Naturwissenschaften (2002) 89:299–301
DOI 10.1007/s00114-002-0338-7

SHORT COMMUNICATION

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Hot spots in the bee hive

Received: 15 January 2002 / Accepted: 28 April 2002 / Published online: 15 June 2002

Abstract Honeybee colonies (*Apis mellifera*) maintain temperatures of 35–36°C in their brood nest because the brood needs high and constant temperature conditions for optimal development. We show that incubation of the brood at the level of individual honeybees is done by worker bees performing a particular and not yet specified behaviour: such bees raise the brood temperature by pressing their warm thoraces firmly onto caps under which the pupae develop. The bees stay motionless in a characteristic posture and have significantly higher thoracic temperatures than bees not assuming this posture in the brood area. The surface of the brood caps against which warm bees had pressed their thorax were up to 3.2°C warmer than the surrounding area, confirming that effective thermal transfer had taken place.

Introduction

Active brood incubation occurs in social insects such as honeybees (*Apis mellifera*), bumblebees (*Bombus* spp.) and vespine wasps (Vespinae), because high and constant rearing temperatures lead to short development times as well as low rates of malformation and mortality (Himmer 1927; Muzalewskij 1933; Seeley 1985). Heat is produced in imagines with the wing muscles located in the thorax (Krogh and Zeuthen 1941; Esch et al. 1991) and is transferred via thorax or abdomen to the developing brood (Esch 1960; Heinrich 1972a, b). In the capped brood area of honeybee colonies, where pupae develop, the temperature is regulated at 35–36°C (Hess 1926). Honeybee workers with high thoracic temperatures in the brood area were described as brood-heating individuals (Esch 1960; Kronenberg and Heller 1982; Schmaranzer et al. 1988), but the mechanism of heat transfer from the warm bee to the brood has not yet been specified. We first analysed thoracic temperatures of bees in the brood area with an infrared camera and found bees with high thoracic temperatures staying almost motionless for several minutes. Subsequently we observed such bees in a modified observation hive with an infrared camera while simultaneously using an endoscope system.

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Materials and methods

Investigations were carried out at the University of Würzburg, Germany, in September 1999 and September 2000. The two queenright study colonies (4,000 and 2,000 individuals of *Apis mellifera carnica*) lived in observation hives that were kept indoors and the bees were allowed to forage in the open. The glass plates on the observation side of the hives were replaced by plastic film, transparent for infrared wavelengths, to allow for thermographic measurements.

First, worker bees in the brood area were recorded simultaneously with an infrared camera [Radiance PM 1/1.5.1b, Raytheon Amber; λ=3.5–5.6 µm, emissivity value ε=0.97, suitable for the bee thorax (Stabentheiner and Schmaranzer 1987), accuracy ± 0.7°C] and a camcorder. Single frames from the infrared camera recordings were captured by a computer every 5 s. A total of 15 bees were traced on the videotapes as long as they remained in the capped brood area or until they visited a cell in the brood area (observation periods between 7.3 and 47.1 min, mean: 20.1 min, SD±10.8 min). Periods of motion and periods of immobility of these 15 bees were recorded. Thorax surface temperatures of the bees were calculated from each single frame using camera-specific software (Ambertherm 1.28) and the temperature scale of the infrared images. No measurements were possible if a bee's thorax was shielded by other bees. The influence of the plastic film was compensated for by measuring thoracic temperatures of dead, artificially heated bees both with the film in place and without it in a parallel set-up.

Second, stationary bees with high thoracic temperatures were spotted in the live thermographic image. Additional close-up observations and recordings of bees were made with an endoscope system (Olympus IV6C5–20), which was introduced from an opening at the side of a modified observation hive with space to move the camera tube between the plastic film and the comb. To

