Thermochimica Acta, 229 (1993) 173–180
Elsevier Science Publishers B.V., Amsterdam

Calorimetric investigations on social thermogenesis in the hornet *Vespa crabro* L. (Hymenoptera: Vespinae) [1]

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(Received and accepted 26 May 1993)

Abstract

Heat production rates of individual hornets were measured at 10, 15, and 20°C by means of direct calorimetry in order to investigate endothermic behaviour and capabilities to contribute to nest heat. Hornet workers showed heat production rates of 49 mW per g wet weight (w.w.) (SD = ±8 mW g^{-1}) at 20°C; drones have lower heat production rates at the same temperature (36 mW g^{-1}, SD = ±5 mW g^{-1}). Nevertheless, the latter may contribute significant portions of heat to the nest at the end of season. The heat production of the whole colony was assessed at 1.8 W at the state of maximum biomass and at 1.3 W later, after the appearance of the reproductive forms, i.e. the drones and queens. The fact that drones and workers lowered their heat production rates with decreasing ambient temperatures in our experiments is discussed.

INTRODUCTION

Hornets are social wasps belonging to the family Vespinae that form annual colonies in northern temperature climates. These colonies are usually founded at the end of April or the beginning of May by a single queen. They consist of a few hundred or less workers at the time of maximum biomass in September. In autumn, after the appearance of drones and virgin queens as reproductive forms, colony life comes to an end and only seminated queens survive and hibernate until they build new nests in the following year.

The ability of hornets to control and maintain their nest temperatures is well documented [1, 2]; thus hornets can be regarded as social homeotherm organisms. In most social insects, the ability to warm up the nests against low ambient temperatures strongly depends on the endothermic behaviour of the colony members, i.e. the workers, drones and queens [3]. (The

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[1] Presented at the Tenth Ulm Conference, Ulm, Germany, 17–19 March 1993.

physiological term "endotherm" in this text denotes the heat produced endogenously in an organism by metabolic processes. Of course, in a thermodynamic sense, this heat is generated by exothermic and not by endothermic processes.)

Individual bees (solitary and social species) can raise their body temperature by antagonistic contraction of their flight muscles and by heat exchange with the abdomen [4], but it is not known to what extent this is true for hornets. Although there is some evidence for endothermic behaviour in hornet workers [5, 6], no heat production rates have been measured in these insects. It was the aim of the present study to determine heat production rates of workers and drones at different ambient temperatures (T_A) by direct calorimetry, in order to investigate the individual thermoregulatory behaviour and the possible capacity to contribute to the nest heat. We also present data for the heat production rates of a whole hornet colony.

MATERIALS AND METHODS

Animals

In the summer and autumn of 1991, two colonies of the hornet *Vespa crabro* were kept in the Institute for Biophysics in Berlin-Dahlem. The nests had already been founded outside and contained workers when they were transferred from their original nest sites to the institute. Colony 1 was relocated from a garden colony in Berlin-Zehlendorf on July 22nd and contained 1 queen, 8 workers, 19 larvae and 15 pupae at one comb. Colony 2 was detected near the airport of Berlin-Tegel and transferred to the institute on August 8th with 1 queen, 36 workers, 41 larvae and 22 pupae at 2 combs. The colonies were each placed in a wooden nest box ($70 \times 35 \times 35$ cm^3). These boxes had two doors with plastic windows so that the colony development could easily be observed. The hornets were able to go outside by means of plastic tunnel system with an inner diameter of 3.2 cm and a length of 1 m. In Germany, hornets are listed as an endangered species and therefore they are protected by governmental law. The Berlin Senator for Environment and Protection of Nature gave us kind permission to pursue these experiments. During our procedures, no animal was killed or harmed, and both colonies developed normally.

