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## COCKROACHES ON A TREADMILL: AEROBIC RUNNING

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**Abstract**—Five species of cockroach were tested on a miniature treadmill at three velocities as  $O_2$  consumption ( $\dot{V}_{O_2}$ ) was measured: *Gromphadorhina chopardi*, *Blaberus discoidalis*, *Eublaberus posticus*, *Byrsotria fumagata* and *Periplaneta americana*. All cockroaches showed a classical aerobic response to running:  $\dot{V}_{O_2}$  increased rapidly from a resting rate to a steady-state ( $\dot{V}_{O_{2ss}}$ );  $t_{1/2}$  on-response varied from under 30 s to 3 min. Recovery after exercise was rapid as well;  $t_{1/2}$  off-response varied from under 30 s to 6 min. These times are faster or similar to mammalian values.  $\dot{V}_{O_2}$  varied directly with velocity as in running mammals, birds and reptiles.  $\dot{V}_{O_2}$  during steady-state running was only 4–12 times higher than at rest. Running is energetically much less costly per unit time than flying, but the cost of transport per unit distance is much more expensive for pedestrians. The minimal cost of transport ( $M_{run}$ ), the lowest  $\dot{V}_{O_2}$  necessary to transport a given mass a specific distance, is high in cockroaches due to their small size. The new data suggest that insects may be less economical than comparable sized vertebrates.

**Key Word Index:** Cockroach, running, oxygen consumption, energy, locomotion, *Gromphadorhina chopardi*, *Blaberus discoidalis*, *Eublaberus posticus*, *Byrsotria fumagata*, *Periplaneta americana*

### INTRODUCTION

Terrestrial locomotion of vertebrates has been vigorously studied, especially in the areas of energetics, respiration and circulation. Comparable exploration of the invertebrates is conspicuously absent, except for a few cases (e.g. Jensen and Holm-Jensen, 1980; Denny, 1980; Houlihan and Innes, 1982). This is unfortunate, for invertebrates are incredibly diverse in their styles of locomotion, number of legs and type of respiratory and circulatory systems, thus offering interesting alternate solutions to the problem of pedestrian travel. Study of such “novelties” should assist the development of general principles of locomotion that cut across major taxonomic lines (Herreid and Fournier, 1981).

The metabolic response of an invertebrate under rigorously controlled exercise conditions was first investigated on a land crab, *Cardisoma guanhumi* (Herreid *et al.*, 1979). Oxygen consumption ( $\dot{V}_{O_2}$ ), carbon dioxide production ( $\dot{V}_{CO_2}$ ), ventilation and heart rate were investigated while the animals ran on a treadmill. Four other treadmill studies have been published, including three on crabs, *Cardisoma carnifex*, *Gecarinus lateralis* and *Ocypode quadricaudii* and one on cockroaches (Herreid *et al.*, 1979, 1981a, 1981b, 1983; Wood and Randall, 1981a, 1981b; Full and Herreid, 1983). The virtue of such studies is that the exercise regime can be carefully controlled by varying the speed of the treadmill while physiological parameters are monitored. Moreover, the use of such procedures allows the data to be directly compared among species and especially with the vertebrates where such methods have been used for years.

In this paper we present data on the oxygen consumption of five species of cockroaches tested over a range of speeds as they travelled on a tread-

mill. Although they only represent a fraction of the 3500 species of cockroaches and a miniscule portion of the million or so extant insects, they are among our best invertebrate runners. In previous papers, we examined the large hissing cockroach of Madagascar, *Gromphadorhina portentosa* (Herreid *et al.*, 1981a, 1981b). Now we present data on its relatives *G. chopardi*, *Blaberus discoidalis*, *Eublaberus posticus*, *Byrsotria fumagata* and *Periplaneta americana*. These species range extensively in size, flight capacity and running ability; yet they are similar enough that comparisons can be readily made without profound changes in ventilation and circulation confounding the picture.

### MATERIALS AND METHODS

#### Animals

The experimental animals were adult cockroaches obtained from laboratory colonies. Each species was raised in its separate communal cage in an environmental chamber maintained at 25°C, relative humidity 75% and given food in the form of dried puppy food and water *ad libitum*. Male cockroaches were used except for those cases mentioned in the Results Section.

#### Apparatus

The experiments were conducted in a miniature airtight respirometer enclosing an axle-driven latex treadmill belt (Herreid, 1981). The latter was powered by an external motor and controlled by a Veriac capable of controlling speed over a range of 0.8–30 cm/s. A switch was built into the system which allowed us to reverse the direction of the treadmill if the animal turned around. Inflow and outflow gas

ports permitted a constant unidirectional circulation of fresh air into the respirometer. Room air was continuously drawn through the respirometer and tubing (effective volume 125 ml) at 50 ml/min. Gas leaving the respirometer passed through a drierite filter to remove water vapour and then was drawn into one sensor cell and flow meter of an S-3A Applied Electrochemistry Oxygen Analyzer. Room air was directly passed at the same rate through a drying filter and into a second sensor cell of the analyzer; this served as a reference gas. The O<sub>2</sub> analyzer flow meters were calibrated with a bubble meter (Fisher and Porter). By measuring the difference between the percentage of O<sub>2</sub> of the room air and the gas leaving the respirometer (usually ranging from 0.020 to 0.200% O<sub>2</sub>) and by multiplying this value by the flow rate, we were able to calculate the instantaneous O<sub>2</sub> consumption ( $\dot{V}_{O_2}$ ) of the roaches corrected to conditions of STPD (see Bartholomew *et al.*, 1981, for the method). A respiratory quotient equal to 1.0 was assumed in the  $\dot{V}_{O_2}$  calculation. The fractional error in  $\dot{V}_{O_2}$  is only  $\pm 3\%$  if RQ is actually 0.85 or 1.15 (Withers, 1977).

