DIRECT CAROUSEL FLIGHT CALORIMETER FOR METABOLIC INVESTIGATIONS OF SMALL INSECTS

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Abstract

An isoperibolic heat flow calorimeter is described for the determination of heat production rates during the tethered flight of small insects such as flies, honeybees or hornets. The insects are fixed with their thoraces to one arm of a low-friction carousel. A sensor counts the number of revolutions per time and determines the speed of flight. Wing sound is monitored by a microphone with an audio recorder, so that wing heat frequencies and hence locomotor activities can be determined. Different illumination means are incorporated to guarantee the illumination levels necessary for flight.

Keywords: direct calorimetry, energy metabolism, flight, illumination, insects

Introduction

The energy metabolism of living organisms is of the utmost interest for physiologists. It even stood as godfather at the cradle of calorimetry [1]. While the standard or resting metabolism of an animal is easy to define and to determine, states of activity vary considerably depending on the external parameters. For many animals, the highest level of activity that limits the metabolic scope is approximately 10 times higher than the resting metabolism [2]. Exceptions are flying organisms and especially insects. Under the conditions of flight, the metabolic rate is more than 20-fold for honeybees, for example [3–6]. The highest energy turnover rates are observed during the hovering flights of humming birds and some insects (e.g. moths), since no support is then given by the surrounding medium, in contrast with the situation during running, swimming or forward flight. Under such circumstances, the rates are increased up to 100-fold [2, 7].

The difficulties involved in determinations of the heat output during activity states arise from different sources. Such states often appear irregularly, in the form of bursts, without a steady state for an exact evaluation. The animals have
to be kept motivated [8] to perform special tasks with a high turnover. This may be attained by long training, as for investigations on a treadmill, for instance, or by continuously stimulating them by mechanical or electrical irritation, but this may lead to artificial conditions [3]. Rewards can be a means to overcome these problems. In the special case of insect flight, it is often difficult to initiate flight and keep it going [9], although many insects are excellent flyers over long distances or long times [6].

The energy turnover during rest or activity can be determined by different methods. These are often classified as ‘direct’ and ‘indirect’ calorimetry methods. Direct calorimetry applies isothermal/isoperibol heat flow calorimeters in most cases, with a few exceptions of the use of quasi-adiabatic or truly adiabatic instruments, while the spectrum of indirect approaches is very broad. The most common procedure is to determine oxygen consumption and carbon dioxide production. These are monitored by the classical manometric Warburg method [5], by paramagnetic or optical sensors and gas-specific electrodes. Their ratio, the respiratory quotient \( RQ \), provides information about the substrate consumed during the metabolism. A value of \( RQ = 1.00 \), \( RQ = 0.83 \) or \( RQ = 0.71 \) indicates that carbohydrates, proteins or fats, respectively, are utilized as fuel. The fat metabolism, with a heat output of up to 39 kJ g\(^{-1}\), affords the highest amount of energy per gram and is thus observed particularly in long-distance flyers or hovering insects (e.g., moths [10]). Carbohydrates and proteins provide only 16 and 13 kJ g\(^{-1}\) respectively, i.e., less than 40% of the level for fat. A carbohydrate metabolism with an \( RQ = 1.00 \) is typical for honeybees; \( RQ \)s between 0.71 and 1.00 are characteristic for hornets [unpublished data].

Other methods of indirect calorimetry include the uptake and consumption of radioactively labeled compounds, very often \(^{14}\)C glucose [11], the determination of metabolites in tissue and/or blood/hemolymph [10], or the measurement of heart beat rates [12]. A typical approach with insects is ‘exhaustion flight’ [5, 11], which is readily applicable when the type of metabolism and the kind of energy substrate are known. An insect is kept flying, e.g., tethered to a carousel, until all of its energy resources (‘fuels’) are consumed. It is then fed with a known amount of energy in the form of a glucose or mixed glucose/protein solution and stimulated to fly again until exhausted. This can be done so effectively that, for example, honeybees will die within a few minutes if they are not fed again immediately [13]. The amount of energy provided divided by the flight duration yields the energy consumption rate and hence the flight metabolism.

An even more indirect physical method is the ‘grab-and-stab’ procedure often applied to measure the energy metabolism of insect flight (see e.g., [14, 15]). An insect is caught during flight, and within a few seconds a very thin thermocouple (installed inside a hypodermic needle) is implanted into its thorax, the main site of heat production. The temperature differences between the thorax and the ambient air are recorded, and the heat loss is calculated from cooling curves evalu-