Calorimetric experiments

Calorimetric experiments were performed in a batch calorimeter (Bioflux, MV Meßgerätevertrieb, München) with vessels of 25 ml capacity. The sensitivity of the instrument was 55 mV W^{-1}. It was adjusted to the temperatures of the three test series: 10, 15 and 20°C. The calorimeter signal was registered with a chart recorder (BD 41, Kipp and Zonen, Delft). The mean heat flow rates of the animals were determined by integrating the heat production rate $P(t)$ over a period of 2–3 h by means of an electronic planimeter (Digikon, Kontron, Munich). Maximum and minimum heat production rates were evaluated dividing the $P(t)$ curves into 10 min intervals. Intervals of highest and lowest heat production rate during each single experiment were selected and the average heat flow rate during these intervals was regarded as P_{MAX} and P_{MIN} for the maximum and minimum heat production intervals respectively.

Hornets were caught when leaving the nest for foraging or mating so that it was reasonable to assume that they had enough food to survive for some hours. Laying queens and larvae were caught directly in the nest with tweezers after they had gained some food from their nestmates. Virgin queens appeared only for a short period in the nest cycle (less than one week). Their individual heat production rates could only be measured at 15°C, because a new temperature adjustment of the calorimeter would have taken about two days. All individuals were weighed before and after the experiments, using a mechanical balance (Type 414/13, Sauter, Ebingen). The mean values of the body weight in each experiment were used to calculate the mass-specific heat production rates of the individual hornets.

During the 1991 season, nest temperatures were measured with thermocouples (T-BMB Ni/Ni–Cr, Linseis, Selb) at two points in the nest and recorded (chart recorder type 2065, Linseis, Selb). At the end of the season when all the hornets had disappeared, a resistor (Dale resistor, 25 W, 10 Ω) was placed in the empty nest under the lowest comb near to the nest entrance. Then the nest was heated up using this resistor to the same temperatures as determined in the intact colony at the same ambient temperatures T_A. In this way, the energy corresponding to the average heat production rate of the whole hornet nest could be evaluated.

RESULTS

Heat production rates in drones and workers at ambient temperatures of 10, 15 and 20°C showed a distinct increase at 20°C (Fig. 1). The mass-specific heat production of workers and drones was 2.5 times higher at $T_A = 20$°C than that at $T_A = 15$°C. Hornets did not increase their heat production at low ambient temperatures, suggesting that they follow an ectothermic behaviour. Nevertheless, it should be noted that heat production during the first 30 min of each experiment could not be measured due to technical reasons: handling the calorimeter vessels to put the hornets inside caused an initial heat overshoot which was equilibrated only after 30 min. It is, therefore, not clear if hornets first behave endothermally and then switch to ectothermy after a while due to exhaustion.

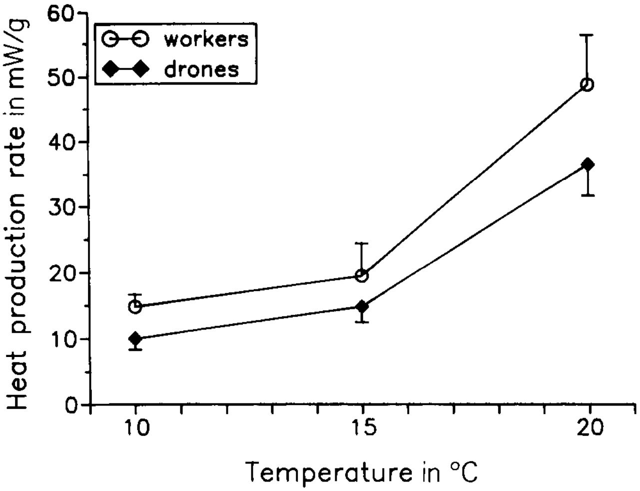

Fig. 1. Mass specific heat production rates of hornet workers and drones as a function of the ambient temperature T_A. Each point is the mean of five independent experiments. Bars indicate the standard deviation.

