SHORT COMMUNICATION

VENTILATION AND OXYGEN CONSUMPTION DURING REST AND LOCOMOTION IN A TROPICAL COCKROACH, *BLABERUS GIGANTEUS*

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The importance of the autoventilation associated with wing movements to gas exchange in the tracheal system of insects is well established (Weis-Fogh, 1967), and data are available on the relative effectiveness of autoventilation and abdominal pumping in ventilatory exchange (Bartholomew & Barnhart, 1984). However, only preliminary information relating ventilatory behaviour and oxygen consumption during terrestrial locomotion have been published (Bartholomew, Lighton & Louw, 1985; Lighton, 1985).

Published information on the minimum energy cost of walking and running in insects exists for five species of cockroaches (Herreid, Full & Prawel, 1981; Herreid, Prawel & Full, 1981; Herreid & Full, 1984) and six species of flightless beetles (Bartholomew *et al.* 1985; Lighton, 1985). Clearly, more data are needed before the relationship between mass and cost of transport in insects can be evaluated.

Our studies took place during July and August, 1984 at the Barro Colorado Island station of the Smithsonian Tropical Research Institute in the Republic of Panama. Adult *Blaberus giganteus* (L.), mean mass 4·33 g, were captured at lights and housed communally in a windowless container measuring $70 \times 50 \times 50$ cm. Water and food (rolled oats, cheese and fruit) were available in excess. All measurements were made at night at 25–27 °C. Temperatures were measured with copper-constantan thermocouples connected to Bailey Bat thermometers. Thoracic temperature (T_{th}) was measured with a 40-gauge thermocouple inserted dorsolaterally into the flight muscles to a depth of about 2 mm and sealed in place with wax.

Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured with an Applied Electro-chemistry S3-A two-channel oxygen analyser using a flow-through system. Airflows were measured with flow meters calibrated against a Brooks mass flow meter. The respirometer was a bottomless box of Lucite (inside dimensions,

55 mm wide, 99 mm long and 35 mm high) to which a Tygon tube for the excurrent airstream was connected. This chamber was enclosed in a second bottomless Lucite box (153 mm wide, 243 mm long and 107 mm deep) to which a Tygon tube for the incurrent airstream was connected. The boxes rested directly on the belt of a treadmill. The outer chamber was continuously flushed with dry outside air. Air was pumped from the inner chamber at $80 \, ml \, min^{-1}$, which was sufficient to prevent a backflow of air even at the highest treadmill speeds. Of the excurrent air $20 \, ml \, min^{-1}$ was pulled through the oxygen sensor after being dried and scrubbed of CO_2. A parallel system without a respirometer chamber was used for baseline calibration.

The rate of travel ($0.02-0.4 \, m \, s^{-1}$) of the treadmill belt was controlled by an electric motor equipped with a stepless speed control. One treadmill roller was coupled to a small electric motor which functioned as a generator-tachometer.

The voltage outputs for thoracic and ambient temperatures, belt speed and the difference between the concentrations of oxygen in the two airstreams were fed to the A/D converter of an Acorn BBC computer and displayed graphically in real time on a CRT monitor. Inputs of each of the four channels were samples at intervals of 2–6 s, depending on the time resolution required (Lighton, 1985). Data files of the oxygen measurements were converted to instantaneous STP values using the procedures described by Bartholomew, Vleck & Vleck (1981).

Pre-running. When the cockroaches were placed in the respirometer chamber with the belt stationary, they usually groomed themselves vigorously for 30–45 s, then remained motionless, but alert. The mean of the lowest sustained values of oxygen consumption of five motionless individuals (mean mass 4.33 ± 0.81 g) was $0.160 \, ml \, O_2 \, g^{-1} \, h^{-1}$ (± 0.02 S.D., $N = 5$).