#### Protocol

All the experiments were 110 min in duration and proceeded in the same manner: a cockroach was removed from its cage and placed within the respirometer for a period of 30 min rest while  $\dot{V}_{O_2}$  was monitored. Typically, the animal settled down rapidly and  $\dot{V}_{O_2}$  reached a low, relatively constant rate within 15 min.

Following the rest, an exercise bout of 20 min occurred. The treadmill was turned on at a specified speed while  $\dot{V}_{O_2}$  was measured continuously. Each species was usually tested at three speeds: the lowest speed chosen was the slowest velocity the animal maintained without wandering on the treadmill; the highest speed was the fastest velocity the animal could maintain for 20 min; the middle speed was approximately midway between the high and low velocities. Most animals ran well on the treadmill, except for those cases mentioned in the Results Section. Occasionally, an insect would become disoriented or agitated, flipping over or lodging against the back of the chamber; in such cases the run was aborted.

After the exercise period, the treadmill was stopped for a recovery period of 60 min or until  $\dot{V}_{O_2}$  had declined to a resting rate. Experiments were conducted at 25°C.

## RESULTS

### *Periplaneta americana*

The resting  $\dot{V}_{O_2}$  of *P. americana* was determined by calculating the average of 32 experiments from 15 males for the 15 min just prior to exercise. At this time the cockroaches were usually resting quietly on the treadmill belt with a  $\dot{V}_{O_2}$  of 0.52 ml O<sub>2</sub> · g<sup>-1</sup> h<sup>-1</sup> ± SD of 0.14 for cockroaches weighing an average of 0.73 g ± 0.08. The resting  $\dot{V}_{O_2}$  is comparable to the value of 0.36 ml O<sub>2</sub> · g<sup>-1</sup> h<sup>-1</sup> reported for *P. americana* by Polacek and Kubista (1960).

*P. americana* ran well on the treadmill. The three speeds chosen for the experiment were as follows: low speed, 0.04 km · h<sup>-1</sup> (10 animals tested); middle speed,

0.13 km · h<sup>-1</sup> (11 animals tested); high speed, 0.22 km · h<sup>-1</sup> (8 animals tested). This species can run at higher speeds, but because of technical difficulties, higher velocities were not used.

Figure 1 shows the abrupt change of  $\dot{V}_{O_2}$  once exercise was initiated. Not represented on the graph but readily apparent in our continuous records was a brief 10-s period just after the treadmill was turned on, when  $\dot{V}_{O_2}$  dropped to low levels. This was probably a startle response, when the cockroach momentarily stopped breathing. After this slight delay the  $\dot{V}_{O_2}$  increased from a resting rate to a peak reading within 1 min. The time to reach one-half of this value,  $t_{1/2}$ , was within 30 s. By the second minute of running,  $\dot{V}_{O_2}$  had decreased somewhat to a steady-state value ( $\dot{V}_{O_{2ss}}$ ), although this level was rather irregular in this species due to its tendency to lag behind then accelerate rapidly. The lag in the  $\dot{V}_{O_2}$  response of the animal is called the O<sub>2</sub> deficit (e.g. Stainsby and Barclay, 1970). Oxygen deficit is the difference between two values: (1) the actual gradual rise in  $\dot{V}_{O_2}$  which occurred as the 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. It is obvious that O<sub>2</sub> deficit is virtually absent in *Periplaneta americana*.

Recovery from exercise was very rapid. At the two lower velocities, it was complete within a minute after the treadmill stopped with the  $t_{1/2}$  time for recovery of no more than 30 s. At the highest velocity, recovery took about 1.5 min with a  $t_{1/2}$  time of 45 s. More variation was present in the "resting"  $\dot{V}_{O_2}$  readings taken after the run than before the run; this was due to some minor activity by the insects during the post-exercise period.

Figure 2 shows that the increase in  $\dot{V}_{O_{2ss}}$  was a direct linear function of the speed of locomotion ( $V$ ). The least-square's regression line based on 29 runs is  $\dot{V}_{O_{2ss}} = 0.30 + 9.83 V$ . The 95% confidence intervals for the  $Y$ -intercept and slope are  $\pm 0.62$  and  $\pm 4.17$ , respectively. Such large confidence intervals for the average data reflects the large variation among individuals, but for each given animal there was a consistent pattern of an increase in  $\dot{V}_{O_{2ss}}$  with velocity. Thus, the correlation coefficient between  $\dot{V}_{O_{2ss}}$  and velocity was  $r = 0.88$ . The  $Y$ -intercept (0.30 ml O<sub>2</sub> · g<sup>-1</sup> h<sup>-1</sup>) at zero velocity falls slightly below the average resting rate. The highest velocity tested produced a  $\dot{V}_{O_{2ss}}$  about 4.7 times higher than the resting rate.

Using the data from the experiments, we may calculate the cost of transport (Taylor *et al.*, 1970). This is the amount of O<sub>2</sub> used per g animal to travel a km. It is determined by dividing the steady-state  $\dot{V}_{O_2}$  by the velocity. As with other running animals, the cost of transport falls as velocity increases. Thus at 0.04, 0.13 and 0.22 km · h<sup>-1</sup>, the cost of transport progressively falls from 16.8 to 12.2 and then to 11.2 ml O<sub>2</sub> · g<sup>-1</sup> km<sup>-1</sup>. The cost of transport approaches a minimal value as velocity increases; Taylor *et al.* (1970) have termed this the minimal cost of transport ( $M_{run}$ ). This value is equivalent to the slope of the line relating  $\dot{V}_{O_{2ss}}$  to velocity seen in Fig. 2. For an average 0.73 g *P. americana* the minimal cost of transport is 9.83 ml O<sub>2</sub> · g<sup>-1</sup> km<sup>-1</sup>.

