ENERGETICS OF COCKROACH LOCOMOTION

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SUMMARY

Cockroaches, *Gromphadorhina portentosa*, were run at different speeds for 20 min on a miniature treadmill enclosed in a lucite respirometer while oxygen consumption ($\dot{V}_{O_2}$) was continuously monitored. The data collected on these 5 g insects are remarkably similar to those obtained on vertebrates.

$\dot{V}_{O_2}$ rises rapidly with the onset of exercise; the $t_{\frac{1}{2}}$ on-response was about 1 min with steady-state reached within 4 min at the fastest speed, 0·12 km/h. Recovery was rapid; the $t_{\frac{1}{2}}$ off-response was 4–6 min, with total recovery achieved in less than 1 h. The tracheal system appears to be a highly efficient mode of O_2 conductance in contrast to the crustacean method of delivery involving gills and circulation.

$\dot{V}_{O_2}$ (ml O_2/g.h) at steady-state running varies directly with velocity (V). The regression equation at 24 °C is $V_{O_2} = 0.45 + 4.92V$. The Y-intercept, at zero velocity, is 2·4 times the actual resting $\dot{V}_{O_2}$ rate of 0·19 ml O_2/g.h. Temperature does not change the slope of the regression line but shifts it up or down in accordance with a simple Q_{10} effect. Incline running produces no changes compared to level running.

The minimum cost of transport, the lowest $\dot{V}_{O_2}$ necessary to transport a given mass a specific distance, is high in cockroaches (4·92 ml O_2/g.km) and comparable to that expected for a small quadrupedal or bipedal pedestrian vertebrate.

INTRODUCTION

Studies on comparative locomotion of terrestrial animals have been growing by leaps and bounds. Special interest has been devoted to the field of pedestrian energetics since the landmark papers of Tucker (1970), Taylor, Schmidt-Nielsen & Raab (1970) and Schmidt-Nielsen (1972). In spite of recent attention to running vertebrates including mammals, reptiles and birds (Taylor, 1973; Fedak & Seeherman, 1979), remarkably little information is available for the great majority of animals in the world, the invertebrates. Three papers are exceptions to the generalization: studies on the land crab, *Cardisoma guanhumi* (Herreid, Lee & Shah, 1979), three species of ants, *Formica fusca*, *F. rufa* and *Camponotus herculeanus* (Jensen & Holm-Jensen, 1980), and the pulmonate slug, *Ariolimax columbianus* (Denny, 1980).

The studies on ants, crabs, and slugs indicate that metabolic rate as measured by oxygen consumption ($\dot{V}_{O_2}$) or carbon dioxide production ($\dot{V}_{CO_2}$) is linearly related to the velocity of running. This is also true for vertebrate locomotion on land (Taylor

et al. 1970). Unfortunately, the potential usefulness of the above generalization (
marred by the fact that in none of the invertebrate studies was it possible to collect
data comparable to the steady-state running which is considered essential in vertebrate
experiments. In the case of the ants, animals were run for given periods of time and
the total CO_2 produced during the exercise bout was used to calculate $\dot{V}_{CO_2}$ (Jensen
& Holm-Jensen, 1980). This procedure assumes that there is little delay in reaching
a steady-state aerobic condition. However, without a continuous measurement of
$\dot{V}_{CO_2}$, this assumption can not be verified. Nevertheless, the assumption is probably
valid in view of the rapid response to flight demands seen in $\dot{V}_{O_2}$ measured for insects
such as *Drosophila* (Chadwick & Gilmour, 1940). In the case of crabs and slugs where
continuous monitoring of $\dot{V}_{O_2}$ was possible, it was clear that neither animal attained
a steady-state. Hence, both Herreid *et al.* (1979) and Denny (1980) calculated the
aerobic cost of running by integrating the total area under the $\dot{V}_{O_2}$ curve during and
after running to estimate aerobic cost. The inclusion of O_2 debt in these calculations
does not seem justified when there is no evidence that the recovery O_2 is a measure
of energy expenditure during running. Certainly in vertebrates this position is no
longer considered valid (Brooks *et al.* 1971*a, b*; Brooks, Brauner & Cassens, 1973;
Segal & Brooks, 1979; Hagberg, Mullin & Nagle, 1980).

Lack of steady-state running has forced the authors of the invertebrate experiments
to calculate a value called net cost of transport to compare with data on the minimum
cost of transport determined for vertebrates (Taylor *et al.* 1970). These cost estimates
are reputed to be the metabolic cost required to transport a gram of animal over a
1 km distance. Slugs appear to use 12 times more energy to travel a given distance
than similar-sized mammals (Denny, 1980), whereas ants and crabs are comparable
to the latter (Herreid *et al.* 1979; Jensen & Holm-Jensen, 1980). These results must
be viewed cautiously in view of the way $\dot{V}_{O_2}$ or $\dot{V}_{CO_2}$ was determined especially when
O_2 debt is involved. Moreover, net cost of transport, even when calculated under
steady-state conditions, is not synonymous with minimum cost of transport (cf.
Taylor, 1973) and the difference between the two values rises in small animals with
relatively high metabolic rates. Also, it should be noted that small animals do not
approach the speeds necessary to attain the theoretical minimum cost of transport
values (cf. Taylor *et al.* 1970).

