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Resting metabolism and critical thermal maxima of vespine wasps (*Vespula* sp.)

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ABSTRACT

Vespine wasps are known for their high endothermic capacity. Endothermic activity is directly linked to respiration. However, knowledge on wasp respiration is sparse and almost nothing is known about their resting metabolism.

We investigated the yellowjackets' CO_2 production in a flow-through respirometer chamber overnight. Endothermic and behavioral activity was observed by real-time infrared thermography. Most resting wasps were ectothermic or only slightly endothermic (thoracic temperature excess against abdomen < 0.6 °C). In the investigated temperature range (T_a = 2.9–42.4 °C) mean CO_2 production rate of resting wasps increased steeply according to an exponential function, from 5.658 μl g^{-1} min^{-1} at 8.3 °C to 8.504 μl g^{-1} min^{-1} at 20.2 °C, 58.686 μl g^{-1} min^{-1} at 35.3 °C and 102.84 μl g^{-1} min^{-1} at 40 °C. The wasps' respiratory critical thermal maximum (CT_{max}), marking the upper edge of their viable temperature range, was 45.3 °C. The respiratory CT_{max} did not differ significantly from the activity CT_{max} of 44.9 °C. CT_{max} values were considerably below that of honeybees (48.9 and 49.0 °C for respiration and activity, respectively). This allows honeybees to kill wasps by heat-balling.

Comparison with other arthropods showed that vespine wasps are among the insects with the highest mass-specific resting metabolic rate and the steepest increase of metabolism with ambient temperature.

1. Introduction

Vespine wasps of the genus *Vespula* are capable of a very impressive thermoregulatory performance (Coelho and Ross, 1996; Heinrich, 1989; Kovac and Stabentheiner, 1999; Kovac et al., 2009). Endothermy improves muscular function (Coelho, 1991), which improves agility and enables them to carry heavy loads during foraging (Kovac and Stabentheiner, 1999; Kovac et al., 2009). Endothermy is also used to regulate the nest temperature (Himmer, 1927; Schmolz et al., 1993; Steiner, 1930). A high nest temperature in honeybees speeds up larval development (Petz et al., 2004). However, in the nest of honeybees, which have a comparable social thermoregulatory capacity, most bees are ectothermic (Stabentheiner et al., 2003, 2010). The same has to be assumed for the nest of vespine wasps. Basal metabolism of the ectothermic insects provides a considerable amount of heat for social thermoregulation (Kovac et al., 2007; Petz et al., 2004; Schmolz et al., 1993; Stabentheiner et al., 2010). As in the wasps' nests temperature varies more than in honeybee nests (e.g. Büdel, 1955; Himmer, 1962; Klingner et al., 2005, 2006; Simpson, 1961; Steiner, 1930) the temperature dependence of their resting metabolism is of special interest. The resting metabolism as a measure of the basal metabolism, however, has not yet been well investigated in vespine wasps. Wasp nests may cool considerably during cold nights (Himmer, 1962; Klingner et al., 2005, 2006; Steiner, 1930), and the individuals' resting metabolism is important also outside their thermal optimum. To gain a comprehensive overview of an insect's physiological reaction to environmental changes, analysis over the animal's entire viable temperature range is a necessity. Therefore we measured the CO_2 production of resting *Vespula vulgaris* and *Vespula germanica* foragers in the entire range of temperatures they are likely exposed to in a breeding season (2.9–42.4 °C) in Central Europe.

Vespula often builds its nests under the roofing tiles of old farmhouses. These nests are sometimes abandoned at an early stage. On the one hand this may be caused by an accident or illness of the nest-founding queen. On the other hand, however, this may be caused by the increasingly higher temperatures in the course of the early breeding season. Temperatures at these locations may become as high as 45.8 °C when the sun shines on the tiles on warm days (our own unpublished observations). This is in the range of the wasps' suggested upper thermal limit (Käfer et al., 2011). Although wasps are known to cool their nests with water spread on the combs (Klingner et al., 2005; Kovac et al., 2009; Steiner, 1930), these nest temperatures may be higher than single insects or small colonies can survive. In this context the wasps' critical thermal maximum (CT_{max}) is of special interest. Some vespine wasps are known to be more susceptible to high temperatures

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than honeybees (Ono et al., 1987, 1995). This allows honeybees to kill wasps by heat-balling (Ono et al., 1987; Papachristoforou et al., 2007; Stabentheiner, 1996; Tan et al., 2005). Stabentheiner (1996) and Stabentheiner et al. (2007) investigated this aggressive interaction between *Apis mellifera carnica* and *Vespula* sp. However, while the upper lethal temperature has been determined in *Vespa mandarinia japonica* (44–46 °C, Ono et al., 1995), *Vespa velutina* (45.7 °C, Tan et al., 2005), and *Vespa orientalis* (50.6 °C, Papachristoforou et al., 2011) the upper thermal limit of *Vespula* has not yet been investigated. Because it is thought to be more relevant to natural conditions we choose the temperature ramping procedure (Terblanche et al., 2011). We applied behavioral observations (Klok et al., 2004) and thermolimit respirometry (Lighton and Turner, 2004) to determine the wasps' upper critical thermal maximum (activity and respiratory CT_{max}).

2. Material and methods

2.1. Animals

Experiments took place in late summer and autumn 2008 (September, October, November) and 2009 (October), and in summer 2010 (August). Foraging yellowjackets (*V. vulgaris* (Linnaeus 1758) and *V. germanica* (Fabricius 1793) – subsequently referred to as *Vespula* sp.) were caught at an artificial feeding station provided with sucrose solution. Animals were collected for immediate analysis. In some cases (8 of 35 wasps) they were stored in cages overnight in a dark and cool area (12–15 °C, food provided) for use on the following day. Individuals were weighed before and after the experiments.

