

SHORT COMMUNICATION

CORRELATION OF SOUND GENERATION AND METABOLIC HEAT FLUX IN THE BUMBLEBEE *BOMBUS LAPIDARIUS*

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Flying insects produce extreme amounts of heat as a by-product during the contractions of their thoracic flight muscles (Heinrich, 1989). Before flight, metabolic heat may serve to warm up the thoracic muscles until the minimum lift-off temperature is reached (Heinrich, 1974*b*; Stone and Willmer, 1989; Esch and Goller, 1991). Social bees and wasps are also able to use the heat produced in their flight muscles for brood incubation and for active regulation of nest temperatures (Heinrich, 1974*a*; Seeley and Heinrich, 1981; Schultze-Motel, 1991).

In this study, we report simultaneous measurements of heat flux and sound generation by wing buzzing in individual bumblebee workers (*Bombus lapidarius* L.). Bumblebees used in the experiments were taken from colonies in observation nest boxes (Schultze-Motel, 1991) and placed into the cylindrical 100 ml stainless-steel vessel of a Calvet-type microcalorimeter (MS 70, Setaram, Lyon; Wadsö, 1987). A small microphone had been installed below the screw cap of the calorimeter vessel. The sensitivity of the calorimeter under these conditions was 41.7 mV W^{-1} . Both the calorimeter and the microphone signals were amplified and recorded on a dual-channel chart recorder.

In 32 out of a total of 36 measurements, the bumblebees showed prolonged periods of sound generation, most frequently at the beginning of experiments. We assume that the sound was not produced in an alarm reaction, but by flight movements of the wings when the animals attempted to lift off inside the calorimeter vessel. The buzzing sounds produced by bumblebees are caused by oscillations of the flight muscles inside the metathorax (Schneider, 1975). Previous endoscopic observations of bumblebees sitting on the bottom of our calorimeter vessel had shown that there was a one-to-one correlation between episodes of wing movements and sound production. The microphone recordings thus allowed an easy way of measuring locomotor activity inside the calorimeter.

The simultaneous recordings of calorimeter and microphone signals showed a very good agreement between periods of sound generation and increased metabolic heat flux from the animals. This was most conspicuous in some experiments without continuous wing buzzing activity but with distinct episodes of intense sound generation that were

Key words: bumblebee, *Bombus lapidarius*, direct calorimetry, acoustic monitoring, locomotion, metabolic rate.

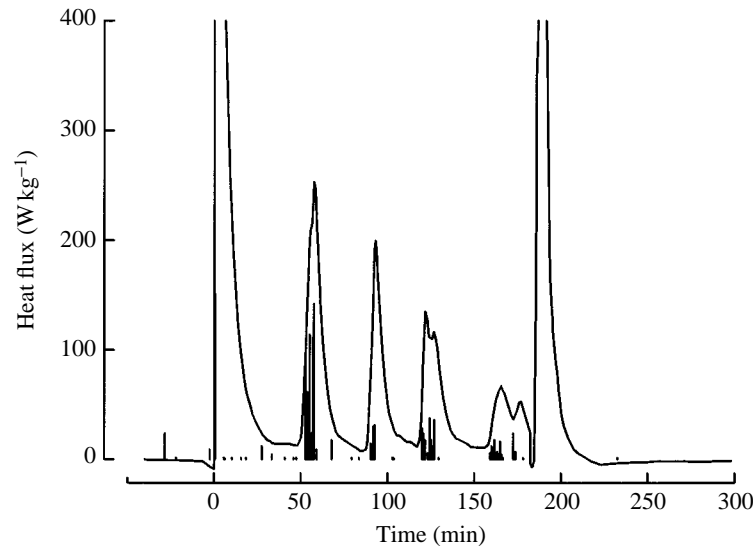


Fig. 1. Time course of heat flux and sound generation of a *Bombus lapidarius* worker. The calorimeter was at 26°C, and the body mass of the bumblebee was 105 mg. The animal was placed into the calorimeter vessel at time $t=0$ min and was removed at $t=185$ min. The heat flux has been recalculated to mass-specific units and is shown as a continuous curve. The vertical lines represent the simultaneously recorded microphone signals (voltage emitted by the microphone; arbitrary units). The large heat flux maxima at the beginning and at the end of the experiment are artefacts due to the temperature differences between the calorimeter vessel and the calorimeter block after reinsertion of the vessel into the calorimeter.