In order to broaden our understanding of terrestrial locomotion in general, and to
eliminate some of the problems plaguing earlier studies on invertebrates, we have
turned to the study of cockroaches. These animals are highly specialized for terrestrial
locomotion and some, such as the case of our experimental animal, *Gromphadorhina
portentosa*, have lost their wings altogether. Moreover, cockroaches as representatives
of the Insecta have open circulation systems, tracheal respiration, and are six-legged
– a dramatic contrast to vertebrates. They seem ideal animals in which to study
comparative terrestrial locomotion, in the hope of demonstrating general principles
that may apply to other taxa. In this paper we present data on the metabolic rate of
cockroaches running freely on a treadmill. We have measured steady-state locomotion
at three different temperatures and have collected data on level and incline running.
In addition, we have calculated the minimum cost of transport for comparison with
vertebrates.

Animals

The experimental animals were adult male hissing cockroaches, *Gromphadorhina portentosa* Schaum, weighing between 3·4 and 6·5 g. Females were not included because reproduction and concomitant hormonal changes can influence metabolic rate. The animals were raised in a communal cage in an environmental chamber maintained at 25 °C, relative humidity of 75 % and given food in the form of dried puppy chow and water *ad libitum*. Once experiments began, the roaches were kept individually in small plastic containers with food and water.

Apparatus

All experiments were conducted within an airtight lucite respirometer enclosing an axle-driven latex treadmill belt. The later was powered by a DC gear motor located outside of the chamber and controlled by a veriac capable of a speed range of 0·8–30 cm/sec. A switch was built into the system which allowed us to reverse the treadmill in cases where roaches turned around in the chamber. Inflow and outflow gas ports allowed for constant unidirectional circulation of fresh air into the respirometer. Room air was continuously drawn through the 125 ml working section of the respirometer at a rate of 56 ml/min. After passing through a drierite filter to remove water vapour, gas leaving the respirometer was drawn into one sensor cell and flow meter of an S-3A Applied Electrochemistry Oxygen Analyzer which was electrically interfaced with a Linear Instruments Model 282 Integrating Chart Recorder. As a reference gas, room air was directly passed at the same rate through a drying filter and into a second sensor cell of the analyser. Thus, we were able to measure differences between the percentage O_2 of the room air and the gas leaving the respirometer. This value multiplied by the flow rate gave us oxygen consumption ($\dot{V}_{O_2}$) of the roaches. Using these values and the flow rate, we were able to calculate the instantaneous oxygen consumption $\dot{V}_{O_2}$ of the roaches corrected to conditions of STPD (see Bartholomew *et al.* (1981), for the method).

Protocol

Single-speed experiments. The purpose of these experiments was to determine the $\dot{V}_{O_2}$ of roaches running at different speeds on different days. Approximately ten animals were tested at three speeds 0·03, 0·07 and 0·12 km/h, the latter being the highest speed this species could maintain for the experimental period. Individuals were generally run at a single speed with a day of rest before being tested again. They had previous experience with the treadmill during pilot studies and gave consistent performances.

Experiments lasted approximately 110 min. A roach was removed from its cage, weighed and placed into the respirometer. It rested in the chamber for 30 min during which time $\dot{V}_{O_2}$ was monitored. Typically, the $\dot{V}_{O_2}$ reached low, relatively constant rates within 25 min.

The rest period was followed by an exercise bout. The treadmill was turned on and $\dot{V}_{O_2}$ measured continuously for a 20 min exercise period. The animals generally ran well on the treadmill, maintaining their position well within the middle of the working

section. Occasionally roaches became agitated, flipped over, or lodged against the back of the chamber causing the experiments to be aborted.

After the exercise period was over and the treadmill was turned off, $\dot{V}_{O_2}$ continued to be monitored for a recovery period of 60 min or until the O_2 consumption had declined to a resting rate. Initial experiments were carried out at $23\cdot6 \pm 0\cdot6$ °C (mean $\pm$ S.D.). In later experiments to determine the effect of temperature, we tested the roaches at 15, 25 and 35 ± 1 °C in an environmental chamber.

Multiple-speed experiments. The purpose of these experiments was to determine $\dot{V}_{O_2}$ of roaches as they were run sequentially at those different speeds during a single test. The experiment began when a roach was weighed and placed into the treadmill respirometer for a rest period of 30 min. The exercise bout lasted 15 min and consisted of three stages. The treadmill was first turned on to the lowest speed $0\cdot03$ km/h for 5 min, then increased to $0\cdot07$ km/h for 5 min, and followed by 5 min at $0\cdot12$ km/h. Recovery was not monitored.

