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A method for continuous direct calorimetric measurements of energy metabolism in intact hornet (*Vespa crabro*) and honeybee (*Apis mellifera*) colonies ☆

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Abstract

The heat production rates of an intact hornet (*Vespa crabro*) colony and a honeybee (*Apis mellifera*) winter cluster were measured by means of direct calorimetry. Two camping cold boxes with Peltier elements as cooling systems were used as simple and inexpensive differential calorimeters. The boxes had a volume of 24 l and sensitivities of between 6.8 mV W^{-1} and 14.8 mV W^{-1}, depending on the experimental setup. They were modified in such a way that the foragers had free access to the outdoor environment. The average daily heat production rate of the hornet colony ranged from 1.2 W at the end of the season in October up to 12.5 W at the stage of maximum biomass in August. The heat production rates of a honeybee winter cluster were measured in the following winter at ambient temperatures of 0-5°C. The maximum heat production rate was attained at 0°C (20.5 W) and the minimum heat production rate at 5°C (11.5 W). These results are compared with data for energy metabolism obtained respirometrically and by artificial heating of empty nests, respectively.

Keywords: *Apis*; Bioenergetics; Calorimetry; *Vespa*

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1. Introduction

It is a well-established theory among biologists that social insect societies may be regarded as superorganisms. The term superorganism implies that these colonies behave and react as a natural entity analogous to individual multicellular organisms. Although the concept of superorganisms is disputed by evolutionary biologists and the term in its original meaning is not appropriate for all social insect species [1], one can assume that at least in some ecological and behavioral aspects, social insect societies can be regarded as superorganisms. For instance, in thermoregulation the colony as a unit gives responses to changes in ambient temperatures in order to keep the nest temperature stable (analogous to body temperatures in individual homeotherm organisms) [2]. For this reason, it is interesting to determine the metabolic rates not only of individual foragers or workers, but of the colony as a whole. There have been some previous attempts to measure the energy metabolism of honeybee and social wasp colonies:

(1) In respirometric measurements, honeybee colonies were placed in an airtight bee hive and oxygen consumption rates were determined [3,4]. This method has to face the problem that the bees were not allowed to forage during the measurements, which is obviously quite an artificial situation for the bees.

(2) The metabolic rates of wasp and hornet colonies have been assessed by artificial heating of the nests at the end of the season [5,6] when the population of the nest had died out for natural reasons because wasps and hornets form only annual colonies in northern temperate zones. The empty nests were heated up by means of an electrical resistor towards temperatures which were obtained in populated colonies during the season. In this way, the average metabolic rate of colonies could be evaluated. The problem of this method is that it is rather cumbersome to calculate the energy expenditure for a whole season, and circadian effects cannot be estimated very exactly.

Therefore, it was the aim of our study to develop a simple method to determine the metabolic rates of undisturbed hornet colonies (and also, for comparative reasons, honeybee colonies) with free access for foragers to the outdoor environment.

2. Material and methods

2.1. Experiments with hornets

Two electric camping cold boxes of 24 l volume each (WAECO TD-24 G-12, Emsdetten, Germany) were used as simple and robust differential calorimeters. These cold boxes carry a Peltier element on the backside wall serving as a heat pump. If a d.c. current of 12 V is applied to the elements a temperature gradient is generated between the inside and the surroundings. Cold boxes with this cooling principle can also be used as inexpensive calorimeters, because the heat flowing through the Peltier element creates a thermoelectric voltage proportional to the heat flow [7]. The boxes were slightly modified for our measuring purposes. Copper foil was glued to the walls of the boxes to improve the heat conduction to the Peltier element. Entrance ducts (diameter, 4 cm) were drilled into the calorimeter boxes and connected to exit holes in nearby windows with a transparent plastic tunnel (length, 40 cm). This walkway was long enough to limit cold draughts from the outside. In a twin-arrangement, one box served as a measuring chamber and contained the nest, the other served as a control chamber. Nest temperatures, as well as the temperature inside the control chamber, were measured by means of thermocouples. All temperature and calorimeter signals were recorded continuously with a chart recorder (Linseis L 2005, Selb, Germany). The boxes were placed in a room at the Institute for Biophysics in Berlin-Dahlem. Room temperatures were stable between 18 and 20°C. To prevent the condensation of water, the calorimeter box was ventilated by opening the door if necessary. A removable metallic grid was placed between the door and the chamber.

The calorimeter was calibrated for all modifications of the interior design of the chamber and all ambient temperatures. The sensitivity of the calorimeter amounted to 14.8 mV W^{-1}.

