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Burrowing energetics of the Giant Burrowing Cockroach *Macropanesthia rhinoceros*: An allometric study

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ABSTRACT

Burrowing is an important life strategy for many insects, yet the energetic cost of constructing burrows has never been studied in insects of different sizes. Open flow respirometry was used to determine the allometric scaling of standard metabolic rate (MR_S) and burrowing metabolic rate (MR_B) in the heaviest extant cockroach species, the Giant Burrowing Cockroach *Macropanesthia rhinoceros*, at different stages of development. At 10 °C, MR_S (mW) scales with body mass (M; g) according to the allometric power equation, $MR_S = 0.158M^{0.74}$, at 20 °C the equation is $MR_S = 0.470M^{0.53}$, and at 30 °C the equation is $MR_S = 1.22M^{0.49}$ (overall $Q_{10} = 2.23$). MR_S is much lower in *M. rhinoceros* compared to other insect species, which is consistent with several aspects of their life history, including flightlessness, extreme longevity (>5 years), burrowing, parental behaviour, and an energy-poor diet (dry eucalypt leaf litter). Energy expenditure during burrowing at 25 °C scales according to $MR_B = 16.9M^{0.44}$, and is approximately 17 times higher than resting rates measured at the same temperature, although the metabolic cost over a lifetime is probably low, because the animal does not burrow to find food. The net cost of transport by burrowing (J m^{-1}) scales according to $NCOT = 120M^{0.49}$, and reflects the energetically demanding task of burrowing compared to other forms of locomotion. The net cost of excavating the soil (J cm^{-3}) is statistically independent of body size.

1. Introduction

The Giant Burrowing Cockroach *Macropanesthia rhinoceros* Saussure 1895 (Blattoidea, Blaberidae, Geoscaphinae) is the heaviest cockroach in the world, with adults weighing up to 35 g and reaching lengths of 80 mm (Brown et al., 2000; Rugg and Rose, 1991). This species, which is endemic to the dry *Eucalyptus* woodland of northeastern Australia, lives in permanent burrows excavated to depths of up to 1 m underground (Woodman et al., 2007). *M. rhinoceros* can live up to 10 years, and adults show a long parenting period of at least 6 months, until nymphs are able to disperse and construct their own burrows (Matsumoto, 1992).

The large size, flightlessness and burrowing behaviour of *M. rhinoceros* makes it ideal for studies on metabolic rate (MR) at rest and during burrowing. It is hemimetabolous and grows through about 12 instars but maintains a similar body shape. Therefore, it is a good candidate for allometric studies on the energetics of burrowing intraspecifically, and for comparison with interspecific investigations on resting, maximum aerobic and burrowing MR in insects (Chown et al., 2007; Niven and Scharlemann, 2005).

Many insect species engage in burrowing behaviour, and it can occur through a variety of substrates, including soil, sand, fruit and wood. In fact, most terrestrial insect species present some form of burrowing behaviour at least once in their lifecycle, because eggs are often oviposited below the surface soil, so nymphs need to burrow to the surface when hatched (Nishide et al., 2013). For many insects, burrowing is also present through their life, as an essential life strategy, and in some it persists into adulthood. Burrows constructed by them provide favourable temperature and moisture levels due to the depth and shape of the chamber (Andres et al., 1998; Kurczewski, 2009).

The benefits of burrowing are obvious, but the energy expenditure during this behaviour is considered to be relatively high, especially because of the small body size of insects. In general, the energy cost of burrowing is much more expensive than other forms of locomotion, including swimming, running and walking (Dorgan et al., 2011). Important factors that can influence burrowing energetics are body size, geometry of the burrow, and soil hardness (Bozinovic et al., 2005; Lovegrove, 1989; White, 2005; Withers et al., 2000). Despite the importance of burrowing to many insects, there is only one study of the cost of burrowing in an insect, the Australian mole cricket *Gryllotalpa monaka* (White et al., 2008), although there are similar studies from an Australian scorpion

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Urodacus yaschenkoi (White, 2001) and a wolf spider *Geolycosa* sp. (Suter et al., 2011).