Incline experiments. In order to determine if the $\dot{V}_{O_2}$ would alter with the incline of the treadmill, we followed the following experimental protocol. Roaches were rested 30 min. Then they were run for 20 min at $0\cdot07$ km/h as $\dot{V}_{O_2}$ was monitored. During the first 5 min of the 20 min run the treadmill was level, followed by successive 5 min periods at $+5°$, $+15°$ and $+25°$ incline. In other experiments the same procedure was followed for $0°$, $-5°$, $-15°$ and $-25°$ slopes. Any runs where the animal visibly slipped on the treadmill were discarded.

RESULTS

The resting $\dot{V}_{O_2}$ of the cockroach, *G. portentosa* was determined by calculating the average of seven individuals for the 15 min just prior to exercise. At this time the animals, having explored the chamber, were resting quietly, their only movements being infrequent antennal cleaning manoeuvres. The resting $\dot{V}_{O_2}$ was $0\cdot19$ ml O_2 g.h $\pm$ standard deviation of $0\cdot05$. There was no apparent trend with body mass; all animals had similar $\dot{V}_{O_2}$. These data are comparable to other values collected for insects (Keister & Buck, 1974). For example, Polacek & Kubista (1960) report a value of $0\cdot36$ ml O_2/g.h for the smaller roach, *Periplaneta americana*, and Bartholomew & Casey (1977) published values of $0\cdot17$ and $0\cdot25$ ml O_2/g.h for two large tropical beetles, *Strategus aloeus* and *Stenodontes molarium*.

Once the treadmill was turned on, the cockroaches rapidly adjusted to its motion with no obvious difficulty in most cases. When animals lagged back far enough to touch the rear of the treadmill chamber, they usually responded by moving forward briskly. During walking or running, roaches did not display any obvious shift in gait. This is consistent with the observations on *P. americana* which only changes gait at very low velocities (Delcomyn, 1971). In *G. portentosa* the only apparent behavioural change occurred between resting and walking. At rest, a roach would lie with its abdomen on the substrate, while during locomotion it raised its body as it walked on all six appendages in a typical tripod gait. At the end of the fast speed tests some individuals showed evidence of fatigue. They occasionally stopped in their run, carried their body closer to the substrate, maintained their spiracles in a wide open position and showed exaggerated abdominal breathing movements.
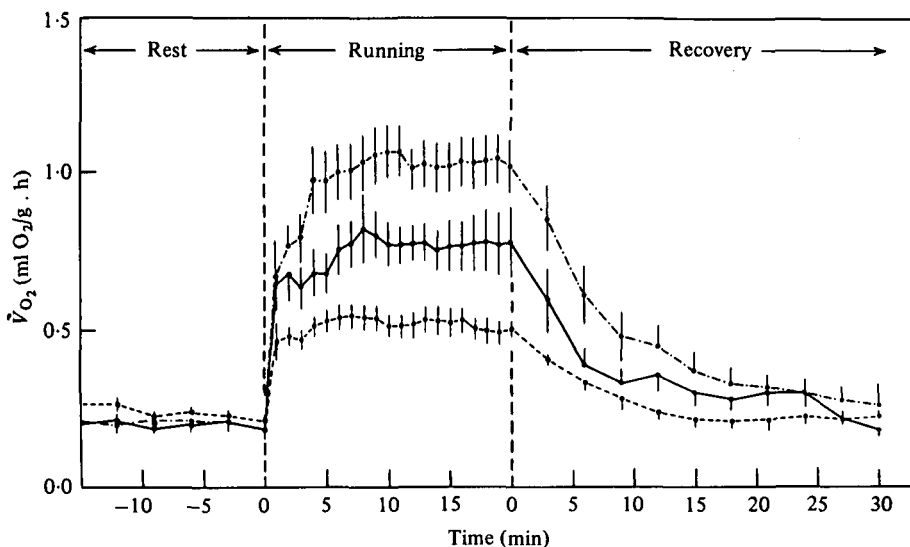
Fig. 1. Oxygen consumption ($\dot{V}_{O_2}$) of cockroaches running on a treadmill. The upper, middle and lower curves represent roaches running at speeds of 0·12, 0·07 and 0·03 km/h respectively. Vertical bars represent 95 % confidence intervals.

At the end of the experiment most roaches abruptly stopped moving and assumed the resting posture. Some individuals began extensive grooming routines, especially involving the antennae, but with little overall motion and apparent affect on the $\dot{V}_{O_2}$.

Fig. 1 shows the rapid change of $\dot{V}_{O_2}$ once exercise was initiated. There were slight differences in the time to reach a steady rate of O_2 consumption at the three different velocities. The time to reach one-half of the steady-state $\dot{V}_{O_2}$ value, $t_{\frac{1}{2}}$, was about 1 min at the two lower speeds and about 2 min at the fastest speed. Steady-state $\dot{V}_{O_2}$ was achieved by 4 min even at the highest speed. The lag in the animals' $\dot{V}_{O_2}$ response is known as the O_2 deficit. Oxygen deficit is the difference between two values: (1) the actual gradual rise in $\dot{V}_{O_2}$ which occurred as an animal began to run at a constant velocity and (2) the abrupt rise in $\dot{V}_{O_2}$ which should occur if the steady-state $\dot{V}_{O_2}$ were reached instantly the moment the run began (e.g. Stainsby & Barclay, 1970).