always coupled to a simultaneous increase of heat flux (Fig. 1). Between episodes of sound generation, heat flux typically returned from maxima exceeding 200 W kg^{-1} to basal values around 10 W kg^{-1} . During one experiment, we recorded a deviation from the usually observed synchronism between metabolic heat flux and sound generation (Fig. 2). The acoustic activity of the animal started about 45 min after the beginning of the experiment. Remarkably, the heat flux signal showed a steep increase as early as 5 min before the first sound generation was observed. During the period of continuous wing buzzing, heat fluxes of more than 350 W kg^{-1} were measured. These fluxes correspond to metabolic rates during free flight in other Hymenoptera: about 300 W kg^{-1} in the carpenter bee *Xylocopa capitata* (Nicolson and Louw, 1982), $300\text{--}500 \text{ W kg}^{-1}$ in honeybees, *Apis mellifera* (Nachtigall *et al.* 1989) and about 350 W kg^{-1} in the bumblebees *Bombus lucorum* and *B. pascuorum* flying in a wind tunnel (Ellington *et al.* 1990). We suggest that the sharp increase in heat flux before the beginning of sound generation represents a preflight endothermic warm-up event. Apparently, the warm-up of flight muscles proceeded without any wing buzzing.

Two alternative hypotheses have been put forward to explain the mechanism of preflight endothermic warm-up in bumblebees without any visible wing movements. It has been suggested that a biochemical 'futile cycle' involving the glycolytic enzymes fructose diphosphatase and phosphofructokinase could account for heat production

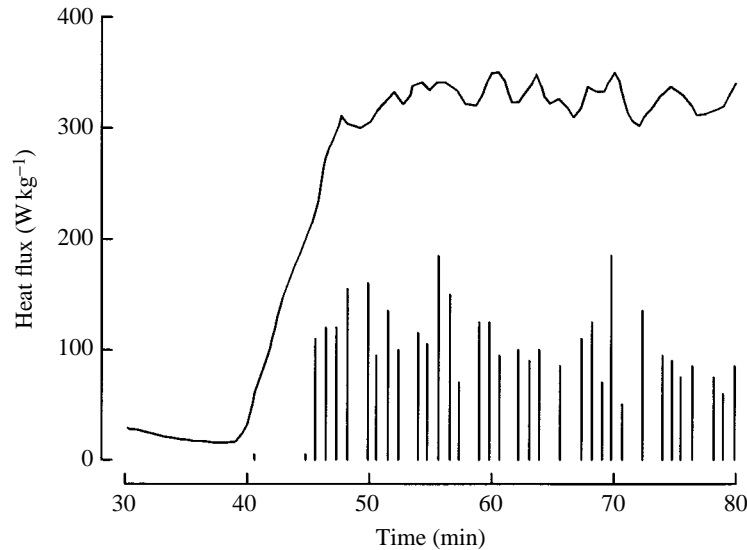


Fig. 2. Detail of the time course of heat flux (continuous curve) and sound generation (vertical lines) of a *Bombus lapidarius* worker with a body mass of 98 mg. The calorimeter temperature was 26 °C. The experiment lasted from $t=0$ min until $t=191$ min. Note the increase in heat flux before the onset of sound production.

without any muscle contractions (Newsholme *et al.* 1972). High activities of both enzymes have been detected in bumblebee flight muscles (Newsholme *et al.* 1972) and substrate cycling may indeed occur during preflight warm-up (Surholt *et al.* 1990, 1991). Most recently, however, it has been shown that heat production is always coupled to contractions of flight muscles (Esch and Goller, 1991). The antagonistic dorsoventral and dorsal longitudinal muscles go into tetanus during preflight warm-up so that there are hardly any externally visible movements (Esch *et al.* 1991). These results corroborate the hypothesis that muscle contractions are the main heat source of endothermic warm-up events without wing movements such as the one witnessed by us in *Bombus lapidarius*.

Both locomotor activity (wing buzzing) of bumblebees and endothermic events without movements could be recorded in our experiments. The heat flux measured in the absence of both types of metabolic heat production provides an estimate of the metabolic rate of inactive bumblebees. Since there is almost always locomotor activity, it is otherwise rather difficult to obtain meaningful data on the resting metabolic rate of insects (Rothe and Nachtigall, 1989; Lighton and Lovegrove, 1990). The combination of direct calorimetry and acoustic monitoring may serve as a suitable method for the direct quantitative measurement of the heat production rate of insects with a simultaneous account of their locomotor status.

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