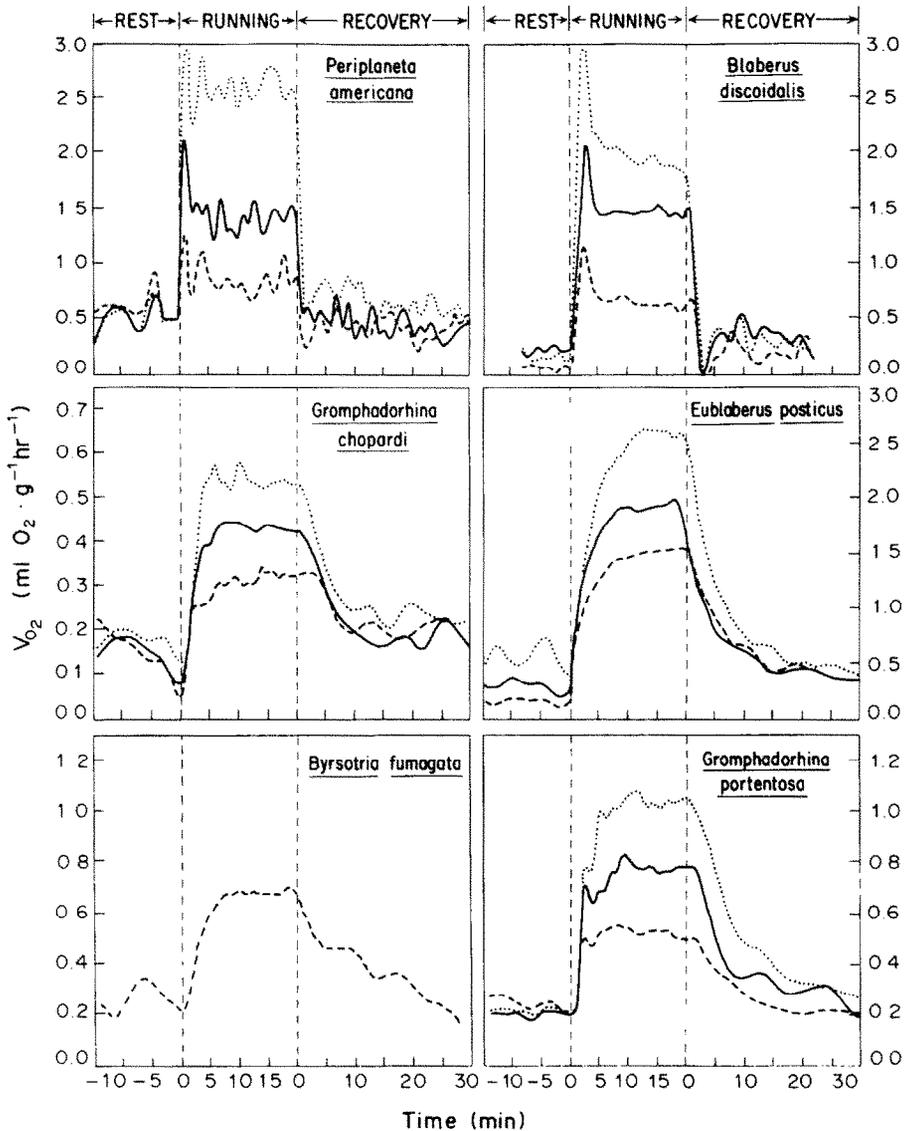


Fig. 1. Oxygen consumption ( $\dot{V}_{O_2}$ ) of 6 species of cockroaches running on a treadmill. The data have been fit by curves using the cubic spline method of interpolation. We used a programme Disk Cs-4804 with an Apple II Plus Computer for this procedure that fits a cubic polynomial through each four successive points to produce a moving average, (Warme, 1981). The upper, middle and lower curves on each graph represent the average  $\dot{V}_{O_2}$  for insects running at high, middle and low speeds, respectively. Data for *Byrsotria fumagata* were only available for a slow run. Data for *Blaberus discoidalis* early in the rest period and late in the recovery period were inadvertently not collected even though the protocol was the same as for other insects. Data for *Gromphadorhina portentosa* are from Herreid *et al.*, 1981b. Note that the ordinate axes differ among the species.

#### *Blaberus discoidalis*

The resting  $\dot{V}_{O_2}$  of *B. discoidalis* was obtained by averaging 16 experiments for 8 males, 15 min prior to exercise. The average  $\dot{V}_{O_2}$  at rest was  $0.17 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  ( $\pm 0.09$ ) for cockroaches weighing an average of  $4.08 \pm 0.76 \text{ g}$ . *B. discoidalis* ran exceptionally well on the treadmill at speeds  $0.10 \text{ km} \cdot \text{h}^{-1}$  (3 animals),  $0.26 \text{ km} \cdot \text{h}^{-1}$  (5 animals) and  $0.48 \text{ km} \cdot \text{h}^{-1}$  (8 animals).

Figure 1 shows a very rapid rise of  $\dot{V}_{O_2}$  once exercise began. Peak  $\dot{V}_{O_2}$  were reached 2.5 to 3 min after the treadmill was turned on with  $t_{1/2}$  times of 60–90 s. At all three speeds there was a striking

overshoot of the steady-state value. It took 4–8 min for  $\dot{V}_{O_2}$  to decline to a clear  $\dot{V}_{O_{2ss}}$ . Peak readings were 1.4–1.6 times higher than the steady-state values which developed shortly thereafter.

Complete recovery after exercise took about 2–2.5 min with  $t_{1/2}$  off responses of about 1 to 2 min. Note an apparent undershoot of  $\dot{V}_{O_2}$  at 6 min with a return to normal resting values a few minutes later (Fig. 1). The reasons for such patterns are obscure.