The steady-state $\dot{V}_{O_2}$ during the test depended directly upon the intensity of exercise: locomotion at 0·03 km/h was 0·58 ml O_2/g.h; at 0·07 km/h was 0·81 ml O_2/g.h and at 0·12 km/h was 1·06 ml O_2/g.h. When compared to the resting metabolism, the exercise values are 3·1, 4·3, 5·6 times higher.

The $\dot{V}_{O_2}$ during recovery was a direct function of the intensity of exercise. The $t_{\frac{1}{2}}$ to recovery was about 4, 4, and 6 min for the slow, medium and fast velocity tests, respectively. Complete recovery was achieved within 15, 30 and 45 min after the cessation of exercise. When the recovery curves are plotted on a log scale, it appears as if the low-speed data fit a simple exponential curve; the two higher speeds seem to be described by a more complex curve of at least two phases: a fast exponential decline in $\dot{V}_{O_2}$ followed by a slower decrease. It is possible to compare the 'O$_2$ debt' with the O_2 deficit values determined earlier by measuring the area under their respective curves. The debt/deficit ratios for the three speeds are as follows: slow, 10·3; medium, 6·9; fast, 6·0.
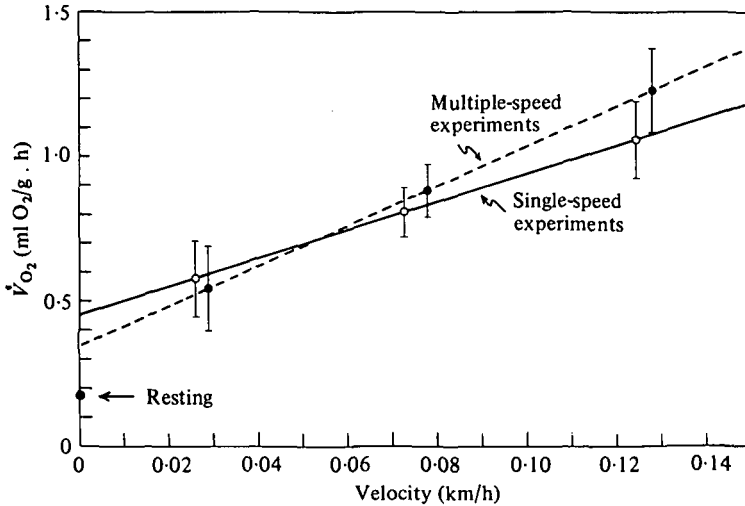
Fig. 2. Oxygen consumption of cockroaches running at different velocities. Data for this graph were obtained from steady-state running at a particular velocity. Data were either collected from roaches running at one speed each day for 20 min (single-speed experiments) or from roaches running successively at three different speeds for about 5 min at each speed (multiple-speed experiments). Vertical bars represent 95 % confidence intervals.

Fig. 2 shows that the increase in $\dot{V}_{O_2}$ with velocity (in km/h) was a direct linear function of the speed of locomotion. The least-squares regression lines based on 25 runs was $\dot{V}_{O_2} = 0.45 + 4.92V$. The 95 % confidence intervals for the slope and Y-intercept are ± 2.19 and ± 0.19. It should be noticed that this line when extrapolated back to zero speed gives a reading of 0.45 ml O_2/g.h or 2.4 times higher than the actual resting $\dot{V}_{O_2}$ of 0.19 ml O_2/g.h.

Fig. 2 also shows the results of the multiple-speed experiments. The equation for the least-squares regression is $\dot{V}_{O_2} = 0.34 + 6.96V$. The 95 % confidence intervals for the slope and Y-intercept are ± 2.30 and ± 0.20. There is no significant difference between the results of the single and multiple-speed experiments. Using the data from the single-speed experiments (Fig. 2), we can calculate the cost of transport (Tucker, 1970). This value is the amount of O_2 used to travel 1 km by 1 g of animal. It is determined by dividing the steady-state $\dot{V}_{O_2}$ by the speed of travel. Similar to most pedestrian species (e.g. Taylor *et al.* 1970), the cost of transport in roaches falls with velocity. Thus, for speeds of 0.03, 0.07, and 0.12 km/h, the cost of transport, progressively falls from 16.3 to 9.9 and to 8.2 ml O_2/g.h. The cost of transport approaches a minimum value as velocity increases; Taylor *et al.* (1970) have termed this the minimum cost of transport (M_{run}). This value is equivalent to the slope of the line relating $\dot{V}_{O_2}$ to velocity seen in Fig. 2. Thus, the minimum cost of transport for an average 5.2 g roach is 4.92 ml O_2/g.km.