This study measures MR with open-flow respirometry and presents the total energy expenditure under standard conditions (MR_S), during rest (MR_R) and burrowing (MR_B) as a function of body mass. The net cost of transport (NCOT) is derived from MR_B minus MR_R and divided by the rate of burrowing to obtain the energy cost to burrow 1 m horizontally. The net cost of excavation (NCOE) is calculated as the energy cost to excavate 1 cm^3 of soil. These measures are then compared between body sizes and species.

2. Materials and methods

2.1. Animals

Giant Burrowing Cockroaches *M. rhinoceros* were purchased from a commercial supplier (Australian Insect Farm, Garradunga, QLD, Australia) where they had been reared from early stage nymphs. Each cockroach was grouped according to age (1–2, 2–3, 3–4, 4–5, and 5+ y.o.), marked on the dorsal thorax with acrylic paint for identification, and maintained in age-specific, soil-filled terraria, under natural lighting conditions, at a constant temperature (25 ± 2 °C). Soil moisture was maintained to prevent desiccation in this tropical species. Cockroaches were also given a constant supply of dry eucalypt leaf litter, which is their natural food source. All cockroaches were weighed to 1 mg on an analytical balance (Sartorius 1265 MP, Göttingen, Germany). Over 6 months of data collection, all individuals gained weight, however none moulted, which is consistent with the slow growth of this species.

2.2. Standard metabolic rate, RQ, and Q_{10}

A flow-through respirometry system recorded resting O_2 consumption and CO_2 production rates in eight cockroaches (1.98–20.1 g body mass) at acutely applied ambient temperatures of 10, 20 and 30 °C (±0.5 °C). These temperature treatments were presented to each cockroach in a random order with a 3 days break between treatments. Food was removed c.a. 24 h prior to the commencement of respirometry, which is approximately the duration of the specific dynamic action in insects (Secor, 2009). Each respirometry session lasted 8–10 h, including a 2 h acclimation period. Briefly, a pump pushed outside air into a pressurised vessel (AT-250A, Sparmax, Taipei, Taiwan), which was coupled to a pressure regulator (140 kPa) that released air downstream along vinyl tubing into a 5 L buffer cylinder, and then into a series of Drierite (W.A. Hammond Drierite Co., Xenia, OH, USA), soda lime and Drierite columns, to remove H_2O vapour and CO_2. This dry, CO_2-free air was then split into a measurement line and a control line, both of which had flow rates regulated (20, 50 or 100 ml min^{-1}_{STPD} depending on temperature and body mass) by a pair of mass flow controllers (GFC-171, 0–100 ml min^{-1}, Aalborg Instruments and Controls, Orangeburg, NY, USA; calibrated with a Gilibrator 2 bubble flow metre, Sensidyne, Clearwater, FL, USA). The control line, on the one hand, was routed through a controlled temperature (CT) cabinet and into the first port of an O_2 analyser operating in the differential mode (FC-2 Sable Systems, Las Vegas, NV, USA; calibrated to 20.95% O_2 with dry, CO_2-free outside air). The measurement line, on the other hand, had its air adjusted to a relative humidity of 75% (at the experimental temperature) with a dew point controller (DG-3 Sable Systems). This humidified air stream was then directed into the CT cabinet and through a sealed plastic metabolic chamber, 30 or 200 ml volume, depending on the size of the cockroach. A bypass line around the chamber allowed for 5–10 min baseline measurements of O_2 and CO_2 every 45 min, and a custom-built infrared motion detector mounted directly above the chamber allowed activity to be continuously monitored. Excurrent air from the chamber passed through a Drierite column to remove the H_2O vapour before entering a CO_2 gas analyser (LI-820, LI-COR Biosciences, Lincoln, NE, USA; calibrated with high purity N_2 and 0.2001% CO_2 span gas). The air stream was then scrubbed of CO_2 using an in-series column of Ascarite (A.H. Thomas Co., Philadelphia, PA, USA) and Drierite, before entering the second port of the O_2 analyser. Analogue outputs from the O_2 and CO_2 gas analysers, the measurement line's mass flow controller, and the activity detector were recorded to a computer at 1 s intervals with a PowerLab data acquisition system and LabChart software (ADInstruments, Bella Vista, NSW, Australia). After correcting for drift, O_2 consumption rates ($\dot{V}_{O_2}$; ml min^{-1}_{STPD}) were calculated as:

