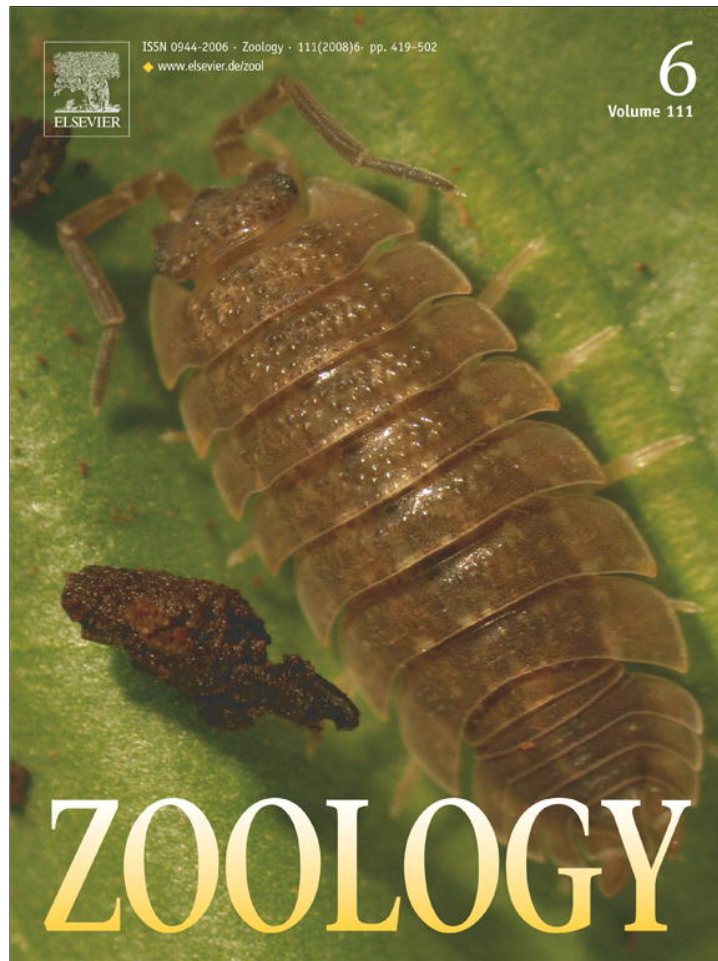


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Zoology 111 (2008) 433–441

ZOOLOGY

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Trophallactic activities in the honeybee brood nest – Heaters get supplied with high performance fuel

Rebecca Basile^{a,*}, Christian W.W. Pirk^b, Jürgen Tautz^a^a*BEEgroup, Department of Zoology II, Behavioral Physiology and Sociobiology, Biocenter, Julius-Maximilians-University, D-97074 Würzburg, Germany*^b*Department of Zoology and Entomology, University of Pretoria, 0002 Pretoria, South Africa*

Received 19 June 2007; received in revised form 21 November 2007; accepted 22 November 2007

Abstract

Honeybees actively regulate their brood temperature by heating between 33 and 36 °C if ambient temperatures are lower. Heat is generated by vibrating the flight muscles. Heating rapidly depletes the worker's internal energy; therefore heating performance is limited by the honey that is ingested before the heating process. Stored honey is the predefined fuel for flying and heating, but it is stored at a distance from the broodcomb, causing a potential logistic problem of efficient energy supply in the brood area. Our study focused on the behaviour and the thoracic temperature of the participants in trophallactic food exchanges on the broodcomb. We found that 85.5% of the recipients in a trophallactic food exchange have a higher thoracic temperature during feeding contacts than donors and after the feeding contact the former engage in brood heating more often. The donor bees have lower thoracic temperature and shuttle constantly between honey stores and the broodcomb where they transfer the stored honey to heating bees. Providing heat-emitting workers with small doses of high performance fuel contributes to an economic distribution of resources consistent with physiological conditions of the bees and the ecological requirements of the hive. The trophallaxis-based system is essential to provide the energy-intensive brood warming activity. The emerging independence from ambient temperatures is not only beneficial for brood rearing during times of sudden cold spells, but also enables the honeybees in temperate regions to raise brood in early spring and might be the decisive factor for the occurrence of honeybees in temperate climates in general.