The fluctuations in instantaneous $\dot{V}_{O_2}$, both when the animals were motionless (Fig. 1A) and during sustained locomotor activity (Fig. 1B), indicate that ventilation was intermittent in both situations. Each ventilatory event consisted of a bout of abdominal pumping. Periods of apnoea, corresponding to an absence of pumping and presumably to periods of spiracular closure, were particularly conspicuous while the insects were motionless. The ventilatory events of motionless animals had a mean period of 51.1 s. The ventilatory discontinuities caused marked fluctions in instantaneous $\dot{V}_{O_2}$ which could be quantified by the coefficient of variation (CV = S.D. expressed as a percentage of the mean). The CV of 22 measurements of the $\dot{V}_{O_2}$ of five resting animals was 81.4 %. The CV of readings from the respirometer without an animal in it at an imposed baseline equal to the lowest cockroach $\dot{V}_{O_2}$ measured was less than 20 %.

Running. When the treadmill was started the cockroaches ran synchronously with the tread speed, either immediately or after 5–10 s of adjustment. *B. giganteus* ran steadily at speeds up to $0.3 \, m \, s^{-1}$. Even during prolonged rapid running, thoracic temperature did not rise by more than 1–1.5 °C. (Fig. 1B).

Because instantaneous $\dot{V}_{O_2}$ fluctuated cyclically while the cockroaches were running, we have based our estimates of the energy cost of locomotion on integrations of instantaneous $\dot{V}_{O_2}$ over periods of 4–10 min (mean 6.9 ± 1.9 S.D.) of
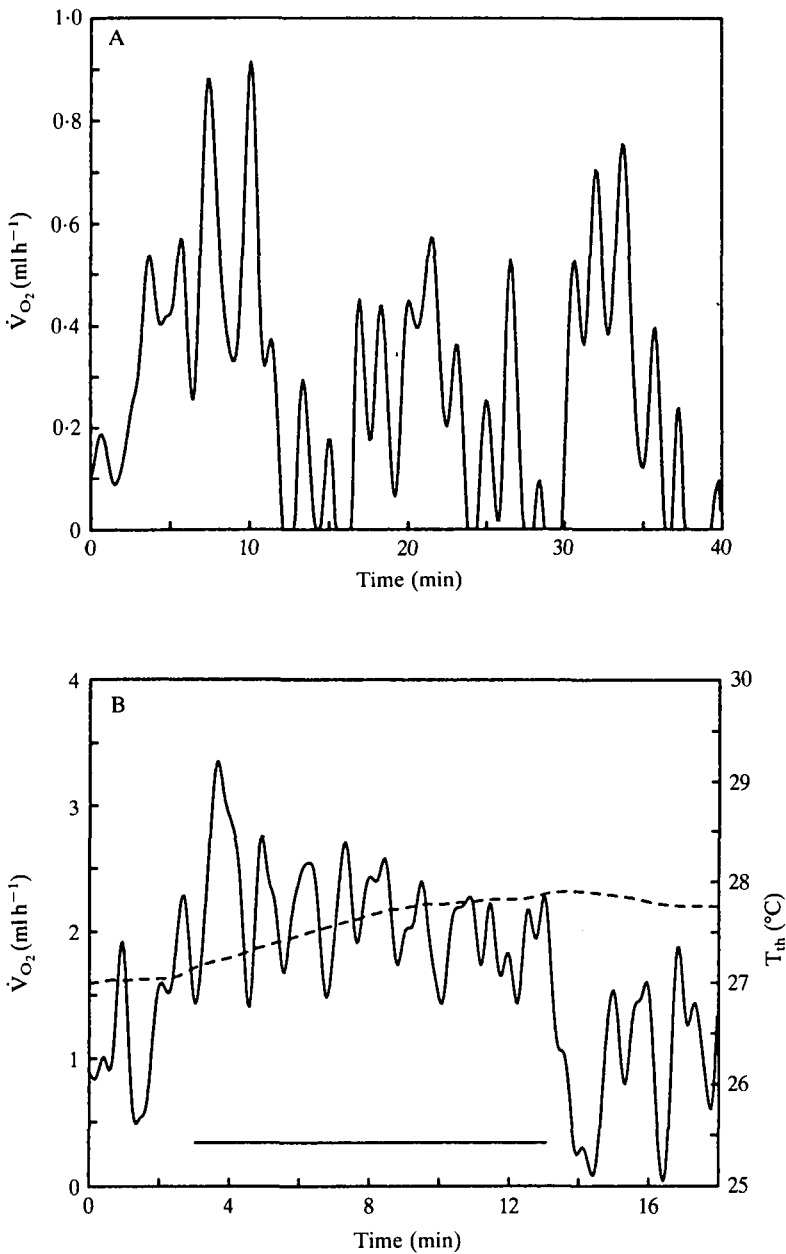
Fig. 1. (A) Instantaneous $\dot{V}_{O_2}$ in a motionless *Blaberus giganteus* (mass, 3·18 g) at an ambient temperature of 26·6 °C. (B) Instantaneous $\dot{V}_{O_2}$ (continuous line) and thoracic temperature (dashed line) in *Blaberus giganteus* (mass, 3·18 g) before, during and after running at a speed of 0·06 m s^{-1}. Horizontal line shows the duration of treadmill movement.