$$\dot{V}_{O_2} = \dot{V}_I(F_{IO_2} - F_{EO_2})/(1 - F_{EO_2}), \quad (1)$$

where $\dot{V}_I$ is the upstream flow rate of the dry CO_2-free air (ml min^{-1}_{STPD}), F_{IO_2} is the fractional O_2 concentration of the upstream dry CO_2-free air (i.e. 0.2095), and F_{EO_2} is the fractional O_2 concentration of the air stream exiting the metabolic chamber following the removal of CO_2 and H_2O vapour (Lighton, 2008; Withers, 2001). Insignificant drift in the CO_2 baseline was nevertheless corrected and CO_2 production rates ($\dot{V}_{CO_2}$; ml min^{-1}_{STPD}) were calculated as:

$$\dot{V}_{CO_2} = \dot{V}_I[(F_{ECO_2} - F_{ICO_2}) - F_{ECO_2}(\dot{V}_{O_2})]/(1 - F_{ECO_2}), \quad (2)$$

where F_{ICO_2} is the fractional CO_2 concentration of the upstream dry CO_2-free air (i.e. 0.0), F_{ECO_2} is the fractional CO_2 concentration of the air exiting the metabolic chamber following the removal of H_2O vapour, and $\dot{V}_{O_2}$ is the O_2 consumption rate calculated in Eq. (1) over the same time sequence (Lighton, 2008). All cockroaches exhibited extended periods of quiescence (c.a. 4–8 h), and any bouts of activity and subsequent recovery were excluded from analysis. The respiratory quotient (RQ) was calculated as the ratio of $\dot{V}_{CO_2}$ to $\dot{V}_{O_2}$. The RQ was then used to calculate standard metabolic rate (MR_S) in units of mW (mJ s^{-1}) using published conversion constants (Withers, 1992). The Q_{10} was calculated for each individual between each 10–20, 20–30 and 10–30 °C interval.

2.3. Metabolic cost of burrowing

In another round of experiments, 15 cockroaches (1.84–23.78 g body mass) were used to quantify the net metabolic cost of burrowing at 25 °C (±0.5 °C). First, the resting CO_2 production rate (MR_R) of these individuals was measured using a flow-through respirometry system involving a train of equipment: a soda lime column, a 200 ml sealed plastic metabolic chamber, a pump (Gilian GilAir Plus, Sensidyne, Clearwater, FL, USA; calibrated with the Gilibrator 2 and set at 285 ml min^{-1}_{STP}), and a CO_2 gas analyser (SBA-5, PP Systems, Amesbury, MA, USA; self-calibrated with soda lime-treated CO_2-free air) coupled to a data acquisition system (DATAQ DI-145 data recorder and Hardware Manager software, DATAQ Instruments, Akron, OH, USA). In these experiments, instead of an activity monitor, a layer of cotton wool was placed over the insect to encourage the inactive state, and the measurements were made for 12–14 h overnight, without food. After correcting for drift, resting CO_2 production rate was derived as above from the lowest readings, integrated over long periods when cyclic gas exchange was observed, according to established equations (Lighton, 2008; Withers, 2001).

Once the resting metabolic rate of these individuals was quantified, their burrowing metabolic rate was measured using a flow-through respirometry system in which a pump (D-79112, KNF Neuberger, Freiburg im Breisgau, Germany) pushed outside air at a mean rate of nominally 285 ml min^{-1}_{STP} through columns of soda lime and Drierite, a mass flow metre (GFM-171, Aalborg, NY, USA;