



Gas exchange pattern transitions in the workers of the harvester termite



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ABSTRACT

The evolutionary genesis and the current adaptive significance of the use of the discontinuous gas exchange cycle (DGC) for respiration by insects is the subject of intense debate. Years of research have resulted in several leading hypotheses, one of which is the emergent-property hypothesis. This hypothesis states that DGC is an emergent property or consequence of interactions between the O_2 and CO_2 set points that regulate spiracular function, i.e. opening and closing. Workers of the harvester termite, *Hodotermes mossambicus* were selected as a model to test this hypothesis. The respiratory patterns of major workers, investigated using flow-through respirometry, were obtained at 100% relative humidity (RH) under varying temperature to evaluate the assumptions of the emergent-property hypothesis. Metabolic rate, measured as VCO_2 increased significantly after 15 °C. As VCO_2 increased in response to increasing temperature and activity, the gas exchange pattern displayed by workers transitioned to a continuous gas exchange. A true DGC, defined as showing all three phases and a coefficient of variation value close to 2, was not expressed under the experimental conditions. The conclusion drawn from this study of termite workers is that changes in respiratory patterns are most likely an emergent property of the insects' nervous and respiratory system.

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1. Introduction

Insect tracheal respiration is renowned for its remarkable efficiency. Insects are capable of extremely high rates of oxidative catabolism and maintain the highest mass specific rates of O_2 consumption in the animal kingdom. The tracheae are capable of supplying 10 times more oxygen per gram of tissue than blood capillaries (Maina, 2002; Lighton and Ottesen, 2005; Matthews and White, 2011). The oxygen needs of an animal are reflected by the respiratory efficiency of their gas exchange system; whereby a highly efficient system would suggest the capacity for a highly energetic lifestyle in which maximum O_2 delivery can occur at high metabolic demands (Maina, 2002; Moerbitz and Hetz, 2010). Physiological systems are designed to maximize performance. Therefore it would seem counter-intuitive to possess a physiological mechanism, such as discontinuous gas exchange (DGC) in insects, which impedes the rate of oxygen delivery to the tissues thus reducing the metabolic capabilities of the insect (Bradley, 2006).

Discontinuous gas exchange is one of three distinct patterns recognized in insect respiration. Insects exhibiting DGC show a distinctive pattern of periodic breathing; a cycle of repeated

spiracular openings and closings that results in the intermittent release of carbon dioxide (Bradley, 2006; Karise et al., 2010; Chown, 2011). DGC is characterized by the behavior of the spiracles, which produce a unique, three-phase pattern of gas exchange (Schneiderman, 1960; Shelton and Appel, 2001; Chown et al., 2006; Chown, 2011). A typical DGC consists of a closed phase (C), a period when the spiracles are sealed and no gas exchange occurs between the environment and the respiratory surfaces (Shelton and Appel, 2001; Chown and Nicolson, 2004; Forster and Hetz, 2010). During this phase O_2 in the tracheal system is consumed and quickly falls to the oxygen threshold while CO_2 accumulates slowly. When the oxygen threshold is reached the spiracles begin to open intermittently, an action described as spiracular fluttering (F). CO_2 still accumulates in this phase while O_2 oscillates around its threshold ensuring adequate oxygen delivery at safe levels, that is, levels that are not toxic to the tissues. Eventually the CO_2 threshold is reached and the spiracles open widely to release a burst of CO_2 . This phase is typically known as the open or burst phase (O/B) (Bradley, 2007; Forster and Hetz, 2010; Chown, 2011). This pattern of gas exchange has been the subject of intensive research, scrutiny and heated debate within the field of insect respiratory physiology (see reviews by Lighton, 1998; Chown et al., 2006). Years of research have resulted in several hypotheses and many, mostly unresolved questions. What is the evolutionary genesis and current adaptive significance of DGC? What is the

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underlying mechanism driving the production of DGCs and is this mechanism the same among all insects? Answers are abundant and varied and yet a consensus remains elusive.

The emergent-property hypothesis is one of these hypotheses and presents a non-adaptive solution to the problem, that is, understanding DGC. This hypothesis states that DGC is an emergent property or consequence of interactions between the O_2 and CO_2 set points that regulate spiracular function, i.e. opening and closing (Chown and Holter, 2000; Chown et al., 2006; White et al., 2007). It has been proposed that the gas exchange patterns in insects are not discrete respiratory forms but instead represent a continuum that reflects the balance between O_2 demand and supply (Bradley, 2007). Aerobic metabolism confers great advancements in the production of metabolic energy; however, this increased metabolic capacity comes at a cost. The utilization of oxygen results in the production of reactive oxygen species that cause deleterious effects within the tissues and are highly toxic (Maina, 2002; Bradley, 2006; Moerbitz and Hetz, 2010). This oxidative damage is reduced when aerobic supply and aerobic demand is matched, i.e. when the respiratory system is functioning at maximum capacity and O_2 is being consumed at the same rate at which it is being supplied to the tissues. A problem occurs when O_2 demand is low, such as, when the insect is at rest, but the respiratory system is still supplying O_2 at maximum capacity (Chown, 2011). Thus necessitating the existence of a physiological mechanism that reduces O_2 supply.