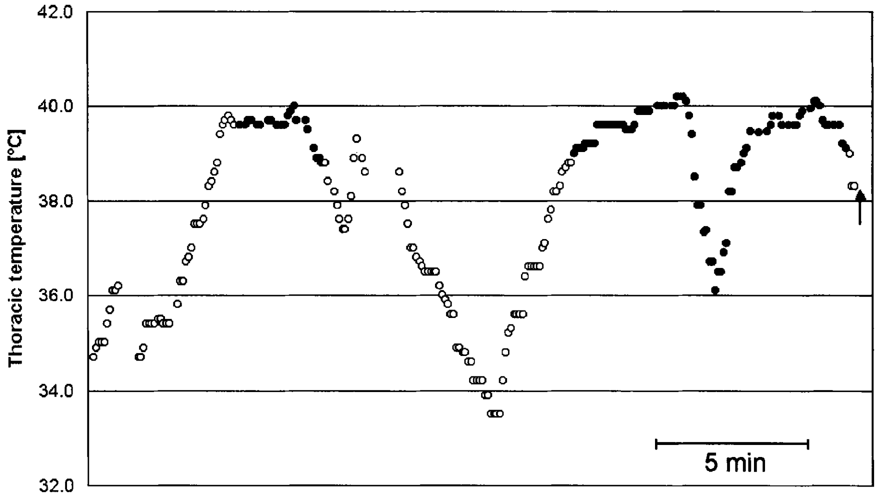

Fig. 1 Time course of the thoracic temperatures of a heating bee in the capped brood area. Thoracic temperatures are high but not constant when the bee is stationary (*filled circles*) and lower when it moves about (*open circles*). Temperature measurements were not possible whenever a bee's thorax was shielded by other bees. An *arrow* marks the point where the bee entered an empty cell in the brood comb

view the temperature distribution on the brood cap surface beneath such bees, altogether 36 bees were pushed aside with the cold tip of the endoscope, which was switched off to prevent artificial warming. The thermographic recordings provided both the thoracic temperatures just before the bees were pushed aside and the temperature of the brood caps on which these bees had been sitting. The temperature difference between the brood cap surface which was in close contact with the bees' thorax (the "hot spot" in the thermographic image) and the average temperature of five surrounding brood caps was recorded. All values are mean ± SD.

Results

Of the 15 analysed bees occupying the capped brood area, we observed 14 that alternated between periods of remaining motionless (apart from respiratory movements of the abdomen and slight antennae movements) for up to 9 min, and periods of moving about. Thoracic temperature values of these bees were not constant but were significantly higher during periods of immobility (mean thorax temperature 38.4±1.3°C, n=14 bees; N=1,210 single temperature values) than during periods of mobility (mean thorax temperature 36.6±1.3°C, n=15 bees, Wilcoxon P <0.002, N=1,781; single temperature values, Fig. 1). During periods of immobility, bees seemed to have their thorax lowered onto the brood caps because of their crouched posture, but the dorsal view of immobile bees did not allow us to determine whether the thoraces touched the caps or not.

However, examination with the endoscope clearly showed that immobile bees with warm thoraces pressed their thoraces firmly onto the brood caps (Fig. 2a), whereas the cooler, mobile bees in the same area did not touch the brood caps with their thorax (Fig. 2b). While the bees pressed their thoraces against the brood caps they pointed their antennae downwards and touched the caps with the tips of both antennae (see Fig. 2a; slow antennae movements over the cap surface may occur). In these bees, fast continuous respiratory movements of the abdomen could also be observed (Heinrich 1972b; Ishay and Ruttner 1971). No activity nor any interaction with other bees in the vicinity took place during this phase of the behaviour.

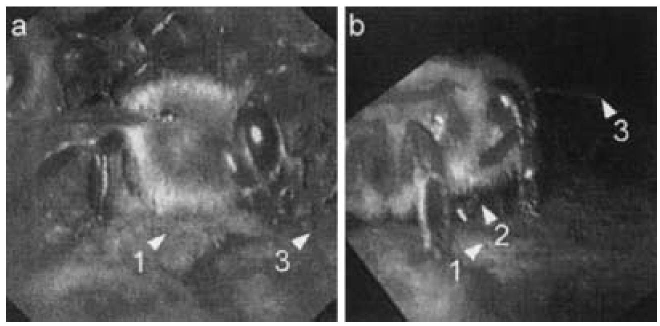

Fig. 2a, b Endoscopic video recordings of bees in the brood area of the hive. **a** One of the stationary bees (n=36) heating the brood caps with its thorax pressed down onto the cell caps. Thoracic temperature = 41.6°C. **b** One of the bees walking over the capped brood with its thorax raised above the cell caps. Thoracic temperature = 35.5°C (mean thorax temperature of walking and resting bees: 33.5±1.4°C, n=32). Key: capped brood surface (*arrow 1*); the gap between thorax and cap surface allows a view of the opposite side of the walking bee and shows one of its legs (*arrow 2*); tip of antenna (*arrow 3*)

