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Temperature- and body mass-related variation in cyclic gas exchange characteristics and metabolic rate of seven weevil species: Broader implications

C.J. Klok, S.L. Chown*

Spatial, Physiological and Conservation Ecology Group, Department of Botany & Zoology, DST Centre of Excellence for Invasion Biology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

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Abstract

The influence of temperature on metabolic rate and characteristics of the gas exchange patterns of flightless, sub-Antarctic *Ectemnorhinus*-group species from Heard and Marion islands was investigated. All of the species showed cyclic gas exchange with no Flutter period, indicating that these species are not characterized by discontinuous gas exchange cycles. Metabolic rate estimates were substantially lower in this study than in a previous one of a subset of the species, demonstrating that open-system respirometry methods provide more representative estimates of standard metabolic rate than do many closed-system methods. We recommend that the latter, and especially constant-pressure methods, either be abandoned for estimates of standard metabolic rate in insects, or have their outputs subject to careful scrutiny, given the wide availability of the former. $\dot{V}CO_2$ increase with an increase in temperature (range: 0–15 °C) was modulated by an increase in cycle frequency, but typically not by an increase in burst volume. Previous investigations of temperature-related changes in cyclic gas exchange (both cyclic and discontinuous) in several other insect species were therefore substantiated. Interspecific mass-scaling of metabolic rate (ca. 0.466–0.573, excluding and including phylogenetic non-independence, respectively) produced an exponent lower than 0.75 (but not distinguishable from it or from 0.67). The increase of metabolic rate with mass was modulated by an increase in burst volume and not by a change in cycle frequency, in keeping with investigations of species showing discontinuous gas exchange. These findings are discussed in the context of the emerging macrophysiological metabolic theory of ecology.

Keywords: Curculionidae; Cyclic gas exchange; Respirometry; Scaling; Sub-Antarctic

1. Introduction

Periodic gas exchange is one of the most characteristic physiological features of insects at rest. Although it is by no means common to all species, it has been recorded in a wide variety of higher insect taxa from cockroaches and termites (Wilkins, 1960; Shelton and Appel, 2001a; Marais and Chown, 2003) to beetles and ants (Lighton, 1990, 1991a). In its most sophisticated guise it takes the form of a series of repetitions of three periods of gas exchange (closed (C), flutter (F) and open (O)), which differ substantially in the rate of exchange of different gasses, and which ultimately result in a partial decoupling of CO_2 release and O_2 uptake (Lighton, 1996). These discontinuous gas exchange cycles (DGCs) were originally documented in lepidopteran pupae (Kestler, 1985) and adult insects (e.g. Punt et al., 1957), and have subsequently been investigated in considerable detail in lepidopteran pupae (e.g. Levy and Schneiderman, 1966a, b; Hetz et al., 1999), a wide variety of adult insects (reviews in Lighton, 1996; Chown and Nicolson, 2004), and several other arthropod groups (Lighton and Fielden, 1996; Klok et al., 2002; Lighton and Joos, 2002). Studies have ranged from comparative (e.g.

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*Corresponding author. Tel.: +27 21 808 2385; fax: +27 21 808 2995.
E-mail address: slchown@sun.ac.za (S.L. Chown).

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Lighton, 1991a; Duncan and Byrne, 2000) to experimental (Schneiderman and Schechter, 1966; Lighton and Garrigan, 1995; Chown and Holter, 2000), and in most instances have been concerned with the physiological mechanisms underlying discontinuous gas exchange and the reasons why insects might show discontinuous gas exchange cycles at rest.

