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Heat loss and thermoregulation in a nest of the bumblebee *Bombus lapidarius* (Hymenoptera, Apidae)

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Abstract

Heat loss and brood cell temperatures in a *Bombus lapidarius* colony were measured by settling the whole nest inside a large calorimeter box. A walkway connected the interior of the box with the outside so that the bumblebees could attend to their normal foraging activities. Brood cell temperatures were maintained between 27 and 32°C, the mean rate of heat loss from the nest varied between 0.3 and 1.4 W. The daily heat loss typically showed a sinusoidal time course.

INTRODUCTION

Unlike the closely related honeybees that exist in large permanent colonies with many thousands of individuals, bumblebees form smaller colonies of a less sophisticated social organisation. In northern temperate climates, a bumblebee nest only exists from spring to autumn, producing a few hundred workers at most. Young queens emerge in late summer; after hibernating underground, they establish new colonies in the spring of the following year.

The ability of bumblebees to raise the temperature inside their nests several degrees above ambient temperature has fascinated biologists for a long time. As early as 1837, Newport measured the temperature inside bumblebee nests with mercury thermometers [1]. Several other authors have reported that the nest temperatures of various bumblebee species were maintained in the range 27–32°C, independent of the ambient temperature [2–7]. The heating of the nest is accomplished by an endothermic [a] warmup of the flight muscles of individual bumblebees. The heat released by this increase in metabolic rate is used for brood incubation [9,10].

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[a] In its physiological sense, "endothermic" refers to heat derived from metabolic processes; in physiology, the terms "endothermic" and "ectothermic" are used in the opposite sense to "endothermic" and "exothermic" in thermodynamics [8]. In a thermodynamic sense, metabolic heat production is of course driven by exothermic biochemical reactions.

Although the temperature balance of bumblebee nests has been studied extensively, the energy expenditure of entire colonies that is necessary to achieve endothermic heating has been largely neglected; there is only one report on the oxygen consumption of bumblebee nests at different ambient temperatures [11].

In this study, I present data for the daily and seasonal time course of the heat flow from a nest of the bumblebee *Bombus lapidarius* measured by direct calorimetry.

MATERIALS AND METHODS

Animals

In spring 1990, hibernated *Bombus lapidarius* queens searching for nest sites in the area of the Botanical Garden in Berlin-Dahlem were captured and placed in the entrance ducts of outdoor nest boxes. Each nest box consisted of a cardboard box, loosely filled with upholstery cotton, placed inside a larger wooden box and covered with dry gardening peat for insulation [12]. Several bumblebee queens accepted the artificial nests and started to build new colonies. The queen whose nest was later selected for experiments had been captured on March 21; the first workers could be observed leaving this nest on April 18.

On May 9, the colony was transferred into the calorimeter box together with a small amount of upholstery cotton. The queen and all 37 workers present were individually marked with plastic numbers glued to the dorsal surface of their thorax. Some of the workers that had been on foraging trips outside the nest at the time of the transfer were trapped when they later entered the old nest box and were also taken to the new nest site.

Procedures

An electric camping cold box (Sunny Cool, Quelle) containing a Peltier element in the bottom was used as a simple, robust calorimeter [13,14]. With a capacity of 8 l, it was large enough to hold a whole bumblebee nest and was suitable as a nest box. The heat flowing through the walls of the closed calorimeter box creates a thermoelectric voltage at the Peltier element that is proportional to the heat flow. A 2 mm brass plate was placed onto the inner bottom of the box in order to improve heat conduction to the Peltier element. A circular opening with a diameter of 25 mm was drilled through the wall of the calorimeter box at one of the corners, as an inlet for an entrance duct fitting tightly into the hole. Four NiCr–Ni thermocouples reaching into the interior of the box were permanently installed into one of the side walls. The brass plate on the bottom was covered with wood shavings and the whole box was placed into a larger styrofoam container.

The calorimeter was set up in a basement room where the temperature showed only small variations between 21 and 23°C. This may have confronted the bumblebees with unnaturally stable temperature conditions but was necessary for the operation of the calorimeter. The entrance duct of the calorimeter box was connected to an exit hole in a nearby window with a walkway 60 cm long made from a thick-walled plastic tube with an inner diameter of 19 mm. A small cardboard box with an opening just large enough to allow the passage of bumblebee workers was fixed as a vestibule in front of the exit hole at the outside of the building in order to restrict the access of parasites.