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Keywords: *Apis mellifera*; Trophallaxis; Food exchange; Brood heating

Introduction

Worker bees of *Apis mellifera* maintain the temperature of their pupae between 33 and 36 °C by heating or cooling (Himmer, 1927; Seeley and Heinrich, 1981; Esch and Goller, 1991; Heinrich, 1993). If temperatures are not kept within these limits, the results may be brain damage and losses in behavioural capability (Tautz et al., 2003; Groh et al., 2004). The heating bees station

*Corresponding author. Current Address: Department of Biology, Institute for Integrated Natural Sciences, Campus Koblenz, University of Koblenz-Landau, D-56070 Koblenz, Germany.
Tel.: +49 931 8884328.

E-mail address: rebecca.basile@biozentrum.uni-wuerzburg.de (R. Basile).

themselves on the broodcomb where they transfer heat either by pressing their hot thoraces onto capped cells (Bujok et al., 2002), or by crawling head first into empty cells within the broodcomb to heat neighbouring brood from the side (Kleinhenz et al., 2003). This uninterrupted cell-heating activity was observed to last up to 32.9 min by Kleinhenz et al. (2003).

In honeybees, heat is produced by “shivering” the flight muscles. During this shivering, wing and thorax vibrations are generally not detectable and the bees may appear to be quiet and “at rest”. Thoracic heat also is a by-product of flight during which up to 60% of the energy is released as heat (Josephson, 1981).

Brood heating and flying rapidly consume the energy reserves of a worker bee. This can be concluded from the equality in oxygen consumption for both the activities, which is 1.16 $\mu\text{l/g/min}$ during flight muscle shivering and 1.14 $\mu\text{l/g/min}$ during flight (Heinrich, 1993). Since honeybees use mostly sugar as energy substrate for muscular activity (Jongbloed and Wiersma, 1934; Loh and Heran, 1970; Sacktor, 1970; Rothe and Nachtigall, 1989), the level of glycogen in the haemolymph must be kept high to provide an adequate fuel supply for the heat-generating flight muscles (Crailsheim, 1988) which are the most metabolically active tissues known (Southwick and Heldmaier, 1987).

In honeybees, food is stored in the crop or “honey stomach”. Any liquid from the crop (nectar, water, honey) can be regurgitated and deposited in cells or transferred to other bees. The crop has a sphincter muscle, the ventriculus, which works as a valve that can release food doses into the midgut, where they are transferred into the bloodstream (Blatt and Rocas, 2001). A crop load of sugar solution can provide a bee with food for several hours. But even inactive, caged honeybees with a full crop held at room temperature die within 7 h after being separated from their food source (Heinrich, 1993). A physiologically challenging activity like flying or heating will consume their sugar fuel even faster, so the crop content and its sugar concentration reflect the demand of the upcoming task (Nixon and Ribbands, 1952; Crailsheim, 1988).

The brood area where the heating activity takes place is usually situated in the centre of the comb and roughly surrounded by pollen-containing cells. The stored honey, which is the best source of carbohydrates in the hive, is kept in the upper corners of the comb which is extended towards the centre in the course of time (Seeley and Morse, 1976). The broodcomb and the honeycomb are separated from each other by several empty cells and the pollen circle. These empty cells between brood and food are kept empty as long as there is enough space for additional nectar deposits in the honeycomb and additional brood cells on the broodcomb (Fig. 1). Seeley (1982) suspected that the spatial segregation of broodnest and food storage regions is initially advantageous

because it facilitates brood incubation and probably economises the nest construction. However, it creates a spatiotemporal gap between brood and food, which must be bridged by the heating bees for a regular reload of honey, because of their increased energy requirement. The expense of heat loss for a heating bee that leaves the brood nest is independent of the distance it needs to bridge between the brood nest and the honeycomb. Since the clustering on the broodcomb serves the same purpose as a winter cluster, i.e. to reduce and prevent heat loss, every movement of heating bees flying in or out reduces the insulation efficiency. Indeed, Southwick and Heldmaier (1987) reported that the tight clustering in winter may reduce the effective area of heat exchange by as much as 88%. Brood incubation in that manner economises the heating activity of the bees by means of an efficient organisation of the cluster.