Figure 2 shows that  $\dot{V}_{O_{2ss}}$  in *B. discoidalis* depends upon the velocity of locomotion with a least square's regression line (16 points) of  $\dot{V}_{O_{2ss}} = 0.52 + 3.1 V$ . The 95% confidence intervals for the  $Y$ -intercept and

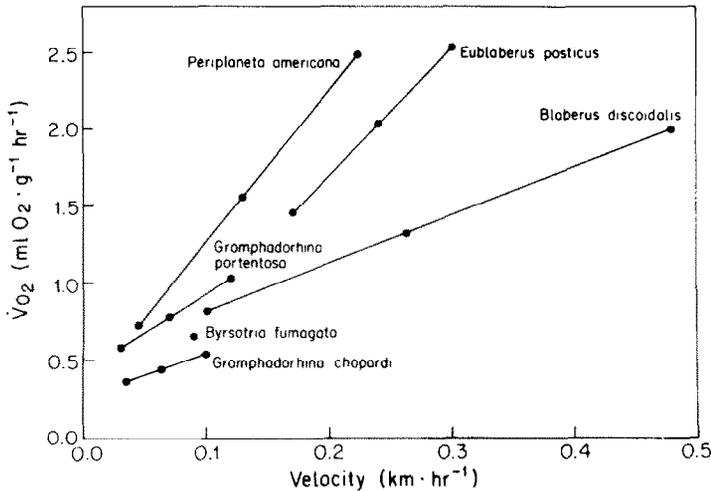


Fig. 2. Best fit regression lines representing the steady-state oxygen consumption ( $\dot{V}_{O_{2ss}}$ ) of cockroaches running at different velocities. Confidence intervals and equations for these lines are represented within the text. The points on the graph show the velocities where the data were obtained. Data for *Gromphadorhina portentosa* are from Herreid *et al.*, 1981b.

slope are  $\pm 0.45$  and  $\pm 1.38$ . The correlation coefficient relating  $\dot{V}_{O_{2ss}}$  to velocity is  $r = 0.79$ . The  $Y$ -intercept value  $0.52 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  is 3.1 times higher than the actual resting  $\dot{V}_{O_2}$  ( $t = 8.3$ ,  $P < 0.01$ ). The highest velocity runs produced a  $\dot{V}_{O_{2ss}}$  11.8 times higher than rest but the peak rate was 17.6 times higher.

Calculating the cost of transport we find at increasing speeds of 0.10, 0.26 and  $0.48 \text{ km} \cdot \text{h}^{-1}$  there is a progressive decrease in  $\dot{V}_{O_2}$  from 8.3, 5.1, and  $4.2 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{km}^{-1}$  (Fig. 3). The minimal cost of transport is  $3.1 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{km}^{-1}$  for an average *B. discoidalis* weighing  $4.18 \text{ g}$ .

#### *Gromphadorhina chopardi*

The resting  $\dot{V}_{O_2}$  of *G. chopardi* was determined by averaging the data from 22 experiments, over 15 min prior to exercise. We noted a resting rate of  $0.14 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \pm 0.05 \text{ ml}$  for male cockroaches weighing an average of  $3.40 \text{ g}$ .

*G. chopardi* ran well on the treadmill. The speeds chosen for the experiment were as follows: low speed,  $0.04 \text{ km} \cdot \text{h}^{-1}$  (6 runs); middle speed,  $0.06 \text{ km} \cdot \text{h}^{-1}$  (5 runs);  $0.10 \text{ km} \cdot \text{h}^{-1}$  (6 runs). Figure 1 shows a rapid rise in  $\dot{V}_{O_2}$  once exercise began. However, there was a momentary decrease in  $\dot{V}_{O_2}$  before the rise began. The  $\dot{V}_{O_{2ss}}$  was reached within about 4–6 min. The  $t_{1/2}$

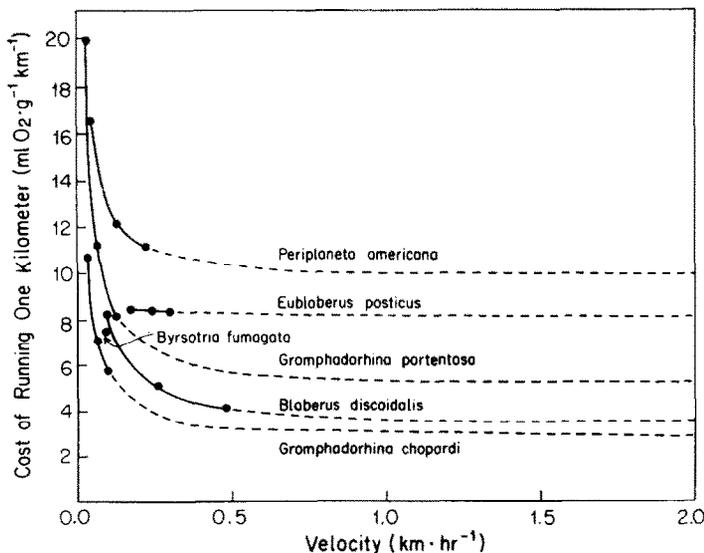


Fig. 3. Cost of transport for cockroaches running at different velocities. The curves are generated from the regression lines relating  $\dot{V}_{O_{2ss}}$  to velocity. The points show the velocities tested. Data for *Gromphadorhina portentosa* are from Herreid *et al.*, 1981b.

on-response was 2–3 min. Consequently, a modest  $O_2$  deficit was present.

Recovery to  $\dot{V}_{O_2}$  values near those of rest took several minutes and true resting rates were never established because of the general activity of the insects during the post-exercise period. But judging from the rate of decline it seems safe to conclude that the  $t_{1/2}$  off-response would be at least 4–6 min, with the longest time being measured at the fastest velocities.