Fig. 3 illustrates the influence of temperature on locomotion. As expected, at all three temperatures $\dot{V}_{O_2}$ increased with velocity as evidenced by their least-squares regression equations: at 15 °C, $\dot{V}_{O_2} + 0.18 + 5.25V$; at 25 °C, $\dot{V}_{O_2} = 0.38 + 4.50V$; at 35 °C, $\dot{V}_{O_2} = 0.67 + 5.16V$. The slopes of the three lines were not significantly different from one another. However, their Y intercept values were significantly different; the highest test temperatures had higher Y intercepts. In addition, th
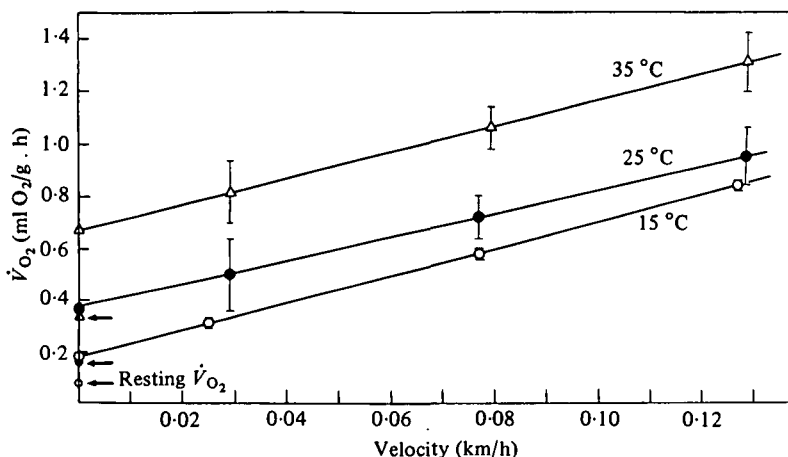
Fig. 3. Effects of temperature on O_2 consumption of running cockroaches. Vertical bars represent 95 % confidence intervals.
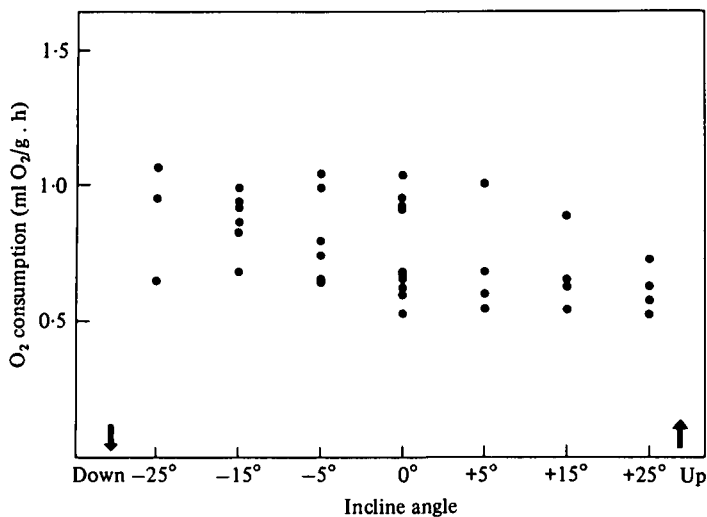

Fig. 4. Effects of incline running on O_2 consumption of running cockroaches.

resting $\dot{V}_{O_2}$ values showed the typical poikilothermic response; $\dot{V}_{O_2}$ was a direct function of temperature. The resting rates ± S.D. in ml O_2/g.h were as follows: at 15 °C, 0·09 ± 0·04; at 25 °C, 0·17 ± 0·06; at 35 °C, 0·37 ± 0·06. The Q_{10} effect was approximately 2 across this temperature range.

Cockroaches running on inclines did not show any differences compared to loco-motion across a level surface (Fig. 4).

DISCUSSION

Oxygen consumption in response to running

The running response of cockroaches seems remarkably similar to that of higher vertebrates. This is first evident from Figs. 1 and 2. There we note that the $\dot{V}_{O_2}$ of roaches rapidly attained a steady-state level once running began. The cockroach $t_{\frac{1}{2}}$ on-response of about 1 min compares favourably with humans (Cerretelli *et al.* 1979) as well as flying locusts (Krogh & Weis-Fogh, 1951). The time lag from the onset of exercise until a steady-state $\dot{V}_{O_2}$ is attained, referred to as an O_2 deficit (Stainsby & Barclay, 1970), may depend upon several factors. It depends upon the O_2 consumption, the efficiency of the O_2 conductance system, the extent of the tissue and blood supplies of O_2, the time to deplete the ATP and phosphagen supply of muscle, the magnitude of anaerobiosis, and the way that $\dot{V}_{O_2}$ is linked to ATP hydrolysis. In addition, it depends upon the sensitivity, position and responsiveness of the sensory reflex systems monitoring tissue gases and acid-base balance. Setting the latter problem aside, if the O_2 conductance system is efficient, the anaerobic contributions small, the stores of O_2, ATP, and phosphogens limited, then we might expect the $t_{\frac{1}{2}}$ on-response to be brief. This is the case for both higher vertebrates and insects. The latter have a tracheal system whereby air is delivered directly to the muscle cells without the participation of a circulatory system. Krogh & Weis-Fogh (1951) and Weis-Fogh (1964, 1967) have shown that this system is remarkably adept at supplying O_2 even during flight which is energetically more demanding per unit time than pedestrian locomotion. In contrast to this effective and rapid O_2 conductance system, we note that the land crab, *C. guanhumi*, running at modest speeds, showed a slow $t_{\frac{1}{2}}$ on-response (2–4 min) as well as a long $t_{\frac{1}{2}}$ recovery (15–20 min) after exercise (Herreid *et al.* 1979). This animal appears to have a poorer O_2 conductance system than the cockroach. In crabs, O_2 must be exchanged across an enclosed gill system, into an open circulation of low carrying capacity before it reaches the muscles. In addition, the O_2 storage of the crab, although unknown, may be relatively high because 30 % of the body weight is haemolymph. Moreover, muscle phosphagen levels may be high and anaerobic contributions large in crustaceans (e.g. Beis & Newsholme, 1975; Phillips *et al.* 1977). In view of such differences, we should not be surprised at the differences in $\dot{V}_{O_2}$ response between the two types of arthropods.