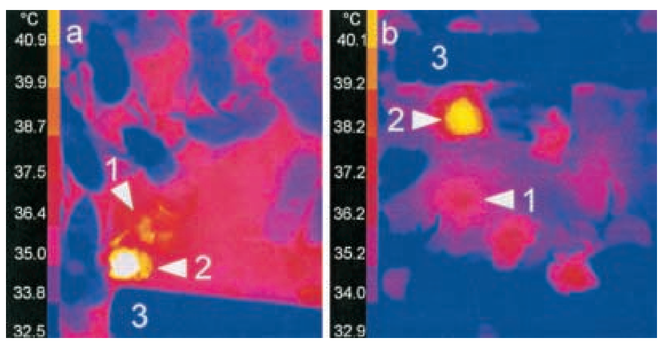

Fig. 3 Thermographic recordings of the capped brood area (**a**, **b**). The infrared images show two "hot spots" (*arrow 1*) on the brood cap surface where warm bees (*arrow 2*) had been pressing their thorax onto the brood cells. Images were recorded immediately after the warm bees (*2*) had been pushed aside with the tip of an endoscope (*3*)

We pushed aside 36 bees that were in close contact with the brood caps to get a view of the brood cap surface beneath them. The infrared images revealed “hot spots” on these brood caps that were up to 3.2°C warmer than the surrounding brood caps (average temperature difference: 1.6±0.7°C, *n*=36 “hot spots”) (Fig. 3a, b). The thorax temperatures of the bees were 38.1–42.4°C just before they were pushed aside (mean = 40.5±1.1°C, *n*=36 bees).

Discussion

Although bees with warm thorax temperatures sitting still in the brood area have been observed before (Esch 1960; Schmaranzer et al. 1988), the mechanism of brood incubation at an individual level – the pressing of the warm thorax firmly onto the brood caps – has not been described. Whereas walking bees (which do not have contact with the comb surface with their thorax) may transfer heat to the comb only via radiation and convection, this behaviour is obviously designed to transfer heat more efficiently by conduction. Resting honeybees have thoracic temperatures at ambient levels (Kaiser 1988) but may appear similar to brood heating bees because both sit quietly on the comb (Esch 1960; Schmaranzer et al. 1988). However, the bees we observed were – apart from their high thoracic temperatures – clearly distinguishable from resting bees because of their crouched posture when they pressed their thorax onto the brood caps and because of the respiratory movements of their abdomens, which were found to be fast and continuous. Such movements are discontinuous with long breaks in resting bees (Kaiser 1988). These observations are consistent with similar observations in bumblebees and hornets (*Vespa crabro*), which were described as performing fast continuous abdominal respiratory movements when incubating (Himmer 1931; Ishay and Ruttner 1971; Ishay 1972; Heinrich 1972a, b). An incubating nest-founding bumblebee queen transfers heat to eggs, larvae and pupae by pressing a specialised hairless “thermic window” of her warm abdomen on to the brood, whereas resting bumblebees keep their body elevated above the substrate (Heinrich 1972a, 1993). The brood-heating queen may remain on the brood for many minutes up to hours and the pressure of the bee creates an “incubation groove” (Heinrich 1993). In this study, the longest period of immobility observed was 9 min; however, incubation periods of up to 1 h in honeybees have been observed in other experiments (data not shown here).

Thermoreceptors on the distal segments of a honeybee’s antenna allow the detection of temperature differences as small as 0.25°C (Heran 1952; Lacher 1964). With the tips of their antennae touching the brood cap surface, incubating workers may receive information about the local brood temperature or chemical signals (Koeniger 1982) from the brood.

All aspects of the behaviour described above suggest that the honeybee workers were engaged in a specialised brood-heating task.

Acknowledgements We thank D. Sandeman for comments on the original manuscript and H. Demmel for support with the experimental set-ups. This study was supported by the German Research Foundation SFB 554 and by the Graduiertenkolleg GK 200. The experiments comply with the current laws of Germany.

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