The locomotor activities of hornets during an experiment can be recognized from typical structures in the calorimetric curves: tranquil animals show no fluctuations in the curve, whereas any locomotor activity causes a rapid increase in heat flux. These peaks can be quantified as portions of locomotor activities during an experiment. Locomotor activity P_{LOC} may be expressed as the difference between the maximum and minimum heat production rates

$$P_{LOC} = P_{MAX} - P_{MIN} \tag{1}$$

In extreme cases, P_{LOC} represents the metabolic scope, which is the difference between minimum and maximum possible heat production rates. It should be noted that the minimum heat production rate differs from the resting metabolic rate (RMR), which is defined as the heat production rate of inactive fasting animals. Because adult hornets, with the exception of virgin queens, cannot fall back upon food reserves when their crop is empty, such a status is lethal. P_{LOC} alone gives no hint of the mean heat production rates (P_{MEAN}) at which locomotor activities occur. Hence, a locomotor quotient L can be introduced

$$L = P_{LOC}/P_{MEAN} \tag{2}$$

L is used to quantify the portion of heat production rate during locomotion or stress in relation to the mean heat production rate.

Figure 2 presents the L values of drones and workers at different ambient temperatures. Drones and workers show increasing activities (indicated by P_{LOC}) at higher T_A, but no significant differences in L values can be detected in mean heat production rates at these temperatures. An exception is the L

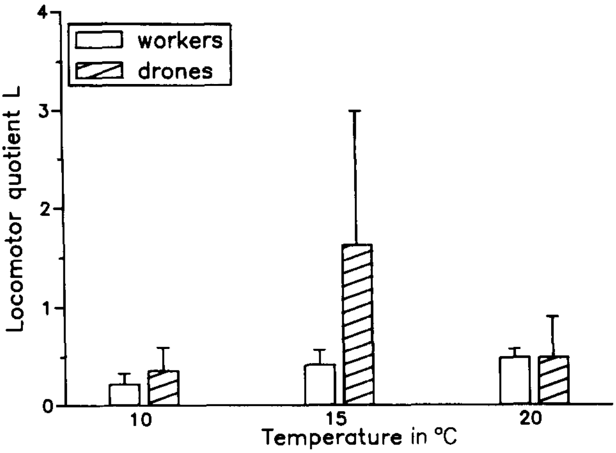

Fig. 2. Locomotor quotient L of hornet workers and drones at three ambient temperatures. Each point is the mean of 5 independent experiments. Bars indicate the standard deviation.

value of drones at 15°C, but as the heat production rates are very disperse at this temperature (note the large standard deviation) no significant differences from the values at 10 and 20°C can be established. Table 1 shows P_{MAX}, P_{MIN} and P_{MEAN} values for drones and workers at $T_A = 20$°C. Mass-specific heat production rates of virgin queens at $T_A = 15$°C have comparative values to those of drones and workers at the same temperature (12.4 mW g^{-1}, SD ± 2.3 mW g^{-1}), with an average body mass (1.164 g, SD = ±0.134 g, $n = 7$) about three times higher than those of workers and drones.

At the end of the season, the abandoned nest of colony 1 was heated artificially by an electric resistor at an ambient room temperature of 16°C. This temperature was equivalent to the average temperatures experienced by the colony during September and October 1991. To heat the colony to an inner temperature of 26°C at this ambient temperature, a power output of 1.8 W was necessary. By mid-October, the mean nest temperature of the still intact colony was 23°C. With a power output of 1.3 W, this temperature

TABLE 1

Body mass (M) and mean, maximum and minimum mass-specific heat production rates (P_{MEAN}, P_{MAX}, P_{MIN}), and locomotor quotient L of hornet workers and drones at 20°C. Each value is the mean of 5 independent experiments

	M in g	P_{MEAN}/M in mW g^{-1}	P_{MAX}/M in mW g^{-1}	P_{MIN}/M in mW g^{-1}	L
Workers	0.45 ± 0.05	48.4 ± 7.5	62.4 ± 9.1	39.2 ± 9.1	0.49
Drones	0.35 ± 0.1	36.5 ± 4.9	53.2 ± 12.6	30.1 ± 6.9	0.49