Figure 2 shows that the increase in  $\dot{V}_{O_{2ss}}$  with velocity was directly related to the speed of locomotion. The least square's regression line (17 points) is  $\dot{V}_{O_{2ss}} = 0.28 + 2.72 V$ . The 95% confidence intervals for the  $Y$ -intercept and slope are  $\pm 0.09$  and  $\pm 1.29$ . The correlation coefficient for  $\dot{V}_{O_{2ss}}$  vs velocity was  $r = 0.76$ . Note that the  $Y$ -intercept,  $0.28 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ h}^{-1}$ , is 2 times higher than the actual resting rate  $\dot{V}_{O_2}$  ( $t = 9.3$ ,  $P < 0.01$ ). The highest velocity runs produced a  $\dot{V}_{O_{2ss}}$  3.9 higher than rest.

Calculating the cost of transport we find at increasing speeds of 0.04, 0.06 and  $0.10 \text{ km} \cdot \text{h}^{-1}$  we see a steady decrease of  $O_2$  consumption from 10.7 to 7.1 to  $5.5 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ km}^{-1}$  (Fig. 3). The minimal cost of transport is  $2.72 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ km}^{-1}$  for an average *G. chopardi* of 3.4 g.

#### *Eublaberus posticus*

The resting  $\dot{V}_{O_2}$  of *E. posticus* was calculated by averaging 9 experiments for 3 males 15 min prior to exercise. We noted a resting rate of  $0.34 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ h}^{-1} \pm 0.25$  for cockroaches weighing an average of  $2.20 \text{ g} \pm 0.32$ .

Three runs were obtained for *E. posticus* at each of the following speeds 0.17, 0.24 and  $0.30 \text{ km} \cdot \text{h}^{-1}$ . Figure 1 shows a rather slow rise in  $\dot{V}_{O_2}$  at all velocities once exercise began. As a result, a significant  $O_2$  deficit can be seen. The delay in the on-response is emphasized by looking at the time required to reach  $\dot{V}_{O_{2ss}}$ : at slow velocity, 6 min was required; at middle velocity, 8 min; at fast velocity, 12 min. These times indicate that the  $O_2$  deficit was greater at high velocities. The  $t_{1/2}$  on-values varied from 2 to 2.5 min.

The recovery from exercise was fairly rapid:  $t_{1/2}$  off-values of 3 min were recorded at all velocities. Complete recovery was accomplished within 10–15 min of the exercise bout.

The  $\dot{V}_{O_{2ss}}$  was a function of the running velocity (Fig. 2). When  $\dot{V}_{O_{2ss}}$  is plotted against velocity, the best fit least-square's regression line (9 points) through the data is  $\dot{V}_{O_{2ss}} = 0.05 + 8.29 V$ . The 95% confidence intervals for the  $Y$ -intercept and slope are  $\pm 1.12$  and  $\pm 4.62$ . The coefficient of correlation  $\dot{V}_{O_{2ss}}$  vs velocity was  $r = 0.75$ . The  $Y$ -intercept value of  $0.05 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ h}^{-1}$  appears much lower than the actual resting rate, but the difference is not significant ( $t = 1.59$ ,  $P > 0.05$ ). The highest velocity runs produced a  $\dot{V}_{O_{2ss}}$  of 7.5 times higher than rest.

Calculating the cost of transport, we find at increasing speeds of 0.17, 0.24 and  $0.30 \text{ km} \cdot \text{h}^{-1}$  there is a slight progressive decrease from 8.60, to 8.51, to  $8.46 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ km}^{-1}$ . The minimal cost of transport is  $8.29 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ km}^{-1}$  for an average *Eublaberus* weighing 2.2 g.

#### *Byrsotria fumagata*

This species was a poor runner in our treadmill respirometer. The males would turn sideways in the chamber or wedge themselves in the corner or in back of the treadmill. They would also cling to the walls of the respirometer, frequently fall on their backs, struggle to right themselves and produce erratic records. In spite of numerous attempts to measure  $\dot{V}_{O_2}$  no successful runs were obtained for males.

Female *B. fumagata* were more consistent performers on the treadmill. The insects would run well at the slow velocities but could not maintain the pace for more than 10 min. After this point, they lagged behind, then upon touching the rear of the chamber, they accelerated rapidly to the front of the treadmill. This was repeated continuously; this irregular sprinting caused a rise in the  $\dot{V}_{O_2}$  over the steady-state values in the early part of the run. After numerous tries we were able to complete only two successful experiments with females at a slow velocity of  $0.09 \text{ km} \cdot \text{h}^{-1}$ ; average mass  $4.95 \text{ g} \pm 0.62 \text{ g}$ .

Figure 1 shows a fairly rapid rise in  $\dot{V}_{O_2}$  once exercise starts from a resting rate of  $0.20 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ h}^{-1}$  to a steady-state of  $0.67 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ h}^{-1}$ . The  $t_{1/2}$  on-response was 2.5 min with steady-state reached in about 7 min, thus a modest  $O_2$  deficit occurred. The  $\dot{V}_{O_{2ss}}$  was 3.4 times higher than the rest.

Recovery was quite slow in *B. fumagata* and not complete until 30 min after rest. However, this was because of periodic activity. One can get a true idea of the recovery potential by noting the rapid fall of  $\dot{V}_{O_2}$  in the first few minutes of recovery; we estimate the  $t_{1/2}$  to be about 6 min.

The cost of transport for the single speed of  $0.09 \text{ km}^{-1}$  was  $7.4 \text{ ml } O_2 \cdot \text{g}^{-1} \text{ km}^{-1}$ .

## DISCUSSION

Consistent with general opinion, cockroaches run well. There are species differences, however. Subjectively, *Blaberus discoidalis* and *Periplaneta americana* were the best runners in our treadmill respirometer. *Byrsotria fumagata* was the worst performer and *Eublaberus posticus* and *Gromphodrhina chopardi* were average. These judgements were based on the ease with which the species adapted to the treadmill chamber, the effort that was required to keep them active and most importantly, the consistency of their running performance.