2.2. CO_2 measurement

Individuals were put into a flow-through respirometer measurement chamber made of brass and immersed into an electronically controlled water bath (Julabo F33 HT) regulated within ±0.1 °C of the set temperature. The chamber volume was 18 ml (3 × 3 × 2 cm). This allowed unrestricted movement of the wasps at a high measurement sensitivity. Because of the wasps' long stay in the chamber (typically overnight, >6 h) they were also provided with a food source (1.5 M sucrose solution ad libitum). Experimental ambient temperature (T_a) for the wasps was set via the water bath from 2.5 to 45 °C in steps of 5 °C. Most individuals (23 of 35) were tested at only one T_a. Six individuals were tested at two T_as, five individuals at three T_as, two individuals at four T_as, and one individual at five T_as. Experiments lasted at least 3.5 h at each set temperature.

Individuals were transferred into the respirometer chamber directly from the outside or from storage and had time to accustom to the adjusted T_a for at least 15 min. Because the chamber was not completely submersed and the chamber's top lid window was covered with a thin plastic film, the inside temperature deviated somewhat from the temperature of the water bath. Therefore, actual ambient air temperature was measured with a thermocouple inside the chamber near the insect (~1 cm), sensing the actual experimental temperature.

The air for the flow-through respirometry was taken from an inlet outside the laboratory. Before entering the measurement system it had to pass a 10 l canister and a 5 l bottle to smooth any variations in outside CO_2 concentration. Relative humidity was kept at 50% down to 15 °C, 60% at 12.5 °C, 70% at 10 °C, 80% at 7.5 °C, 90% at 5 °C and 100% at 2.5 °C. To control relative humidity, the measuring gas was passed through two humidifying bottles filled with distilled water prior to the measurement chamber, saturating the air with water vapor. The bottles were submersed in a second Julabo F33 HT water bath adjusted to the according dew point temperature required for the desired relative humidity in the measurement chamber (Stabentheiner et al., 2012).

CO_2 production was measured with a differential infrared gas analyzer (DIRGA) sensitized to carbon dioxide in serial mode (Advance Optima URAS14, ABB; compare Kovac et al., 2007; Stabentheiner et al., 2012; Petz et al., 2004). Air flow was set to 150 ml min^{-1} and regulated by a Brooks 5850S mass flow controller (0–1000 ml/min; Brooks Instrument, Hatfield, USA). As a result of the tube length between the measuring chamber and the URAS a delay of 35.0 s was measured. The wasps' CO_2 production was recorded at intervals of 1 s. The amount of CO_2 production (μl g^{-1} min^{-1}) reported in this paper refer to standard (STPS) conditions (0 °C, 101.32 kPa = 760 Torr). Considering the duration of each experiment, the URAS gas analyzers were set to automatic zero and end point calibration every 3 h using the internal calibration cuvettes. During evaluation, the data were corrected for any remaining offset and drift.

2.3. Activity and body temperature

The top lid of the measurement chamber was covered with a plastic film transparent to infrared (IR) radiation in the range of 3–13 μm. It enabled us to record both the wasps' body surface temperature and activity with an infrared thermography camera (ThermaCam SC2000 NTS; FLIR Systems Inc.). An IR emissivity of 0.97 of the wasp cuticle was used to calculate surface temperatures (for details see Kovac et al., 2007; Schmaranzer and Stabentheiner, 1988; Stabentheiner et al., 2012; Stabentheiner and Schmaranzer, 1987). The measurement accuracy of 0.7 °C was achieved by using a self-constructed Peltier driven reference source of known temperature and emissivity. Infrared data were recorded digitally on hard disk at 3, 5 or 10 frames s^{-1}. Evaluation of the surface temperatures of head (T_{hd}), thorax (T_{th}) and abdomen (T_{ab}) was done with AGEMA Research software (FLIR Systems Inc.) controlled by a proprietary Excel (Microsoft Corporation) VBA macro. The thermographic video sequences also allowed judgment of active and resting periods without behavioral impairment. Endothermy was assessed by the difference between T_{th} and T_{ab}. As these temperatures were both surface temperatures measured via IR, we minimized measurement errors which possibly might occur when calculating T_{th} from IR and T_a from thermocouple data. Our definition of rest (classification according to Crailsheim et al., 1999; Stabentheiner and Crailsheim, 1999; Stabentheiner et al., 2003) was: (1) The individual was ectothermic (no visibly heated thorax) and (2) there were no or marginal signs of bodily activity (i.e. movements of antennae, single movement of legs allowed) for a duration of at least 10 min (reduced to 5 min at temperatures >27.6 °C if no 10 min intervals were available). However, we were forced to take into account that individuals, although being obviously at rest (sitting still for an hour or more), could be slightly endothermic. Therefore we had to define "rest" in terms of "scarce movement" and "only weak endothermy" with $T_{th} - T_{ab} < 2$ °C during a few periods of the experiment.

2.4. CO_2 production calculation

Before we determined the amount of carbon dioxide produced in a certain experimental trial, the IR video sequences were analyzed concerning the wasps' activity. Sections assessed as "resting periods" (defined in Section 2.3) were divided up into 10 min intervals. At high T_a (27.6 °C and above) phases of inactivity in some individuals decreased in duration as well as in number to such an extent that we had to reduce the minimal interval for our definition of "rest" to 5 min. URAS 14 CO_2 data from these time intervals were used for further calculations. Integrating the gas