The food intake to fuel a honeybee's activity is either done by the worker bee itself, i.e. by taking up food from the honeycomb, or by getting fed by another bee which regurgitates food from her crop and transfers it mouth to mouth. This feeding activity between two individuals is called trophallaxis (Free, 1956).

There are two ways of starting a trophallactic contact. Firstly, a bee can beg for food by extending its proboscis and thrusting its tip towards the mouthparts of another bee. If the begging bee is successful, the other bee responds by regurgitating food, thereby initiating a trophallactic contact. Secondly, a bee can offer food by opening its mandibles, raising the proximal part of its proboscis and regurgitating a droplet of food that is displayed between the mandibles and the proboscis (Free, 1956). If a recipient bee touches that droplet with its antennae and then thrusts its proboscis between the mouthparts of the donor, this also results in a trophallactic contact (Montagner and Pain, 1971).

Not all trophallactic contacts in the hive are feeding contacts. Nectar foragers, for example, make trophallactic contacts with nectar-receiving bees. These contacts are used for nectar transport rather than for nourishment of the recipient, as the passed-on nectar is finally deposited in the nectar cells and usually not consumed by the nectar-receiving bee.

Trophallactic contacts occur all over the hive, but more frequently on the broodcomb (Seeley, 1982). Most likely, these feeding contacts on the broodcomb are intended for the nourishment of the recipient. The nectar-passing contacts between foragers and nectar-receiving bees are usually limited to an area near the hive entrance (Seeley, 1982) and distant from the broodcomb where the observations in this study were focused (Fig. 1).

The tasks of worker bees and their energetic requirements vary (Nixon and Ribbands, 1952; Crailsheim, 1988). Foraging or heating bees spend more energy than, for example, pollen-storing or cell-cleaning bees. Consequently, the bees' task partitioning system

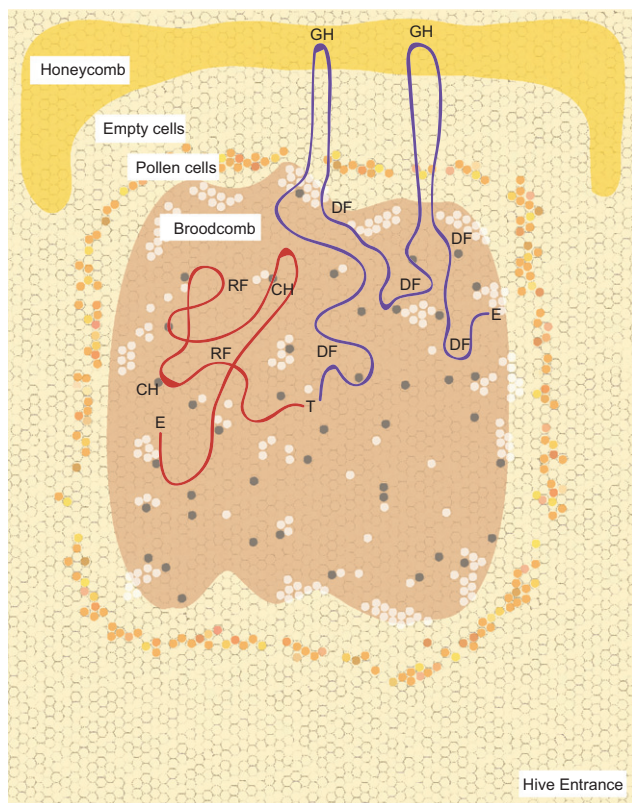


Fig. 1. Map depicting the position of broodcomb and honeycomb in a two-frame observation hive. The different areas and the cell contents in the hive with tracks of a donor bee (blue line) and a receiving bee (red line) after the trophallactic contact give an example of how the data was collected. The different behaviours of donor and receiving bee are abbreviated (T = trophallaxis, RF = receiving food, DF = donating food, CH = cell-heating, GH = gathering honey, E = end of observation). The “shuttling” behaviour of the donor bee is noticeable by the tracks which lead to the honeycomb and back to the broodcomb which is how they bridge the spatiotemporal gap between brood and food while recipients stay on the broodcomb. Cell contents in the brood area are differentiated by colour: dark grey = empty cell in the brood area, white = larvae or egg-containing cell, light brown = capped brood cell.