The highest measured $\dot{V}_{O_2}$ of cockroaches running at the fastest speed (0·12 km/h was approximately 6 times higher than the resting rate (Fig. 2). This metabolic scope is similar to values recorded for most vertebrates and the land crab *C. guanhumi* (Young *et al.* 1959; Segrem & Hart, 1967; Wunder, 1970; Pasquis, Lacaisse & Dejours, 1970; Bennett, 1978; Lechner, 1979; Herreid *et al.* 1979). Nevertheless, the peak metabolic scope of these species is considerably inferior to those of flying insects which often range from 25 to 150 times higher than their resting rates (see Polacek & Kubista, 1960).

The explanation of these species differences lies in the enormous metabolic capacity of insect flight muscle. It is by far the most active tissue known (e.g. Weis-Fogh, 1967). When flight muscle is quiescent, insects, regardless of their activity, are poikilothermic with body temperatures (T_B) approximating ambient temperatures (T_A). However, once flight muscles begin to contract during preflight warm-up

during flight itself, T_B is regulated at high levels and $\dot{V}_{O_2}$ is comparable to a homeotherm (e.g. Heinrich, 1974). Consequently, the difference between the poikilothermic and homeothermic $\dot{V}_{O_2}$ rates leads to spectacular metabolic scopes. Running in cockroaches clearly did not generate enough heat to produce unusual scopes nor was the T_B raised in our experiments according to measurements made with implanted copper–constantan thermocouples. We should note, however, that Bartholomew & Casey (1977) did find walking tropical beetles, *Strategus aloeus* and *Stenodenetes molarium*, with elevated T_B. Nevertheless, this appeared to be caused by contracting flight muscle.

Recovery from locomotion

Recovery from locomotion in cockroaches seems similar to the pattern described for many higher vertebrates. Thus, the magnitude of the O_2 debt is a direct function of the intensity of exercise. This is seen if one integrates the area under the recovery curve or considers the maximum time to achieve full recovery (i.e. resting $\dot{V}_{O_2}$). This pattern is consistent in animals as different as humans and crabs (Hagberg *et al.* 1980; Herreid *et al.* 1979). It is less evident when one examines the slight differences in $t_{\frac{1}{2}}$ off-response varying between 4 and 6 min.

The briefness of the $t_{\frac{1}{2}}$ off values for cockroaches indicates that much of the O_2 recovery is comparatively rapid. Although the $t_{\frac{1}{2}}$ off-response does not seem as rapid as in humans or dogs, which have values well under 1 min (e.g. Piiper & Spiller, 1970; Cerretelli *et al.* 1979; Hagberg *et al.* 1980), nor as long as the 20 min seen in that data for kangaroo rats or crabs (Yousef *et al.* 1970; Herreid *et al.* 1979), it does seem definitely comparable to rats and lizards (Brooks *et al.* 1971 *b*; Moberly, 1968; Dmi'el & Rappeport, 1976; Gleeson, 1980). Regardless of the variations in $t_{\frac{1}{2}}$ values among animals, almost all experiments reported within the literature indicate that $\dot{V}_{O_2}$ recovery lasts for periods up to an hour in length. This is certainly true of the cockroach data, as well as in the locust following flight (Krogh & Weis-Fogh, 1951). This is not the case for *Drosophila*, which had an almost immediate recovery (within 1 or 2 min) after flight (Chadwick & Gilmour, 1940).

The cause for such differences in O_2 recovery pattern is subject to considerable debate. Within the literature on vertebrates, where the subject has received extensive discussion, the recovery O_2 ('O_2 debt') has been traditionally divided into two parts. A fast component exists lasting 20–30 s, which is presumably due to replacement of O_2 within tissues and body fluids (including O_2 depleted from respiratory pigments during locomotion), and the additional O_2 required to replenish ATP and phosphagens such as creatine phosphate or arginine phosphate in the case of most invertebrates. The slow component, lasting for periods over 1 h, has been traditionally assumed to be due to the O_2 required to convert lactic acid into glycogen. This view seems no longer tenable for higher vertebrates at least (Brooks *et al.* 1971 *a*, *b*, 1973; Segal & Brooks, 1979; Hagberg *et al.* 1980). Much of the lactic acid generated during strenuous exercise is not resynthesized into glycogen but directly oxidized after exercise. Also it has become clear that as much as 70 % of the recovery O_2 is not directly due to the metabolic demands of locomotion. Rather, body temperatures are elevated by locomotion and these persist long after the exercise bout causing $\dot{V}_{O_2}$ to be increased by a Q_{10} effect. Additionally, high T_B reduces the phosphorylative

efficiency (ADP:O ratio), requiring that much more O_2 be consumed for a given amount of ATP produced than at rest.