This would suggest that the type of gas exchange employed, be it discontinuous, cyclic or continuous, is dictated by the interaction between an insect's metabolic rate and the capacity of the respiratory system to deliver oxygen to this metabolically active tissue (Contreras and Bradley, 2011). If O_2 entry exceeds the rate of O_2 being consumed by aerobic metabolism, the spiracles will close and the closed phase of discontinuous gas exchange will be observed. This closed phase is required to lower the internal partial pressure of O_2 around the tissues to a safe level. This low level of O_2 is maintained during the flutter phase (F) of DGC, where the spiracles open and close rapidly. The length of this phase is determined by the rate at which CO_2 accumulates as a result of metabolism within the tissues. When CO_2 reaches a critical level the spiracles open (Forster and Hetz, 2010). As metabolic rate increases this critical CO_2 level is reached more rapidly until the closed phase becomes so short that it is no longer experimentally demonstrable and a continuous gas exchange pattern is displayed (Bradley, 2007). By decreasing the time over which the spiracles are closed, the volume of O_2 entry and CO_2 release are adjusted to meet metabolic demands (Contreras and Bradley, 2010, 2011).

An implication of this hypothesis is that cycle frequency increases with metabolic rate such that the gas exchange pattern displayed by an insect transitions from discontinuous to cyclic to continuous as metabolic rates increase (Bradley, 2006, 2007; White et al., 2007; Moerbitz and Hetz, 2010). Conditions that affect metabolic rate, such as temperature and activity, will therefore influence respiratory patterns through their effects on the rate of O_2 consumption and CO_2 production. All terrestrial animals also face a gas-water tradeoff, as it is a fundamental cost of living that gas exchange with the environment results in a loss of water. The higher the rates of gas exchange the higher the rate of water loss (Woods and Smith, 2010). The need to expel sufficient CO_2 requires the spiracles to be open longer or more frequently than is necessary for the uptake of adequate O_2 . Thus water loss was also measured as it could indicate the level of spiracle opening which has an influence on the pattern of gas exchange.

We chose the grass-harvester termite species, *Hodotermes mossambicus*, to provide clarification of this DGC hypothesis. The workers of *H. mossambicus* forage mostly during the day and as such are exposed to varying temperature and humidity conditions

(Coaton and Sheasby, 1975; Myburgh, 1989; Uys, 2002). In an initial study (Inder, 2010); the respiratory pattern of workers of *H. mossambicus* exhibited a cyclic gas exchange pattern when recorded at 25 °C. However, termite workers have been observed foraging at temperatures ranging from 21.2 °C to 37.8 °C. Underground they are likely exposed to more moderate temperatures. Under the emergent-property hypothesis the experimental temperature of 25 °C would represent an intermediate metabolic rate (Bradley, 2007). Thus, in support of this hypothesis workers of *H. mossambicus* exposed to lower temperatures should exhibit a DGC. To test this assumption, an experiment was designed to manipulate metabolic rate, using temperature. We report on the effect of temperature on metabolic rate, gas exchange pattern and water loss in the harvester termite workers.

2. Methods and materials

2.1. Study species

H. mossambicus is a southern African termite species, often considered a pest, which is widely distributed and occur frequently in areas of low rainfall. This species has subterranean nests, which can occur up to 6 m underground. They are found primarily on savannas and are grass harvesters. Foraging in this species generally takes place at night during summer and by day in the dry winter months, and is done by the worker caste (Coaton and Sheasby, 1975; Uys, 2002; Myburgh, 1989). The worker caste is the only caste to leave the colony and they can be separated into the major and minor workers, which are differentiated by head width and perform different roles (Watson, 1973). Major workers are responsible for cutting the plant material while the minor workers are responsible for the transport of material (Duncan and Hewitt, 1989).

Actively foraging workers of *H. mossambicus* were collected in the field in the Highveld area from Emmerentia Dam, South-West entrance (−26.160264 S, 27.998067 E) in Johannesburg, South Africa. Workers were collected between the months of May and November 2011 and April and May 2012, between 9 am and 3 pm. Temperature and humidity were measured during each collection (PH1000 Zeal Thermohygrometer). Termites were housed in Petri dishes with moist cotton wool and placed in a temperature chamber maintained at 25 °C. Termite workers are unable to feed themselves (Watson, 1973) and as such were left unfed. However, water was provided in the form of moist cotton wool. All measurements were performed within a period of 2 weeks after collection. During this period starvation was shown to have no significant impact on measurements of VCO_2 . Major workers were used for all experiments as a result of the difficulty of finding minor workers as opposed to major workers foraging at the field site. Major workers also had a tendency to survive longer in the lab conditions.

2.2. Respirometry

Flow-through respirometry was used to assess CO_2 output under different temperatures. The following temperatures were used: 5 °C, 10 °C, 15 °C, 25 °C and 35 °C. Individual termites were only used once at a randomly assigned temperature. Ten major workers were measured at each temperature. Termite workers were weighed (Libror AEG-455M) before and after each respirometry experiment. Experiments were run using humid air (100% RH) as it was found that termites survived for longer under humid conditions. Respirometry measurements were taken between the hours of 9 h and 20 h in order to take account of the possible influence of circadian rhythm. Room air was scrubbed of carbon dioxide

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