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Oxygen partial pressure effects on metabolic rate and behavior of tethered flying locusts

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Abstract

Resting insects are extremely tolerant of hypoxia. However, oxygen requirements increase dramatically during flight. Does the critical atmospheric P_{O_2} (P_c) increase strongly during flight, or does increased tracheal conductance allow even flying insects to possess large safety margins for oxygen delivery? We tested the effect of P_{O_2} on resting and flying CO_2 emission, as well as on flight behavior and vertical force production in flying locusts, *Schistocerca americana*. The P_c for CO_2 emission of resting animals was less than 1 kPa, similar to prior studies. The P_c for flight bout duration was between 10 and 21 kPa, the P_c for vertical force production was between 3 and 5 kPa, and the P_c for CO_2 emission was between 10 and 21 kPa. Our study suggests that the P_c for steady-state oxygen consumption is between 10 and 21 kPa (much higher than for resting animals), and that tracheal oxygen stores allowed brief flights in 5 and 10 kPa P_{O_2} atmospheres to occur. Thus, P_c values strongly increased during flight, consistent with the hypothesis that the excess oxygen delivery capacity observed in resting insects is substantially reduced during flight.

Keywords: Oxygen; Flight; Force; Hypoxia; Metabolism

1. Introduction

The high tolerance of metabolic rates and motor behavior exhibited by resting insects in response to hypoxia suggests that the oxygen delivery capacity of the tracheal system is excessive in comparison to demand, meaning that the safety margin for oxygen delivery is large (Keister and Buck, 1964; Greenlee and Harrison, 2004; Schmitz and Harrison, 2004). However, tissue oxygen demands are much higher during activity such as flight, so the tracheal system may not be as overbuilt as it first appears. Flight is by far the most energetically costly activity and it is known to raise metabolic rate 10–100 times in comparison to resting rates (Weis-Fogh, 1952; Kammer and Heinrich, 1978; Harrison and Roberts, 2000). Moreover, safety margins for oxygen delivery during flight appear to be smaller than for resting insects (Joos et al., 1996; Harrison and Lighton, 1998). To our knowledge, no studies have directly compared the safety margin for oxygen delivery for an insect species in a resting and active state. In this study, we tested the effect of atmospheric oxygen on metabolic rate and motor behavior of resting and tethered flying American locusts, *Schistocerca americana* Drury.

Specifically, the oxygen safety margin is the range of oxygen partial pressures (P_{O_2}) for which metabolic activity is constant and is defined by the critical P_{O_2} (P_c). The P_c is the oxygen tension at which function (e.g. flight behavior or metabolic rate) becomes compromised (Kam and Lillywhite, 1994). A large oxygen safety margin for oxygen delivery is equivalent to a low P_c, and a small safety margin corresponds to a high P_c. Adult insects at rest generally have a P_c for metabolic rate of 2–5 kPa O_2 (Galun, 1960; Keister and Buck, 1964; Greenlee and Harrison, 2004). Resting adult *Schistocerca*

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americana grasshoppers have a P_c for metabolic rate of approximately 1.3 kPa (Greenlee and Harrison, 1998; Greenlee and Harrison, 2004), and a P_c for abdominal pumping at rest of 4 kPa (Greenlee and Harrison, 2004), indicating that the safety margin for oxygen delivery for these resting grasshoppers is quite large.

One hypothesis is that excess oxygen delivery capacity observed in resting insects exists to allow activities that require higher oxygen fluxes such as flight. Oxygen consumption rates ($\dot{M}_{O_2}$, μmol g^{-1} h^{-1}) depend on the partial pressure gradient for oxygen from air to mitochondria and on the summed diffusive and convective conductance, G (μmol g^{-1} h^{-1} kPa^{-1}), of the tracheal system for oxygen:

$$\dot{M}_{O_2} = (\text{air } P_{O_2} - \text{mitochondrial } P_{O_2})G. \qquad (1)$$