The mean heat production rates of the colonies were determined by integrating the heat production rate $P(t)$ over a period of 22–24 h by means of an electronic planimeter (Digikon. Kontrol, Munich). These heat production rates were regarded as the average daily heat production rate. In addition, the stage of nest-building was noticed and the weight of the hornet colony was evaluated. The entrance ducts were closed, and the complete measuring chamber was weighed, always at the same time of day (3 pm), using a mechanical balance (Soehnle Domestic scale, Murrhardt, Germany). Because this procedure disturbed the colony, it was repeated only about once a week. At the end of the season, the complete chamber with the empty nest was weighed again, after preparing the nest to a state which looked identical to that noted after the weight measurements during the season. From the values obtained in this way, the mass-specific heat production rates were calculated.

The hornet (*Vespa crabro*) colony used for the experiment was relocated from the original nest site in a shed at a youth camp in Berlin-Tegel. Unfortunately the nest was only detected on August 14, after the season for hornets had started. The nest contained 1 laying queen, about 250 workers and 4 combs. The nest was glued to a removable plate at the top of the measuring chamber. All workers were set in the chamber after cooling them in a refrigerator for a short time in order to immobilize them. On the day after the relocation procedure, the entrance of the nest was opened, and the workers continued to forage after reorientation flights. All measurements were performed between August 18 and October 17 in 1993.

2.2. Experiments with honeybee winter cluster

The calorimetric experiments with the honeybee (*Apis mellifera*) winter cluster were performed between December 10, 1993 and February 15, 1994. The experimental setup was identical to that of the hornet measurements, the calorimeter was placed in a small hut in the garden of the Institute for Zoology. To achieve identical experimental conditions, the entrance duct was connected to exit holes in the same manner as we did for the hornets, although we did not expect the bees to forage in winter (indeed they did not). The ambient temperatures ranged between 0 and 5°C and the sensitivity of the calorimeter was 6.8 mV W^{-1}. The difference in the sensitivities is explained by the fact that some heat produced in the calorimeter chamber gets lost through the entrance ducts. The heat loss is greater when the temperature gradient is higher in winter at low temperatures. In order to check if changing ambient temperatures had an influence on the sensitivity of our calorimeter, an electrical resistor was placed in the control chamber on wax frames. Using an automatic timeswitch connected to a power supply, the resistor was heated up periodically with a frequency of 4 h. The heat production rate $P(t)$ was integrated over periods when the ambient temperature remained stable. Because in the first 14 days of our experiments we found only a small number of dead bees, we assumed a constant weight of the colony for calculating the mass-specific heat production rates for this period.

The honeybee winter cluster was relocated on December 8 from a normal bee hive in the garden of the Institute for Zoology. The cluster had a weight of 1 kg and was placed on 10 food frames (22 cm × 28 cm) with sufficient sugar syrup to survive the winter.

3. Results

3.1. Hornets

The hornet colony developed as expected in the time from August 18 to October 17. The average daily heat production rate of the colony showed a slight increase up to 12.5 W in August (Fig. 1), followed by a slow decrease during September. One week after the first reproductive forms appeared in the nest (September 20) the heat production rate drastically decreased. Simultaneously, the colony biomass became smaller (Fig. 2). By the middle of October the weight of the colony was reduced by 55% compared with values from the end of September. Decreases in both heat production rate and in colony biomass were expected and are caused by the natural seasonal decline of the hornet colony. Nevertheless, the decrease in the mass-specific heat production rate was surprising because the nest temperatures were stable until October and one would expect a higher heat production rate per unit biomass at the end of the season. Fig. 3 shows the power–time curves on three selected days during the period of measurements. In August at the peak of colony development, one can see a circadian rhythm of the heat production rate. During the evening and the night, heat production as well as nest temperatures decrease slowly and increase during the morning until midday. Obviously, the food reserves of the colony are used up, and during the morning most workers start to collect food again. In September, the daily $P-t$ curves show no pronounced profile, probably due to the fact that at this time a greater percentage of workers continued to forage during the night. In October heat production is low and thermoregulation in the nest is weak.

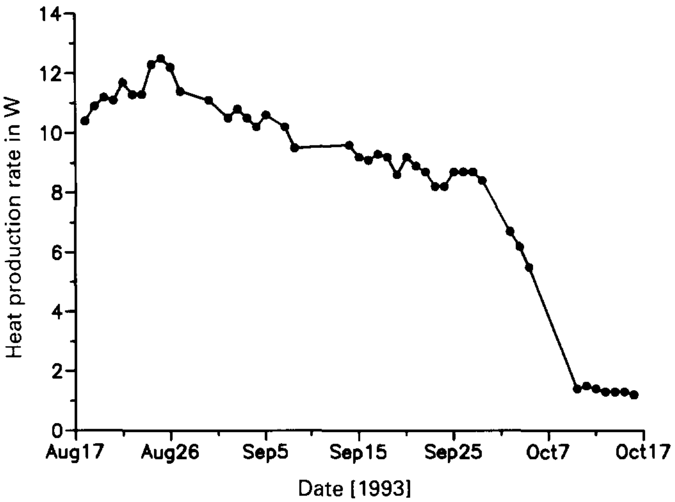

Fig. 1. Average daily heat production rate of the hornet colony.