requires some sort of resource management that assures an ideal distribution of the available resources. A honeybee that goes on a foraging flight needs a certain amount of food to reach her destination and return to the hive. Foragers do not fill their crops at the honeycomb nor do they use the nectar they collect for flying. Brandstetter et al. (1988) found that foragers get refuelled between foraging flights by worker bees in the hive via trophallaxis.

In the same way that the foragers have to balance the distance and fly against the fuel needs (Beutler, 1950; Sacktor, 1970), heater bees need a mechanism to bridge the spatiotemporal gap between heating the brood and replenishing their energy resources. As for foragers, the

area where their task is accomplished is separated from the honeycomb where the energy they need to fulfil their task is stored.

Assuming that the distribution of energy resources has to be in line with the demand as it is in foraging flights (Scholze et al., 1964; Crailsheim, 1988) the question is raised how the heating performance and the nourishment tasks are regulated efficiently without mispending stored honey or wasting produced heat by leaving the heating cluster. Therefore, trophallactic food dispersal and heating have to be interrelated by a task-sharing system and must be distinguishable by the behaviour and the temperature of the participants in a trophallactic contact.

Materials and methods

All observations were made at the Beestation of Würzburg University (Biocenter) from May to July 2005 with *A. mellifera carnica* in four standard two-frame observation hives (3000–4000 bees) in a shaded room under red light. Unrelated, artificially inseminated queens were heading these observation hives.

Behavioural observations

Tracking of the honeybees was done in two-frame observation hives through a transparent foil placed over the pane and with a stopwatch. The participants of a trophallactic contact were identified as donors or receivers and tracked for as long as possible but not exceeding 20 min.

These tracks were sketched on the foil with a marker. The different behaviours were listed on the foil with graphic symbols and the duration of the performed behaviours was noted. The tracking, together with a detailed map of the hive (i.e. cell contents: broodcomb, honeycomb, empty cells, etc.), gives full information about time, space and behaviour of the observed bees at all times (Fig. 1).

The behavioural patterns associated with food transmission (Ribbands, 1953; Crailsheim, 1988) and heat production (Bujok et al., 2002) were distinguished and the durations were recorded and noted as percentages of the whole observation time. The observed behaviour patterns include (1) trophallaxis which was differentiated into donating food and receiving food as described by Free (1956); (2) sticking the head into a cell containing honey, which is necessary to unload or gather honey; and (3) cell-heating, i.e. crawling into an empty cell while continuously pumping the abdomen as described by Kleinhenz et al. (2003). We counted only this form of cell-heating behaviour as “heating”, because it provides a definite indication of heating behaviour without measuring the thoracic temperature of the bee and because the second experiment with a thermal imaging camera provided accurate data

concerning this issue. In addition, the absolute percentage of behavioural actions of donors and recipients, i.e. whether an observed bee ever showed a special behaviour or not, was noted.

Thermal imaging

In addition to the behavioural data, thermal images of trophallactic contacts on the broodcomb were recorded. Both the experiments were performed at the same hives and during the same period (from May to July 2005). With the thermal imaging camera S40 (FLIR Systems Inc.), close-up shots were taken of the capped brood area at two-frame observation hives in a darkened room. The panes were replaced by heat radiation permeable foil. The film footage consists of 32 h (128 sequences à 15 min) taken on 15 different days between 11:00 and 14:00 h. After each sequence, the camera was moved to another part of the broodcomb in order to avoid pseudo-replicates. The recorded images were analysed with the software ThermoCamTM Researcher Pro2.7 (FLIR Systems Inc.). We used an emissivity of the honeybee cuticle of 0.97 as described by Stabentheiner and Schmaranzer (1987).