Temperatures near incubated brood cells were measured with one of the thermocouples attached to a digital thermometer (T-DLIN-U, Linseis; accuracy ±0.5°C) and were recorded together with the calorimeter signal on a two-channel recorder. After the completion of the experiments, the calorimeter was calibrated with a heating resistor placed on top of the empty nest inside the calorimeter; the sensitivity of the calorimeter under these conditions was 18.3 mV W^{-1}. The open connection of the calorimeter box with the outside did not significantly influence the calorimeter signal, as the baselines taken before and after the measurements with bumblebees remained remarkably constant. The walkway was apparently long enough to limit cold draughts from the outside.

After the bumblebee colony had been moved into the calorimeter, the box was opened every 1–3 days in order to observe which marked bumblebees were present in the nest, to mark all newly emerged bees and to check the correct placement of the thermocouples between incubated brood cells. At these times, single bumblebees could be taken out of the nest to determine their individual metabolic rate using a combination of Calvet microcalorimetry and respirometry; the results of these experiments will be reported elsewhere. If necessary, the calorimeter box was ventilated for some time to prevent the formation of condensed water. The time between the day of the first marking of a young bumblebee and the last day it was observed inside the nest was recorded and used for the calculation of the number of bumblebees present in the nest on each day. This method allowed for foragers that were absent at census times but returned to the nest at night.

RESULTS

After their transfer into the calorimeter box, the bumblebees soon adapted to the new surroundings, and the development of the colony continued normally. At first the workers kept pulling out the tips of the thermocouples sticking in the wax between brood cells. After a few days,

View of the bumblebee nest inside the opened calorimeter box on June 3, 1990. Note the large queen (q) incubating brood cells at the upper left and the numerous empty cocoons used as honey pots in the middle. Three thermocouples (arrows) sticking in the brood area are partly covered with a wax canopy. The Lego brick at the right (16 mm × 32 mm) could be filled with sugar solution and served as a feeding trough.

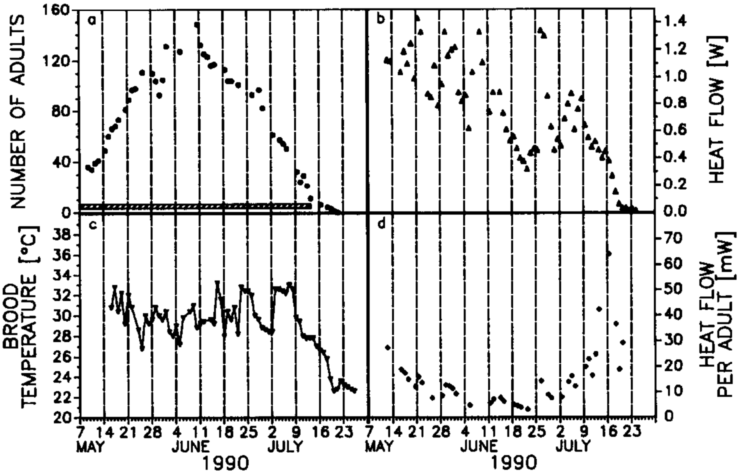

Fig. 2. (a) Calculated number of adult bumblebee workers and males present in the nest. The lifetime of the queen is given by a hatched bar. (b) Mean total heat flow from the nest. Results of 24-h-measurements on days without disturbance of the nest are given by closed symbols. Estimates of the mean daily heat loss on days when the calorimeter box was opened were calculated from measurements during the undisturbed period between midnight and 6 a.m. (open symbols). (c) Temperature at incubated brood cells at 2 a.m. (d) Mean heat flow per adult bumblebee. Calculated from data presented in (a) and (b).

however, they seemed to accept the thermocouples and started to cover them with wax. Sometimes they even constructed extended wax canopies using the thermocouples as fixations (Fig. 1).

On June 25, it was noted that the vestibule in front of the exit hole contained several brood cells. About 25 workers that had not been observed inside the nest box for several days were also present in the vestibule. Apparently some workers had evaded the control of the queen and had started to lay eggs. Brood cells and workers were removed from the vestibule and placed into the calorimeter box next to the main nest. As could be expected, only males developed from the vestibule brood cells.