#### Oxygen consumption response to locomotion

All cockroaches showed the same general response to exercise (Fig. 1).  $\dot{V}_{O_2}$  rose rapidly and reached a steady-state. This persisted until the exercise bout was finished and recovery was relatively rapid thereafter. This pattern was one we identified earlier in the Madagascar cockroach *Gromphodrhina portentosa* (Herreid *et al.*, 1981a and b and shown in Fig. 1 for comparative purposes) and the ghost crab *Ocypode quadricaudii* (Full and Herreid, 1983). Also the pattern is the classical aerobic response displayed by higher vertebrates during running. It is in distinct contrast to the  $\dot{V}_{O_2}$  pattern shown by several running

land crabs (e.g. *Cardisoma guanhumii*, *Gecarcinus lateralis*; Herreid *et al.*, 1979, 1983); these species never reach a  $\dot{V}_{O_{2ss}}$  even during modest exercise.

The general aerobic nature of the cockroach running is underscored by the  $t_{1/2}$  on-response values. All cockroaches reached  $t_{1/2}$  on in less than 3 min quite comparable to typical higher vertebrates. In fact, the fastest times, 30 s or less, as demonstrated by *P. americana* may be superior to that of humans (c.f. Cerretelli *et al.*, 1979).

The lag in  $\dot{V}_{O_2}$  from the start of exercise until a  $\dot{V}_{O_2}$  is reached is said to create an  $O_2$  deficit (Stainsby and Barclay, 1970). During this period there are three sources of energy to compensate for the shortfall of oxygen: (1)  $O_2$  stored in the tissue fluids (probably of minor importance in insects); (2) high energy phosphate stores such as arginine phosphate; and (3) anaerobic metabolism. The relative importance of the latter sources of energy in cockroaches is not known; however, if vertebrates are a clue, the phosphagen reserves are probably used first, followed by anaerobic input (Karlsson, 1979). In addition to the above factors, the magnitude of the  $O_2$  deficit depends upon the efficiency of the  $O_2$  conductance system, and the sensitivity, position and responsiveness of the sensory systems monitoring tissue gases and acid-base balance. In general, if the  $O_2$  conductance system is rapid with sensitive receptors, we might expect the  $O_2$  deficit to be small. Such is the case for both higher vertebrates and insects. The latter depend upon a tracheal system whereby air is delivered directly to the muscle cells without intervention of a circulatory system. This system is so effective that it readily supplies flight muscle, the most metabolically active tissue known (e.g. Weis-Fogh, 1964, 1967).

In contrast to insects, many crabs which rely on chitin-covered gills and an open circulatory system appear to have a comparatively less effective  $O_2$  conductance system. The response of land crabs *G. guanhumii* and *G. lateralis* seems to support this argument: they never reach  $\dot{V}_{O_{2ss}}$  during 10–20 min of modest exercise (Herreid *et al.*, 1979, 1983). Not all crabs respond with so sluggish an aerobic pattern. The pedestrian ghost crab, *Ocypode quadricaudii*, has rapid on-response and is highly aerobic (Full and Herreid, 1983).

The differences between resting and running  $\dot{V}_{O_2}$  varies greatly among cockroaches. The difference is highlighted by the factorial scope values ranging from 3.4 to 11.8. We must stress several caveats concerning such a comparison, however. (1) The low value for *Byrsotria* is not a maximum because the behaviour of this cockroach was so erratic that it was impossible to test at the higher speeds. (2) *Periplaneta* values are also undoubtedly low. Our more recent work indicates we did not test this species at the highest sustainable velocities in this experiment. (3) Finally, it should be emphasized that any measurement of factorial scope is clearly dependent upon the conditions set up to measure resting and active  $\dot{V}_{O_2}$ . Lower resting  $\dot{V}_{O_2}$  might have been measured if a longer pre-trial rest period had been given. Similarly, higher active  $\dot{V}_{O_2}$  would have resulted if we had used data from brief high intensity sprints or if we had used peak  $\dot{V}_{O_2}$  measurements such as that seen for *B. discoidalis* (Fig. 1) which produced a factorial

scope of 17.6. Consequently, one should not get unduly enamoured with data of this sort unless they are collected under identical conditions. For direct comparison with cockroaches only one study is available. The ghost crab, *O. quadricaudii* produced a steady-state  $\dot{V}_{O_2}$  factorial scope of 8 but a maximum of 12, (Full and Herreid, 1983). For less aerobic crabs which do not reach  $\dot{V}_{O_{2ss}}$  we have found maximal scope values of 5 and 3.5 for *C. guanhumii* and *G. lateralis* (Herreid *et al.*, 1979, 1982). Also using different measurement standards: mammals sustain exercise for many minutes at levels around 10 times their resting rate (Taylor *et al.*, 1980). Running ants may have metabolic rates 7 times higher than at rest (Jensen and Holm-Jensen, 1980). Much higher values are reported for flying insects with  $\dot{V}_{O_2}$  factorial scopes varying from 25 to 150 (Polacek and Kubista, 1960). Such scopes are both a reflection of the enormous metabolic capacity of flight muscle but are also due to a rise in body temperature (e.g. Heinrich, 1974). Clearly running cockroaches do not develop such scopes nor have we measured elevated body temperatures. However, Bartholomew and Casey (1977) measured the  $\dot{V}_{O_2}$  of running beetles up to 113 times rest but a rise in body temperature produced by a contraction of the flight muscles was involved.