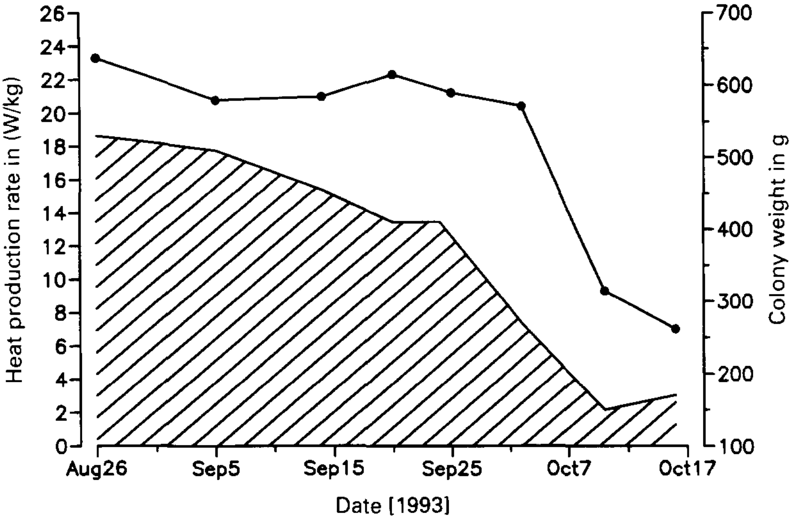

Fig. 2. Mass-specific heat production rate (upper curve, points) and development of colony weight (curve below, hatched) of the hornet colony.

Comparing the average number of incoming foragers per minute with the heat production rate, as shown in Fig. 4, a slight correlation between the increase of returning foragers and the increased heat production rate can be observed.

3.2. Honeybee winter cluster

To check the results obtained for hornets with this simple and inexpensive calorimetric device, we determined the heat production rates of honeybee winter

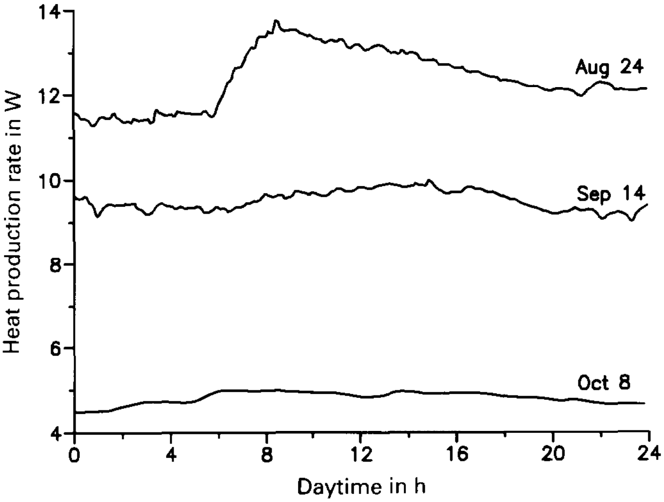

Fig. 3. Typical $P-t$ curves of the hornet colony on three selected days during the 1993 season.

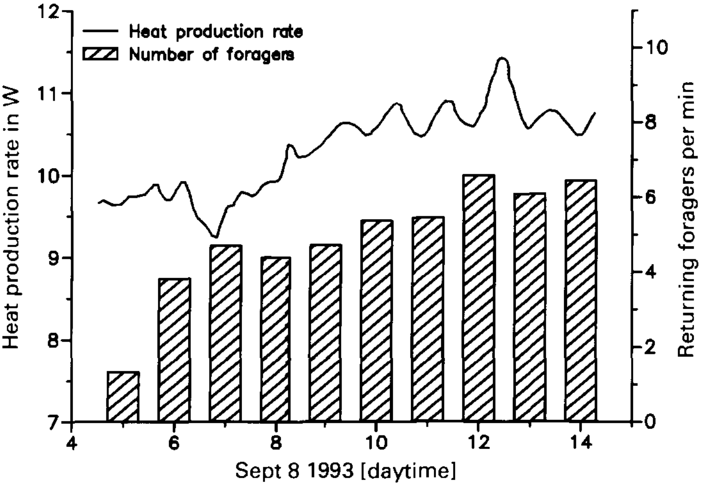

Fig. 4. Correlation between heat production rate and traffic rate of returning foragers of the hornet colony. Each bar presents the average number of returning foragers per minute, observed over 1 h.

clusters between December 1993 and February 1994 and compared them with previous data [3]. The honeybee winter cluster behaved normally in the calorimeter box, although in February a number of bees died probably because of the high humidity in the calorimeter chamber. Data from this period were not considered in our results.