When oxygen begins to limit metabolic rate at the P_c, it is reasonable to assume that the animal is recruiting its physiologic capabilities in order to maximize tracheal oxygen delivery; thus, we define tracheal conductance at this point as the maximal tracheal conductance (G_{max}). Under specific conditions in which oxygen limits mitochondrial respiration, mitochondrial P_{O_2} is believed to be near 0.1 kPa (Richmond et al., 1999), which can be approximated as zero. Consequently, G_{max} can be described as

$$G_{max} = \dot{M}_{O_2\text{-c}} P_c^{-1}, \qquad (2)$$

where $\dot{M}_{O_2-c}$ is the oxygen consumption rate at the P_c. If resting and flying G_{max} were equivalent (in other words, that the low P_c of resting insects is completely due to utilization of the large G available for flight), then Eq. (2) would hold for both flight and non-flight conditions, and

$$G_{max} = \dot{M}_{O_2\text{-rest}} P_{\text{c-rest}}^{-1} = \dot{M}_{O_2\text{-flight}} P_{\text{c-flight}}^{-1}, \qquad (3)$$

where $\dot{M}_{O_2\text{-}x}$ is the oxygen consumption rate at rest and during flight, respectively, and $P_{\text{c-}x}$ is the critical P_{O_2} under the respective conditions. The migratory locust, *Schistocerca gregaria* Forskål, increases oxygen consumption rates 14 times over resting rates during tethered flight (Weis-Fogh, 1952; Armstrong and Mordue, 1985). If $\dot{M}_{O_2}$ increases by 14 times during flight, Eq. (3) predicts that $P_{c-\text{flight}}$ should be near 18 kPa O_2 ($P_{\text{c-flight}} = 14 \times 1.3$). This is an intriguing prediction, as it suggests that there would be a minimal safety margin for oxygen delivery during flight in locusts.

An alternative hypothesis is that G_{max} may increase linearly with $\dot{M}_{O_2}$ during activity, resulting in a similar P_c at rest and during flight. In support of this hypothesis, resting and flying locusts utilize different methods of ventilation. A resting locust ventilates the tracheal system primarily through abdominal pumping (Miller, 1960; Greenlee and Harrison, 1998), while flying locusts add thoracic autoventilation, in which wing movements cause volume changes in the thorax that ventilate thoracic air sacs (Weis-Fogh, 1967). In *S. gregaria*, abdominal pumping contributes about 40 l air kg^{-1} h^{-1} of ventilation at rest. During flight, this increases to 186 l kg^{-1} h^{-1}, while thoracic autoventilation adds an additional 310 l kg^{-1} h^{-1}, suggesting a total increase in ventilation of about 12-fold, similar to the increase in $\dot{M}_{O_2}$ (Weis-Fogh, 1967). This hypothesis is also supported by the similar P_{O_2} found in the resting and active flight muscle of some insects (Komai, 1998, 2001). If G_{max} is proportional to ventilation, these data suggest that the P_c should be similar in resting and flying locusts.

In this study, we measured the effect of atmospheric oxygen on the P_c for carbon dioxide emission rate for tethered flying and non-flying locusts. To further characterize the safety margin for oxygen delivery during flight, we measured the effect of air P_{O_2} on vertical force production and on flight behavior. In addition, we calculated maximal tracheal conductance for oxygen during flight.

2. Materials and methods

2.1. Animals and experimental design

Schistocerca americana were reared from eggs in culture at Arizona State University as previously described (Harrison and Kennedy, 1994; Krolikowski and Harrison, 1996). Only adult male grasshoppers were used because they exhibited a more horizontal position when attached to the force transducer compared to females. Animals were attached to the force transducer using a low-temperature glue gun (FPC Corporation, Buffalo Grove, IL) and an all-purpose hot adhesive. Mean live mass of the animals was 1.22 ± 0.02 g. All animals had intact wings.

The experimental apparatus consisted of a force transducer that was mounted within a 1 l Lucite respirometry chamber (Fig. 1; chamber not shown). The Lucite respirometry chamber was placed inside an incubator set at 35 ± 1 °C, the maxima of the preferred temperature range (25–35 °C) for flying locusts (Weis-Fogh, 1967). We reasoned that the use of a relatively high temperature would produce the highest possible metabolic rates and therefore the best contrast to resting conditions. The chamber was dimly lit and contained an artificial horizon constructed of black and white paint (not shown), conditions previously shown to maximize vertical force production (Wortmann and Zarnack, 1993).

The chamber was sealed and air containing the test atmospheric oxygen level flowed through the chamber. After a 3 min period to allow for oxygen equilibrium of the chamber, we measured the carbon dioxide emission