Because the reduction of respiratory water loss was originally thought to be an important function of discontinuous gas exchange, but has since been vigorously contested (reviews in Lighton, 1996, 1998; Chown, 2002), many comparative studies have examined among-species variation in the relative durations and contributions of each of the three periods to total gas exchange, and their variation with temperature, to assess whether this variation is consistent with a water conservation hypothesis (Lighton, 1991a; Duncan and Dickman, 2001; Chown and Davis, 2003). These studies have shown that in all of the species examined to date, temperature-related increases in metabolic rate are accompanied by an increase in DGC frequency. However, in some insects, such as adult *Camponotus vicinus* ants (Lighton, 1988), several species of *Pogonomyrmex* harvester ants (Quinlan and Lighton, 1999), the fire ant *Solenopsis invicta* (Vogt and Appel, 2000), adult carabid beetles (Duncan and Dickman, 2001), and some species of lepidopteran pupae (Buck and Keister, 1955; Schneiderman and Williams, 1955), the volume of the water profligate O-period declines with increasing temperature. In others, such as *Cataglyphis bicolor* ants (Lighton and Wehner, 1993), several species of dung beetles (Davis et al., 1999), and two cerambycid beetle species (Chappell and Rogowitz, 2000), it does not.

Likewise, owing to the physiological, ecological and evolutionary implications of mass scaling (Peters, 1983; Schmidt-Nielsen, 1984; Gillooly et al., 2001; Allen et al., 2002), considerable attention has been given to the scaling of metabolic rate and gas exchange characteristics of species showing DGCs (Lighton, 1991a; Davis et al., 1999; Chappell and Rogowitz, 2000). At the interspecific level, the positive scaling of metabolic rate is well known, though the value of the exponents and constants of the relationship for the insects (and higher taxa within them) continues to be debated (Lighton and Fielden, 1995; Lighton et al., 2001; Addo-Bediako et al., 2002; Duncan et al., 2002; Terblanche et al., 2004), a characteristic of the field as a whole (Dodds et al., 2001; Symonds and Elgar, 2002; Savage et al., 2004). The scaling of DGC characteristics is not as well investigated, but in the few studies that have been undertaken it is clear that $\dot{V}CO_2$ and O-period CO_2 emission volume scale similarly with body mass, resulting in mass-independence of DGC frequency: a situation different to the scaling of ventilation frequency in vertebrates (Lighton, 1991b; Davis et al., 1999). Other characteristics of the DGC vary considerably in their scaling with mass, depending on the taxa that are being investigated (review in Chown and Nicolson, 2004). Thus, despite some inadequacies, both temperature- and body mass-related variation in the characteristics of the DGC have been documented.

However, DGCs are not the only form of periodic gas exchange characteristic of insects at rest. Many species show less complex forms of cyclic gas exchange (CGE) with a burst period, analogous to the O-period in DGCs, and an interburst period of decreased CO_2 release. The latter is different in character from both the C- and F-period of DGCs, where the spiracles often do not close completely nor exhibit fluttering. Such cyclic gas exchange is characteristic of several species, including cockroaches (Marais and Chown, 2003), termites (Shelton and Appel, 2000, 2001a–c), and flies (Williams and Bradley, 1998), and is also apparent in other arthropod taxa (Klok et al., 2002). How this cyclic gas exchange is related to discontinuous gas exchange is not well known, although CGE may be the basal, or original, form of gas exchange in insects and other arthropods that has since been pressed into service for other purposes and modified by selection to produce DGCs (for a full discussion see Chown and Nicolson, 2004; Marais et al., submitted). Exploring temperature- and body mass-related variation in the characteristics of cyclic gas exchange, as has been done for DGCs, might provide insight into whether these two different forms of periodic gas exchange share characteristics, and in so doing inform the hypothesis that cyclic gas exchange is basal. However, to date, such explorations are rare and have been restricted entirely to investigations of several species of termite (Shelton and Appel, 2001a, c).

Here, we increase the number of investigations of the characteristics of cyclic gas exchange by examining temperature- and body mass-related variation of metabolic rate and the characteristics of gas exchange in seven species of weevils. In doing so not only do we contribute substantially to the number of species for which such investigations are available, but we also provide information on an insect group that is entirely unrepresented in the gas exchange literature. To date, gas exchange studies of beetles have been restricted to the carabids, trogids, scarabs, tenebrionids, and cerambycids, despite the fact that there are at least 166 beetle families (Lawrence and Newton, 1995), of which the largest, in terms of species richness, is the Curculionidae.

2. Materials and methods

2.1. Study animals and sites

The *Ectemnorhinus*-group of weevils is a monophyletic unit, comprising 36 species, which is restricted to