continuous running at a constant speed. $\dot{V}_{O_2}$ increased linearly with tread speed over the range of velocities ($0.02-0.3 \text{ m s}^{-1}$) investigated (Fig. 2); $y = 0.029 + 2.5x$, $r^2 = 0.93$, where y is in $\text{ml O}_2 \text{ g}^{-1} \text{h}^{-1}$ and x is in km h^{-1}.

Variations in $\dot{V}_{O_2}$ during running were smaller (CV = 44.8 %) than when the animals were motionless (CV = 81.4 %).

The mean periodicity of the ventilatory events of running animals ($49.7 \text{ s} \pm 9.1$ S.D., $N = 24$) was not significantly different from that of motionless animals ($51.1 \text{ s} \pm 22.1 \text{ S.D.}$, $N = 22$) but its variance was significantly less (F = 4.458; n1,n2 = 21,23; $P < 0.001$). The $\dot{V}_{O_2}$ of running animals (Fig. 2) was much higher than that of motionless animals and the volume of air moved during each ventilatory event was much greater. Our data do not allow us to rule out the possibility that leg movements autoventilate the tracheal system. In fact, the sharp decrease in the variability of $\dot{V}_{O_2}$ during rapid locomotion (Fig. 3) suggests that limb movements may enhance tracheal ventilation and that abdominal pumping accounts for a progressively smaller proportion of total ventilation as $\dot{V}_{O_2}$ increases.

Post-running. At the end of 6–10 min of running, the $\dot{V}_{O_2}$ of the motionless cockroaches ($0.16 \text{ ml g}^{-1} \text{h}^{-1}$, ± 0.02 S.D., $N = 5$) did not differ from that measured before running began, but the CV of post-running $\dot{V}_{O_2}$ (94.0) was double that of the running $\dot{V}_{O_2}$ (44.9). Ventilatory rates were essentially the same before, during and after running.

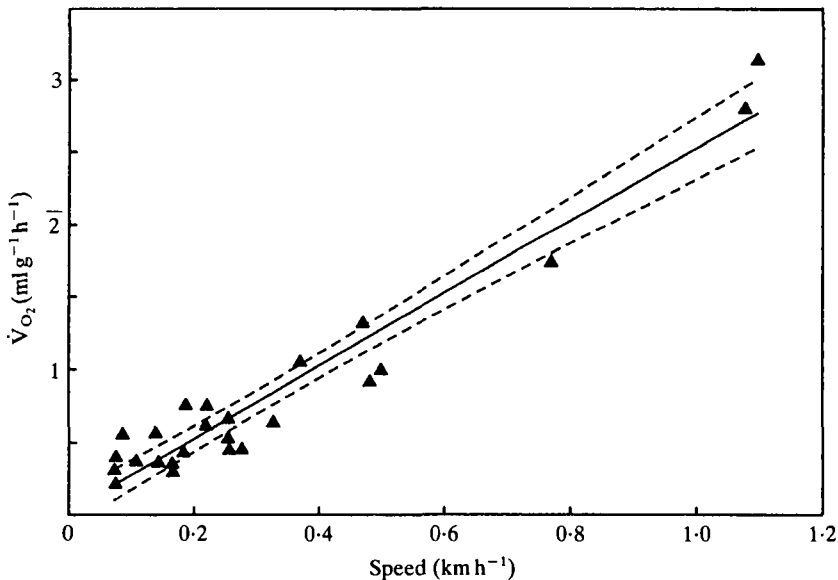The intermittent nature of ventilation in *B. giganteus*, and presumably in other