The average heat production rate at ambient temperatures of 0–5°C was 16.7 ± 3.3 W ($n = 11$). The maximum value was achieved at 0°C and amounted to 20.5 W; the minimum value at 5°C was 11.5 W. In order to check the sensitivity of the calorimeter during the experimental period, the control chamber was frequently calibrated by means of an electrical resistor which was placed on food frames inside the control chamber. The data for the sensitivity were 6.8 ± 0.3 mV W^{-1} ($n = 16$). The small standard deviation indicates that the sensitivity remained stable even with changing ambient temperatures.

4. Discussion

The mass-specific heat production rates in the present experiments for the honeybee winter cluster as well as the values for the hornet *Vespa crabro* are in good agreement with previous literature data (Table 1). The data for two *Dolichovespula* species [5] differ notably from the hornet data, although they were achieved in one case with the same method (heating up the empty nest by using an electrical resistor). It is unclear if the difference between these data has methodical or biological reasons. The quality of data for mass-specific heat production assessed with the electrical resistor method depends on several factors, for instance the position of the resistor and the thermocouples inside the nest. Wasps tend to alter the internal architecture of their nests at the end of the season, and it is not known to what extent this has an influence on the measuring method. There is also a possible biological explanation for the much lower heat production rates of *Dolichovespula* because these species build free-hanging nests whereas *Vespa crabro* usually place their nests in cavities [8,9]. Free-hanging nests should demand better insulating capabilities than nests in cavities. Data for the heat conductivity of the

Table 1
Mass-specific metabolic rates of social insect colonies

T_A [a] in °C	Metabolic rate in W kg^{-1}	Method	Ref.
Honeybee winter cluster			
0-5	4.2-15.1	Respirometry	[3]
0-5	11.5-20.5	Direct calorimetry	This study
Honeybee swarm			
0-5	9.5-18.9	Respirometry	[14]
Dolichovespula arenaria			
30	3.3 and 4.1	Heating with an electrical resistor	[5]
Dolichovespula maculata			
30	5.4 and 6.4	Heating with an electrical resistor	[5]
Vespa crabro			
23	26.7	Heating with an electrical resistor	[6]
26	23	Direct calorimetry	This study

The weight of the *V. crabro* colony determined by Schmolz et al. [6] was 63 g (Schmolz, unpubl. data). For both *Dolichovespula* species, two nests were measured. All mass specific metabolic rates for hornets and wasps were obtained at maximum biomass stage.

[a] Ambient temperature.

nest envelopes as well as the physiology of different wasp species are lacking, so that it is unclear to what extent the insulation properties of nest envelopes influence the energy metabolism of wasp colonies.

The mass-specific heat production rate of the hornet colony decreased markedly from the end of September onwards, although the nest temperatures remained stable for a longer period. This was surprising because a high mass-specific heat production rate per unit biomass at the end of the annual nesting cycle was expected. Two things have to be considered when regarding this phenomenon: firstly, hornets reduce the inner volume of their nests simultaneously with the decline of the population in the nest [Schmolz, unpublished data] and reduce the energetic demands for nest thermoregulation by doing so; and secondly, at the end of the season larvae represent a large portion of the colony biomass [9], but do not contribute much heat to the nest [10]. One would expect that the heat production rate per remaining worker is higher than the mass-specific heat production rate presented here as shown elsewhere for the metabolic rates of bumblebee colonies [11]. The average heat production rate of a bumblebee nest measured using a method that was very similar to that presented in our study varied between 0.3 and 1.4 W, i.e. much lower than the heat production rate of our hornet colony.

There are previous reports about temperature drops in wasp and hornet nests during the night [12,13]. As shown in these papers, the decline of temperature in the nest can be reduced by artificial food supply to the colonies. This indicates that the low heat production rates found in August during the night (Fig. 4) are due to a limited food supply when the workers ceased their foraging activities with the beginning of the night, because the ambient temperatures in our measuring room remained stable. Later in the season, the hornets were observed to continue foraging at night, and the heat production rate remained stable over a 24 h period. The reason for these observations has to be examined more closely in further studies although there is some evidence that heat production rates and foraging activity are correlated (Fig. 4).

The data found for heat production rates in honeybee winter clusters are somewhat higher than the data reported by Southwick [3]. Heat production rates of honeybee swarms at 0–5°C measured by Heinrich [14] were 9.5–18.9 W kg^{-1}, in the same range as our data. The differences may be explained by the different size of the bee clusters which is known to have an influence on the metabolic rates [4], rather than by the different measuring methods.

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