TABLE 2

Temperatures (°C) in an occupied hornet nest (colony 1)

Week (1991)	Ambient temperature		Nest temperature	
	Max	Min	Max	Min
2.09–8.09	17.6	15.2	26.6	23.8
9.09–15.09	17.2	15.0	26.8	25.4
16.09–22.09	16.9	15.7	26.2	24.5
23.09–29.09	17.0	15.1	26.6	23.8
30.09–6.10	16.4	15.0	25.6	22.8
7.10–13.10	16.5	15.0	25.7	21.2
14.10–20.10	16.2	14.6	22.5	20.7

could be achieved at $T_A = 16°C$ (Tables 2 and 3). After the appearance of the reproductive forms (virgin queens and drones), temperatures inside the nest decreased at stable room temperatures.

DISCUSSION

The endothermic behaviour of hornet workers and drones could not be detected by means of direct calorimetry, because of two probable reasons.

1. The heat production rates of hymenopterans strongly depend on experimental conditions because these animals respond sensitively to external factors, such as light, optical signals, temperature or even the presence of conspecifics. Our experiments showed that hornets like other hymenopterans have a wide range of metabolic performance [7, 8], but it should be expected that the metabolic scope of hornets may be even larger than that evaluated in our experiments, because the calorimeter vessels were rather small. Hornet workers have maximum heat production rates

TABLE 3

Electrical heating of an empty hornet nest at an ambient temperature of 16°C, n = number of experiments

Electric power in W	n	Temperature obtained in °C	
		Inside nest	Surface of nest
1.3	5	25.6	23.5
1.4	5	25.9	23.1
1.6	5	26.4	23.8
1.8	5	26.1	23.2
2.2	5	26.7	23.5

that are about twice as high as the minimum heat production rates. This difference can be up to ten times in honeybees under suitable experimental conditions [9].

2. Direct calorimetry is an excellent, but rather "slow" measuring method, and the first experimental results cannot usually be obtained before 30–60 min. We are now developing a "drop in" batch calorimeter, in which the animals are placed directly in the calorimeter without moving the vessels, thus avoiding friction heat of the vessel and any other heat artifact that can appear during their manipulation.

The mass-specific heat production rates of hornet workers at $T_A = 20°C$ can be compared with the heat production rates of honeybee foragers at the same T_A, because all the hornets measured were foragers (see above; note that hornets, unlike honeybees, show no division of labour). The heat production rates in honeybees were 280 mW g^{-1} [8] compared to 49 mW g^{-1} for hornets. The heat production rates of hornet drones at $T_A = 20°C$ (36 mW g^{-1}, SD = ±5 mW g^{-1}) were smaller than those of workers, but the difference between drones and workers in honeybees is much higher (honeybee drone; 118 mW g^{-1}) [8]. This indicates that heat production in honeybee workers is more than twice that in drones, whereas in hornets the difference amounts to only 30%. It is therefore not unlikely that drones contribute significant portions to the heat production in the nest at the end of the season, when they represent approximately 20% of the colony biomass.

The heat production rates of the colony were 1.8 W when the maximum biomass was reached in September and decreased to 1.3 W at the end of the season in October. This is in accordance with other data [10] from two *Dolichovespula* species. Generally, the thermoregulatory abilities of hornet and wasp colonies decrease after the appearance of reproductive forms [2, 11]. Interestingly, the heat production rate of a whole bumblebee colony, measured by means of direct calorimetry, ranges from 0.3 W up to 1.4 W [12] and is thus within the range of heat production rates of hornet colonies with similar size and biomass.

ACKNOWLEDGEMENTS

We thank Norbert Langer for help in relocating the hornet colonies and Paul Schultze-Motel for critical discussions.

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