In view of the turmoil in the literature and our general ignorance about invertebrate metabolic mechanisms, we are dubious about the cause of 'O_2 debt'. Certainly, lactic acid is generated in cockroaches such as *Periplaneta orientalis* and other arthropods both in hypoxia and exercise (Davis & Slater, 1928; Sacktor, 1974; Phillips *et al.* 1977). But no direct tie-in with O_2 debt is evident. Moreover, lactate is not the only end product of anaerobic metabolism thus making the relationship woth O_2 debt even more speculative.

$\dot{V}_{O_2}$ *versus velocity*

Another point of similarity between vertebrate and cockroach performance is evident in Fig. 2; the rate of $\dot{V}_{O_2}$ increases linearly with the velocity of locomotion. This pattern is common in most pedestrian locomotion (Segrem & Hart, 1967; Yousef *et al.* 1970; Taylor *et al.* 1970; Taylor, 1977) but there are important exceptions such as walking humans that show a curvilinear response (e.g. Margaria *et al.* 1963) and kangaroos that show no increase or even a decrease with the velocity of locomotion (Dawson & Taylor, 1973; Taylor, 1977). The possible reasons for these patterns are discussed by Taylor, 1977 and Cavagna, Heglund & Taylor, 1977.

When the line representing $\dot{V}_{O_2}$ v. velocity of locomotion in cockroaches is extrapolated to zero velocity, we note that the predicted $\dot{V}_{O_2}$ at rest is 2·4 times higher than the actual resting rate (Fig. 2). This result is not unexpected for it is common among vertebrates (Taylor *et al.* 1970; Taylor, 1977), although there are notable exceptions including lions, dogs and elk calves (Chassin *et al.* 1976; Raab, Eng & Waschler, 1976; Cohen, Robbins & Davitt, 1978). The reason for the discrepancy between the Y-intercept and the resting rate has received little attention. Among the numerous possibilities, we can mention the following several: Schmidt-Nielsen (1972) proposed that there is an undefined postural cost of locomotion which elevates the $\dot{V}_{O_2}$. There is little evidence for this concept. More likely, the work of Margaria *et al.* 1963 on human walking and Hoyt & Taylor (1979) on pony locomotion suggests that when careful measurements of slow locomotion are made, the $\dot{V}_{O_2}$ v. velocity curve is not linear. Very slow speeds are relatively expensive to maintain, thus deflecting the Y-intercept value upward. This elevation may occur because of the relative inefficiency of moving at slow speeds, the irregular walking patterns produced by some animals, the 'excitement factor' generated by running (e.g. heart rate, Baudinette, 1978) or because of the increased T_B and decreased P/O ratio generated during exercise (Brooks *et al.* 1971 *a*, *b*). Other possibilities exist and the problem awaits clarification.

Effect of temperature on locomotion

Temperature had a decided effect upon the energetics of cockroach locomotion. At higher temperatures the cost of locomotion as expressed by $\dot{V}_{O_2}$ in ml O_2/g.h at a given velocity was elevated. However, the regression lines of Fig. 3, differ only by their Y-intercept values. Since the slopes of the lines are similar at 15, 25 and 35 °C, there probably was no change in efficiency with temperature. The increased cost of locomotion at higher temperatures is simply a function of the Q_{10} effect. High

emperatures affected both resting and exercise $\dot{V}_{O_2}$ values to a comparable degree; a 10° rise in temperature doubled both rates. These results resemble the data for the common iguana, *Iguana iguana*, during treadmill studies (Moberly, 1968). Experiments with the lizard, *Uromastix aegyptius* across a temperature range of 35–42 °C showed a more complex picture. T_B did not affect resting $\dot{V}_{O_2}$. Both slope and Y intercept values were equivalent at all T_A; nevertheless, in this lizard there were some interesting gait changes at high velocities that were correlated with temperature (Dmi'el & Rappeport, 1976).

Incline running

Cockroaches do not seem to use significant amounts of energy to run up or down inclines compared to a level surface (Fig. 4). Again, these data are consistent with information from vertebrate experiments. Taylor *et al.* (1972) found that mammals as small as mice showed no significant increase in $\dot{V}_{O_2}$ with incline running. They reasoned that the cost of lifting a given weight a specific distance remains constant 9·8 joules for 1 kg per vertical metre) regardless of the size of the animal. But since the total metabolic rate per gram and the cost of transport varied inversely with body size, the relative cost to raise a weight would be harder to detect in small animals. Using data from mice and chimpanzees Taylor, Caldwell & Rowntree (1972) found that both expended 14·8 J/kg running up an 15° incline for an efficiency of about 60 %. If we assume roaches are similar, we can calculate that running uphill should produce a shift in the slope of $\dot{V}_{O_2}$ v. velocity curve from 4·92 for level running to 5·12 for a 15° positive incline. This amounts to a minor 4 % rise in $\dot{V}_{O_2}$. It is no surprise that such a change was not detected with our experimental procedure.