#### Recovery from locomotion

As judged by  $O_2$  consumption, recovery from exercise was rapid in all species of cockroaches. The  $t_{1/2}$  off-responses at the fastest speeds varied from 1 to 6 min and complete recovery ranged from 2 to 15 min. The data are very similar to mammalian values: humans and dogs have  $t_{1/2}$  off times under 1 min, but kangaroo rats respond slowly,  $t_{1/2}$  around 20 min. (Piiper and Spiller, 1970; Yousef *et al.*, 1970; Cerretelli *et al.*, 1979; Hagberg *et al.*, 1980). The slowest recovery times for cockroaches was *B. fumigata* and *G. portentosa* (Herreid *et al.*, 1981) which were comparable to rats and lizards (Brooks *et al.*, 1971b, Moberly, 1968; Dmi'el and Rappoport, 1976; Gleeson, 1980). Thus, we can conclude that cockroaches are unquestionably aerobic in their recovery characteristics and the best of these (*P. americana* and *B. discoidalis*) certainly rival or exceed the performance of the best vertebrate runners and *Drosophila* recovering from flight (Chadwick and Gilmour, 1940). Cockroaches are definitely superior to crabs such as *C. guanhumii* and *G. lateralis* which have recovery periods that last for periods over an hour (Herreid *et al.*, 1979, 1983).

The  $\dot{V}_{O_2}$  that is used during recovery above the resting rate has been called " $O_2$  debt" by vertebrate physiologists. Investigators have proposed that this excess  $O_2$  was used to repay the shortfall in  $O_2$  that occurred in the  $O_2$  deficit period at the beginning of exercise. That is, high energy phosphates must be regenerated,  $O_2$  stores replenished and lactic acid recycled back into glycogen. This traditional view has been seriously challenged (Brooks *et al.*, 1971a, 1971b, 1973; Segal and Brooks, 1979; Hagberg *et al.*, 1980), and it is now evident that other factors are undoubtedly involved: (1) tissue repair, (2) temperature effects, (3) ion redistribution, and (4) costs of increased circulation and respiration that persist after exercise. One clue to the presence of such factors

is the fact that in many species (such as the case in cockroaches), "O<sub>2</sub> debt" is considerably larger than O<sub>2</sub> deficit. Moreover, it has become clear that lactic acid generated during strenuous exercise is not necessarily resynthesized into glycogen but may be directly oxidized (Brooks and Gaesser, 1980).

In light of the confusion in the literature and sheer ignorance about invertebrate metabolism, we are not in a position to evaluate the cause of O<sub>2</sub> debt in cockroaches. Nevertheless, it is relevant to note that lactic acid is produced in *Periplaneta americana* and other arthropods both in hypoxia and exercise (Davis and Slater, 1978; Sactor, 1974; Phillips *et al.*, 1977). But no direct link with O<sub>2</sub> is evident as yet.

#### $\dot{V}_{O_{2s}}$ vs velocity

$\dot{V}_{O_{2s}}$  increases linearly with the velocity of locomotion in all cockroaches (Fig. 2). This relationship was identified earlier in the roach *G. portentosa* (Herreid *et al.*, 1981) which is shown in Fig. 2 for comparison and the ghost crab *Ocyropsis guadichaudii* (Full and Herreid, 1983) as well as most pedestrian vertebrates (Segre and Hart, 1967; Yousef *et al.*, 1970; Taylor *et al.*, 1977). Important exceptions exist among walking humans that show a curvilinear response (e.g. Margaria *et al.*, 1963) and kangaroos that show no increase or an actual decrease with velocity (Dawson and Taylor, 1973; Taylor, 1977). The possible reasons for such patterns are discussed by Taylor (1977) and Cavagna, Heglund and Taylor (1977).

#### Y-intercept Problem

When the lines representing the equations for  $\dot{V}_{O_{2s}}$  vs velocity are extrapolated back to zero velocity, we notice that the predicted  $\dot{V}_{O_2}$  at rest are well above the actual resting rate for some species. Thus, the Y-intercept for *G. chopardi* is 2 times higher and for *B. discoidalis* 3.1 times higher than rest. Elevated Y-intercepts are common although not invariable among vertebrates (Taylor *et al.*, 1970; Taylor, 1977) and we noted it previously in the cockroach *G. portentosa* (Herreid *et al.*, 1981). However, the elevated Y-intercept is not present in two species of cockroach, *P. americana* and *E. posticus*. The deviation of the Y-intercept from resting rates is correlated ( $r = 0.82$ ) with body mass ( $W$ ) in cockroaches; i.e. animals with the largest body size tended to have the greatest elevation of the Y-intercept relative to their resting O<sub>2</sub> consumption:  $Y\text{-intercept}/rest \dot{V}_{O_2} = 0.58 W - 0.17$ . The reason for the relationship is obscure and may be spurious; such a correlation is not present in mammals (Taylor *et al.*, 1970).

Schmidt-Nielsen (1972) proposed that the elevated Y-intercept might be due to a "postural cost" of locomotion. Unfortunately this term and concept have been uncritically adopted by several investigators whenever an elevated Y-intercept is found. Indeed, the situation in the literature has become so strained that even investigators of fish locomotion refer to an elevated Y-intercept as a "postural effect" (e.g., Priede and Holliday, 1980; Duthie, 1982). This terminology is totally inappropriate for there are multiple reasons why an Y-intercept might be elevated (Herreid, 1981). For

example, any experimental stress associated with treadmill running clearly could elevate the regression line above the predicted resting rates. Also, irregular walking patterns at slow speeds, a common phenomenon for all animals, including cockroaches, will elevate  $\dot{V}_{O_2}$  over the expected levels and thus deflect the regression line upward. Or as a final example, if anaerobic metabolism plays an increased role in powering fast running velocities,  $\dot{V}_{O_2}$  at the high end of the scale will be lower than expected, again producing an elevated Y-intercept. Since there may be multiple reasons for the elevated Y-intercept and no data exists to evaluate any argument at this time, we strongly urge abandoning the explanatory term "the postural cost of locomotion" unless there is evidence to support the contention. Instead, simply label the phenomenon with the descriptive term, "the elevated Y-intercept".

