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 x 50 x 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 (VO₂) were measured with an Applied Electrochemistry 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 incumbent 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 \(\dot{V}_{O2}\), 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 motion-
less animals had a mean period of 51.1 s. The ventilatory discontinuities caused
marked fluctuations in instantaneous \(\dot{V}_{O2}\) 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 \(\dot{V}_{O2}\) 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 \(\dot{V}_{O2}\) 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 \(\dot{V}_{O2}\) fluctuated cyclically while the cockroaches were
running, we have based our estimates of the energy cost of locomotion on
integrations of instantaneous \(\dot{V}_{O2}\) 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. $\dot{V}_\text{O}_2$ increased linearly with tread speed over the range of velocities (0.02–0.3 m s$^{-1}$) investigated (Fig. 2); $y = 0.029 + 2.5x$, $r^2 = 0.93$, where $y$ is in ml O$_2$ g$^{-1}$ h$^{-1}$ and $x$ is in km h$^{-1}$.

Variations in $V_\text{O}_2$ 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 s ± 9.1 s.d., $N = 24$) was not significantly different from that of motionless animals (51.1 s ± 22.1 s.d., $N = 22$) but its variance was significantly less ($F = 4.458; n_1, n_2 = 21, 23; P < 0.001$). The $\dot{V}_\text{O}_2$ 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 $V_\text{O}_2$ 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 $\dot{V}_\text{O}_2$ increases.

Post-running. At the end of 6–10 min of running, the $\dot{V}_\text{O}_2$ of the motionless cockroaches (0.16 ml g$^{-1}$ h$^{-1}$, ± 0.02 s.d., $N = 5$) did not differ from that measured before running began, but the CV of post-running $\dot{V}_\text{O}_2$ (94.0) was double that of the running $\dot{V}_\text{O}_2$ (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
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 $\dot{V}_{O_2}$ (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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REFERENCES