Cost of transport

The minimum cost of transport (M_{run}) is the minimum $\dot{V}_{O_2}$ (or its energetic equivalent) used to move 1 g of an animal over a distance of 1 km (Taylor *et al.* 1970). Use of this value has permitted investigators to compare animals of radically different size, running velocities, and standard metabolic rates. As Taylor *et al.* (1970) have pointed out, large animals can approach a true M_{run}: the cost of transport is high at low speeds, but as the rate of locomotion increases the cost decreases until a minimum value is reached. Small mammals such as mice and rats never approach the necessary velocities to reach a true M_{run}. This is the case for cockroaches as well. The lowest realized cost of locomotion of the cockroach was 8·2 ml O_2/g.km. This is 1·7 times higher than the theoretical minimum cost of transport of 4·9 ml O_2/g.km determined from the slope of the $\dot{V}_{O_2}$ v. velocity line. In fact, the M_{run} value would be achieved only at velocities over 0·5 km/h or four times the actual maximum speed of the roaches.

In spite of the hypothetical nature of M_{run}, it still has heuristic value to compare locomotion among animals. Fig. 5 (upper line) shows the regression line representing M_{run} for mammals of different body weight (W) determined by Taylor *et al.* (1970). The empirical equation developed for the relationship was $M_{run} = 8.46W^{-0.40}$. Small mammals have a higher M_{run} than large; the physical and physiological parameters producing this relationship have been recently discussed by Taylor *et al.* (1980). When the minimum cost of transport data for cockroaches (M_{run} = 4·92 ml
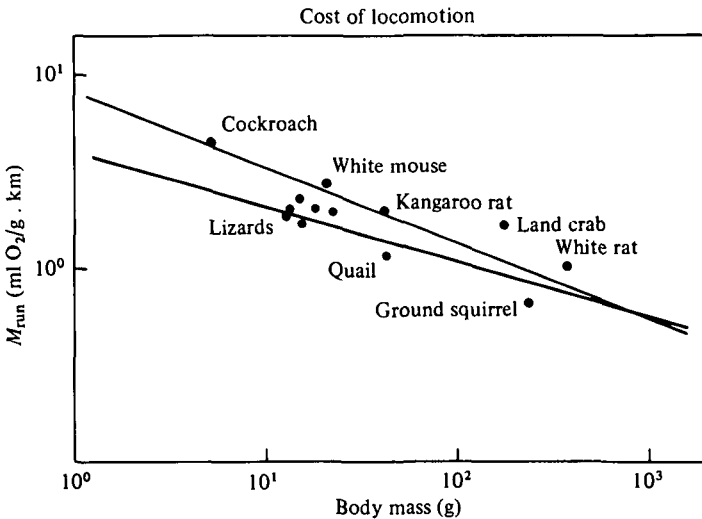
Fig. 5. Minimum cost of transport in ml O_2/g.km for animals of different body mass. The upper line represents data calculated for mammals by Taylor *et al.* (1970). The lower line represents data for birds and mammals summarized by Fedak & Seeherman (1979). The data for the cockroach are from this paper at 24 °C, the data for the land crab are from Herreid *et al.* (1979), and values for reptiles are from Taylor (1973).

O_2/g.km) is plotted in Fig. 5, it clearly falls close to the predicted value of 4·37 based on the Taylor *et al.* (1970) data. Also, the net cost of transport data for the land crab, *Cardisoma guanhumi*, lie nearby, as does the value for ants (Herreid *et al.* 1979; Jensen & Holm-Jensen, 1980).

Recently, Fedak & Seeherman (1979) have reexamined the data for a large variety of terrestrial vertebrates including birds and mammals. They concluded that bipedal and quadrupedal M_{run} values were not significantly different from one another and generated an equation for the pooled data on 69 species, $M_{run} = 3.89W^{-0.28}$, shown as the lower line in Fig. 5. When we use this equation to predict a value for a 5·2 g animal, the average size of our cockroach, we obtain a value 2·45 or about ½ the actual value. Nevertheless, the cockroach data still fall within a reasonable range of the Fedak & Seeherman (1979) line; in fact, these authors state 'for any given size animal, energy cost may vary by a factor of nearly 2'. Thus, it is gratifying to see that eight-legged crabs and six-legged cockroaches and ants fit the pattern for vertebrate quadrupeds and bipeds. This suggests that the minimum cost of locomotion is neither a function of the number of appendages nor the nature of the circulatory or respiratory system. Within broad limits, we clearly see the principle that the minimum cost of transport increases as the size of the animal decreases. This generalization extends across animals ranging from 100 kg horses to 10 mg ants, spanning more than seven decades on the body mass scale and includes two phyla separated by more than 0·5 billion years of evolution.

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