#### Cost of transport

We can calculate the oxygen that is used by an animal to travel a given distance. This cost of transport may be compared among species by adopting the common units ml O<sub>2</sub> · g<sup>-1</sup> · km<sup>-1</sup>, obtained by dividing the  $\dot{V}_{O_{2s}}$  by the velocity of travel. As pointed out by Taylor *et al.* (1970, 1982) first for vertebrates, the cost of transport drops rapidly with increasing velocity. Such is the case for most of our cockroaches (Fig. 3) an exception being *Eublaberus* with only slight changes. A dramatic decrease in the cost of transport with velocity was also experienced by the roach *G. portentosa* (Herreid *et al.*, 1981b).

The fact that the cost of transport declines with velocity is solely a function of the Y-intercept value. That is, in animals with a Y-intercept of near zero such as seen with *Eublaberus* ( $\dot{V}_{O_{2s}} = 0.05 + 8.29 V$ ), there is virtually no change in the cost of transport with velocity. For animals with large Y-intercepts values such as *Periplaneta* ( $\dot{V}_{O_{2s}} = 0.30 + 9.83 V$ ), or *Blaberus discoidalis* ( $\dot{V}_{O_{2s}} = 0.52 + 3.1 V$ ) the decline in the cost of transport with velocity is striking (Fig. 3). Thus, shifts in the cost of transport over a velocity range can only occur if the Y-intercept is altered; this means that any factor raising the resting  $\dot{V}_{O_2}$  will increase the steepness in the cost vs velocity curve. For instance, animals with small body size usually have high resting  $\dot{V}_{O_2}$  per gram and high Y-intercepts and so it is not surprising that small mammals have more dramatic shifts in cost with velocity than do large mammals (Taylor *et al.*, 1970, 1982). Also changes in temperature would raise the resting  $\dot{V}_{O_2}$  and Y-intercept and consequently produce a more profound decrease in the cost of transport with velocity. Data on *G. portentosa* (Herreid *et al.*, 1981) at three temperatures support this contention as do the results on lizards (John-Alder and Bennett, 1981). Finally, we should note that any of the factors that might be responsible for producing an elevated Y-intercept (Herreid, 1981) will also be responsible for a steeper cost vs velocity curve.

All cost of transport curves approach some minimum level at the highest velocities. This minimal cost of transport ( $M_{\text{min}}$ ) is equivalent to the slope of the  $\dot{V}_{O_{2s}}$  vs velocity line (Taylor *et al.*, 1970). This value is useful because it allows investigators to compare animals of different size, running velocities and stan-

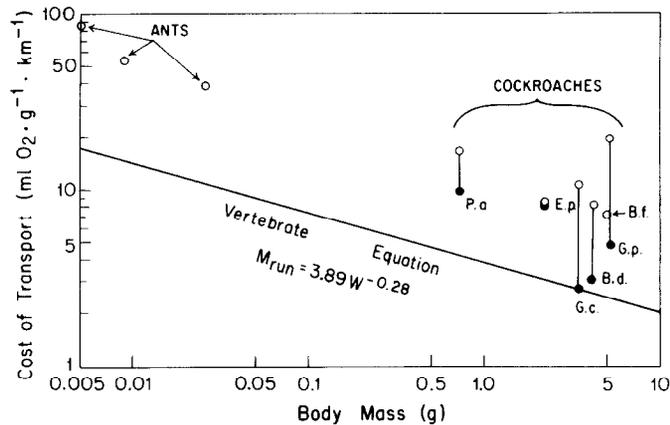


Fig. 4. Minimal cost of transport for running insects of different body mass. The line represents the least squares regression line for birds and mammals (Fedak and Seeherman, 1979). The solid circles represent cockroach species with sufficient data to calculate  $M_{run}$ . The open circles used for cockroaches are cost of transport data for running at the slowest velocities. Data for 3 species of ants are from Jensen and Holm-Jensen, 1980; they do not represent  $M_{run}$  values. Data for *Gromphadorhina portentosa* are from Herreid *et al.*, 1981b.

standard metabolic rates. As we pointed out above, some animals (those with low resting  $\dot{V}_{O_2}$  and low  $Y$ -intercept values) have actual costs of transport which lie close to  $M_{run}$ , while others never approach the theoretical minimum. In mammals, large species are an example of the former and small species are examples of the latter (Taylor *et al.*, 1970). In cockroaches the size relationship is not clearly present; but *Eublaberus* is an example of a species with the actual cost lying near  $M_{run}$  whereas in *G. chopardi* the actual cost at its fastest velocity is still about twice the  $M_{run}$  value. In fact *G. chopardi* would have to run four times its maximal sustainable velocity in order to approach  $M_{run}$ .

The minimal cost of transport varies inversely with the body mass in mammals, birds and reptiles (Taylor *et al.*, 1970, 1982; Fedak and Seeherman, 1979). Cost of transport values for ants and the cockroach *G. portentosa* were sufficiently close to this line for Jensen and Holm-Jensen (1980) and Herreid *et al.*, 1981 to conclude that these insects seemed to fit on the same regression line as pedestrian vertebrates. Our new data on cockroaches does not strongly support that contention (Fig. 4). Note that 8 out of 9 insects now tested show cost of transport measurements that lie above the vertebrate line. It should be emphasized that only 5 species out of 9 are represented by  $M_{run}$  values; the other 4 species (ants and the cockroach *Byrsotria*) are represented by points above the  $M_{run}$  because insufficient data were collected to develop a  $\dot{V}_{O_{2s}}$  vs velocity equation. Therefore, actual  $M_{run}$  values would be lower than these cost values. Nevertheless, it begins to appear that insects may have minimal cost of transport values that are as much as twice those of pedestrian mammals, birds and reptiles.

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