The first male had emerged on June 14 from the main nest; a total of 21 males but no young queens were produced by the colony. During the few days before they left the nest, several males could be observed incubating brood cells by pressing their abdomen against the wax cocoon in the same way as did the workers and the queen [15]. The number of adult bumblebees present in the nest reached a maximum around the middle of June; after that it declined constantly (Fig. 2(a)). The queen died on July 13 and the nest was empty on July 21.

The comb temperature near the brood cells and the heat loss of the nest on a representative day during the incubation period are presented in Fig. 3. The temperature was maintained between 29 and 33°C (31.7 ± 1.0°C;

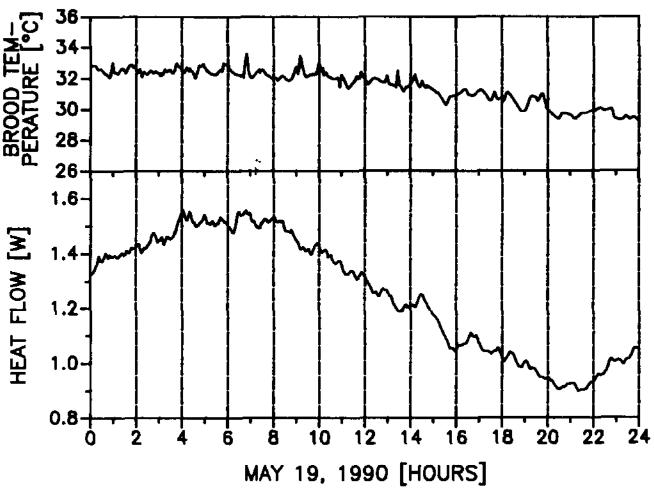

Fig. 3. Typical time course of the temperature measured between brood cells and the heat loss of the nest over a 24-h period.

mean ± SD), and the heat flow showed a maximum during the early morning hours and a minimum in the evening.

The heat flow during the period between midnight and 6 a.m. was measured on all days, even when the calorimeter box would be opened for inspection later during the day. On days without disturbance, the heat flow could be measured over 24 hours. For these days, the following regression function was calculated: $y = 0.90x + 0.02$ ($r = 0.89$; standard error of estimate $s_{y \cdot x} = 0.19$ [16]), where x is the mean heat flow in W between midnight and 6 a.m. and y is the mean heat flow in W over 24 hours. Using this equation, estimates for the mean daily heat flow could be calculated from the measurements made in the early morning on days when the calorimeter was opened (Fig. 2(b)). The mean daily heat flow during the lifetime of the queen ranged from 0.3 to 1.4 W. The large heat loss of the nest after June 25 was due to an increased activity of the bumblebees after the transfer of the vestibule brood cells to the main nest.

The temperatures taken between incubated brood cells at 2 a.m. showed variations from day to day but were maintained within a range from 27 to 33°C (30.1 ± 1.7°C; mean ± SD) during the lifetime of the queen (Fig. 2(c)). After the death of the queen on July 13, there was a rapid decline towards room temperature.

The mean heat flow calculated per number of adult bumblebees present in the nest follows a roughly U-shaped time course (Fig. 2(d)). The data for the days preceding June 25 may be slightly too low, because an unknown number of workers may have stayed outside the main nest on the brood cells in the vestibule although they had been counted as present in the nest; consequently, they would not have contributed to the heat production inside the calorimeter box.

DISCUSSION

According to a classification by Hasselrot [5], a "period of upbuilding", a "period of equilibrium" and a "period of decline" can be distinguished during the development of a bumblebee nest. The first of these phases is characterised by the small number of bumblebees present in the nest, comparatively large excursions of the nest temperature and a small honey store. This period could not be examined in this study as it was not possible to transfer the young colony before the emergence of the first workers.

The following equilibrium period coincides approximately with the time between the first measurements and the death of the queen in the present study. It is characterised by a large number of workers providing plenty of honey, stable nest temperatures and the production of sexual forms (only males in this study). During the final period of decline, the dwindling number of workers is no longer able to provide sufficient honey supplies. The nest temperature shows larger fluctuations and gradually decreases towards ambient temperature. The nest becomes increasingly susceptible to the attack of parasites such as the bumblebee wax moth, *Aphomia sociella*.