Fig. 2. Relationship between mass-specific $\dot{V}_{O_2}$ and running speed in *Blaberus giganteus*. Ambient temperature, 25–27 °C. Each point is the mean value for one animal at a given velocity. $N = 25$ measurements on five individuals. The regression line was fitted by the method of least squares. The dashed lines enclose the 95 % confidence interval for the line: $t = 17.8$, DF = 23. 95 % confidence interval for the slope, 2.213–2.797.
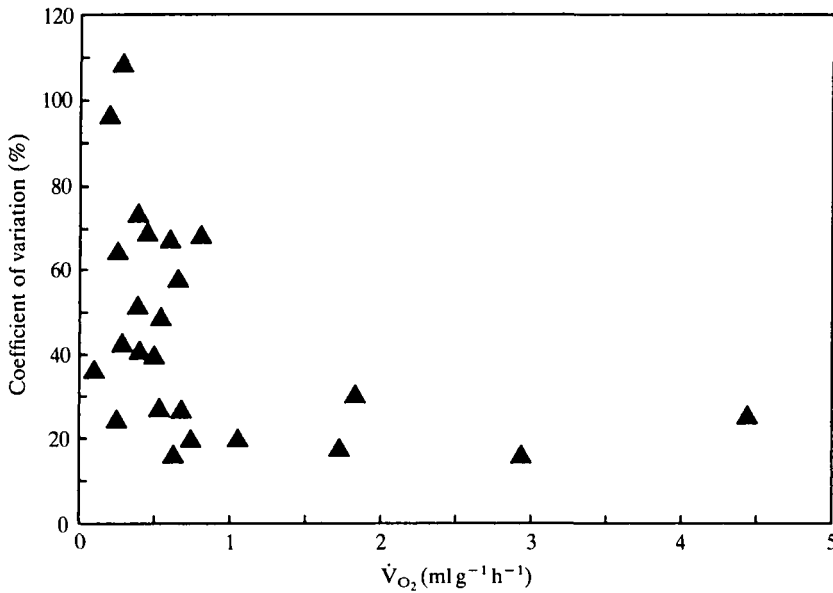
Fig. 3. The relationship of the coefficient of variation of oxygen consumption to $\dot{V}_{O_2}$ in running *Blaberus giganteus*.

cockroaches (Miller, 1981), complicates measurement of the time required for a running individual to reach some fixed percentage of its plateau value of $\dot{V}_{O_2}$ even when instantaneous rates of oxygen consumption are calculated. These ventilatory events are reliably detected only if samples are taken at intervals of less than half the characteristic period of the ventilatory cycles. Our sampling schedule met this criterion. Measurements of instantaneous $\dot{V}_{O_2}$ based on sampling intervals of 2 and 2·5 s indicate that $\dot{V}_{O_2}$ in *B. giganteus* is strongly oscillatory, increases rapidly as soon as the insect begins to run, peaks within 1–3 cycles, oscillates repeatedly during the period of running and then declines precipitously as soon as running stops (Fig. 1).

Metabolic scope for activity. Our data on $\dot{V}_{O_2}$ does not necessarily represent either absolutely minimal, or completely maximal, values. The measurements were made during the active (nocturnal) phase of the daily activity cycle, and even though motionless, the animals were alert and aroused (the antennae often moved, the legs were extended, and the body was partly elevated). However, by comparing the integrated data from motionless animals with data integrated over periods of 4–10 min from animals that were running rapidly we can obtain conservative estimates of factorial scope. The mean value of this quantity for four individuals was $17·57 \pm 8·35$ s.d. which is similar to that reported for *Blaberus discoidalis* (Herreid & Full, 1984), but only one-fifth that known to occur during flight in endothermic moths of similar size (Bartholomew, 1981).

Oxygen debt. We observed no evidence of oxygen debt in *B. giganteus*. The values of oxygen consumption before and after running were statistically indistinguishable.

Cost of transport. The slope of the relationship between mass-specific $\dot{V}_{O_2}$ $(\text{ml}\,O_2\,g^{-1}\,km^{-1})$ and velocity represents the minimum cost of transport. The value of this quantity for *B. giganteus* (2·5) is slightly less than the value of 3·1 reported for its smaller congener, *B. discoidalis*, by Herreid & Full (1984).

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