambridge, MA: Harvard University Press. pp. 194–197.
- CHASSIN, P. S., TAYLOR, C. R., HEGLUND, N. C. AND SEEHERMAN, H. J. (1976). Locomotion in lions: energetic cost and maximum aerobic capacity. *Physiol. Zool.* **49**, 1–10.
- COHEN, Y., ROBBINS, C. T. AND DAVITT, B. B. (1978). Oxygen utilization by elk calves during horizontal and vertical locomotion compared to other species. *Comp. Biochem. Physiol.* **64A**, 43–48.
- FULL, R. J. (1989). Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Animals* (ed. W. Wieser and E. Gnaiger), Stuttgart: Thieme. (pp. 175–182).
- HERREID, C. F. AND FULL, R. J. (1983). Cockroaches on a treadmill: aerobic running. *J. Insect Physiol.* **30**, 395–403.
- HERREID, C. F., FULL, R. J. AND PRAWEL, D. A. (1981). Energetics of cockroach locomotion. *J. exp. Biol.* **94**, 189–202.
- HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Science Progress* **38**, 209–230.
- LIGHTON, J. R. B., BARTHOLOMEW, G. A. AND FEENER, D. H., JR (1987). Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol. Zool.* **60**, 524–537.
- MARGARIA, R. (1938). Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varie velocita ed inclinazioni del terreno. *Atti. Accad. Lincei Memorie, serie VI* **7**, 299–368.
- NIELSEN, M. G., JENSEN, T. F. AND HOLM-JENSEN, I. (1982). Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). *Oikos* **39**, 137–142.
- RAAB, J. L., ENG, P. AND WASCHLER, R. A. (1976). Metabolic cost of grade running in dogs. *J. appl. Physiol.* **41**, 532–535.
- SCHMIDT-NIELSEN, K. (1983). *Animal Physiology: Adaptation and Environment*. Cambridge: Cambridge University Press. p.438.
- SCHMIDT-NIELSEN, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press. pp. 175–176.
- TAYLOR, C. R. (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. exp. Biol.* **115**, 253–262.
- TAYLOR, C. R., CALDWELL, S. L. AND ROWNTREE, V. J. (1972). Running up and down hills: some consequences of size. *Science* **178**, 1096–1097.
- TAYLOR, C. R., HEGLUND, N. C. AND MALOIJ, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 1–21.
- TAYLOR, C. R., HEGLUND, N. C., MCMAHON, T. A. AND LONNEY, T. R. (1980). Energetic cost of generating muscular force during running: a comparison of large and small animals. *J. exp. Biol.* **86**, 9–18.
- TAYLOR, C. R., SCHMIDT-NIELSEN, K. AND RAAB, J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107.
- VOGEL, S. (1988). *Life's Devices: The Physical World of Plants and Animals*. New Jersey: Princeton University Press. p. 312.
- WARNCKE, G., BANDHOLTZ, J. AND SCHULTZE-MOTEL, P. (1988). Metabolic cost and body temperature of grade running in quail (*Coturnix coturnix*). *Comp. Biochem. Physiol.* **89A**, 93–96.
- WUNDER, B. A. AND MORRISON, P. R. (1974). Red squirrel metabolism during incline running. *Comp. Biochem. Physiol.* **48A**, 153–161.
- YOX, D. P., DICAPRIO, R. A. AND FOURTNER, C. R. (1982). Resting tension and posture in arthropods. *J. exp. Biol.* **96**, 421–425.