In the present study, the brood comb temperature was maintained between 27 and 33°C during the equilibrium period (Fig. 2(c)). This agrees well with previous studies on the temperature inside *Bombus lapidarius* nests. Hasselrot reported nest temperatures ranging from 29 to 35°C and 20 to 28°C, for two small nests, and a range from 27 to 34°C for three larger colonies of *B. lapidarius* [5]. Wójtowski measured a mean temperature of 32.5°C (range 27–33°C) in a *B. lapidarius* nest during the period of equilibrium [6].

Although its presence inside an artificial nest box may represent an unnatural condition to a bumblebee colony with respect to thermoregulation, the above results are very similar to temperature measurements that were made inside the nests of two other bumblebee species at natural locations. Temperatures inside a *B. agrorum* colony nesting in a garden shed ranged from 28 to 32°C [2]; in a nest of *B. hypnorum* that had been found in a bird nesting box, temperatures varied between 29 and 32°C [3].

During the equilibrium period, the mean daily heat loss from the *B. lapidarius* colony ranged from 0.3 to 1.4 W (Fig. 2(b)). There were considerable variations from day to day, and the heat loss showed a slowly decreasing tendency. It was not correlated to the number of nest inhabitants which increased towards a maximum around June 10 and gradually decreased again (Fig. 2(a)). It appears that the total heat loss was independent of the number of bumblebees: the few workers at the beginning of this period produce slightly more heat than the many workers present at the time of maximal worker density.

This is further illustrated by the U-shaped time course of the data for heat loss per individual (Fig. 2(d)). Even if the heat produced by the queen and possibly by the brood is not taken into consideration in this graph, the average heat production by an individual worker is clearly larger at the beginning and at the end of the colony cycle when fewer bumblebees are present in the nest.

During the equilibrium period, the heat loss per individual ranged from about 5 to 30 mW. This is equivalent to a metabolic rate between 30 and 200 W kg^{-1}, assuming an average body mass of 150 mg per worker. The heat flow values above 50 mW per animal during the period of decline may be an overestimation owing to inaccuracies in determining the exact number of nest inhabitants.

The oxygen consumption of several small colonies of the American species *Bombus impatiens* and *B. affinus* averaged about 25 ml O_2 g^{-1} h^{-1} at 30°C [11]. Assuming a caloric equivalent of 21 J ml^{-1} O_2, this corresponds to a metabolic rate of 145 W kg^{-1}. This is in accordance with the data from the present study. When the American colonies were exposed to ambient temperatures below 15°C, an increase in oxygen consumption up to about 45 ml O_2 g^{-1} h^{-1} (260 W kg^{-1}) was observed while the brood temperature remained in the range between 28 and 32°C. A large number of workers usually engaged in brood maintenance behaviour were recruited for thermoregulation and switched to brood incubation. These results indicate that bumblebees are capable of finely adapting their metabolic heat production in order to keep the nest temperature constant.

Although bumblebee colonies appear to regulate the nest temperature around a set point between 28 and 32°C, the mechanism of nest thermoregulation is still an unsettled question. Heinrich suggested that it was not nest temperature but abdominal temperature of individual bumblebees that was regulated [9]. While incubating, the bumblebees would simply replace the heat lost from their abdomen to the brood by an endothermic warmup of their flight muscles. This would, however, not explain the wing fanning behaviour that can be observed when bumblebee workers try to cool their overheated nest with outside air [11]. Brood temperature or other unknown cues may thus play a role in the social thermoregulation of bumblebees.

The sinusoidal time course of the 24-h heat flow record presented in Fig. 3 is typical for the data obtained during the equilibrium period. On most days, heat flow from the nest was maximal around 6 a.m. and minimal in the evening, even though the total daily heat flow varied. The fact that all foragers usually returned before sunset and stayed in the nest during the night, as well as small fluctuations in the ambient temperature, may have contributed to this cyclic circadian pattern. There may also have been an endogenous component causing a rhythmic variation in the metabolic rate of the colony. A similar phenomenon has been observed in winter clusters of honey bees [17]. The oxygen consumption of these swarms showed a pronounced periodicity with maxima around 2 p.m. and minima during the early morning hours, even when ambient temperature was held constant.

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