The collected data includes the thoracic temperature of the participants at the beginning of the contact and the duration of the food exchange. The temperature was only measured at the beginning of the contact, as our study focused on the thermal cause and not on the effect of a trophallactic contact. Using thermal imaging, the thoracic temperatures of donor and recipient worker bees in the capped brood area were measured at the initiation of the food transfer, as was the duration of the contact and the temperature difference between a pair. Donors and recipients were recognised by the way in which they manipulate their mouthparts (Free, 1956) and were categorised by the direction of the food exchange.

The thorax has a three-dimensional shape, which produces differences in thermal radiation at the edges. We measured the maximal thoracic temperature, which is usually radiated in the middle of the thoracic surface in top view (Fig. 2A).

Behavioural patterns like feeding and getting fed can only be distinguished in close-up shots that produce a frame of 7.5×11 cm. Bees, especially donors, tended to leave the frame of the camera when taking close-up shots; therefore the tracking had to be done by a person, not with the thermovision camera.

Results

Behaviour of donors and recipients

Both donors and recipients were observed to move between broodcomb and honeycomb. On average,

donors moved back and forth between broodcomb and honeycomb twice in one observation, while recipients stayed on the broodcomb (Figs. 1 and 3). The difference was significantly different (Mann–Whitney *U*-test: donors ($N = 46$), recipients ($N = 41$), $U = 395.5$, $Z = 4.65$, $p < 0.000003$).

A set of behavioural patterns could be distinguished that was performed more often by donors during the first observed contact. The repeated donation of food (median in donors 8.9% of the observation time, median in recipients 0% of the observation time) and the insertion of the head into a honey cell that is required to refill the crop with honey (median in donors 5.3% of the observation time, median in recipients 0% of the observation time) were almost exclusively performed by donors (Fig. 4A and C) (Mann–Whitney *U*-test: donors ($N = 75$), recipients ($N = 75$); donating food: $U = 185.0$, $Z = 9.87$, $p < 0.001$; gathering honey: $U = 1242.0$, $Z = 5.90$, $p < 0.001$).

To exclude the possibility that the observed bees were actually nurse bees, and therefore the feeding of other bees was part of their nursing behaviour, we compared nursing behaviour in donors and recipient bees. There were no significant differences in their nursing behaviour. The median in donors was 1.9% of the observation time; the median in recipients was 0% of the observation time. This indicates that the trophallactic interactions represent a different and distinct behavioural pattern (Mann–Whitney *U*-test: donors ($N = 75$), recipients ($N = 75$) inserting head into larva-containing cell: $U = 2339$, $Z = 1.78$, $p < 0.07$).

Workers that were acting as recipients in the first observed contact repeatedly received food (median in recipients 9.5% of the observation time, median in donors 0% of the observation time), and showed cell-heating behaviour (median 7.2% of the observation time; median in donors 0% of the observation time) for a longer period of time and more frequently than donors (Fig. 4B and D). Mann–Whitney *U*-test: donors ($N = 75$), recipients ($N = 75$); donating food: $U = 185.0$, $Z = 9.87$, $p < 0.000001$; receiving food: $U = 311.5$, $Z = -9.40$, $p < 0.000001$; gathering honey: $U = 1242.0$, $Z = 5.90$, $p < 0.000001$; cell-heating: $U = 1701.5$, $Z = -4.17$, $p < 0.0003$.

Some bees “switched” tasks during the observation, i.e. they were acting as donors in the first observed feeding contact, but were afterwards observed getting fed by other bees (13 bees out of 75, i.e. 17.3% vs. 100% of the recipients) or engaging in cell-heating (12 bees out of 75, i.e. 16% vs. 52% of the recipients). Likewise, there were recipients, which engaged in feeding other workers (23 bees out of 75, i.e. 30.6% vs. 100% of the donors) or gathering honey after the first observed contact (13 bees out of 75, i.e. 18.6% vs. 66.6% of the donors). Nevertheless, the median percentage of the time spent with the “wrong” task in donors or recipients was still 0%.

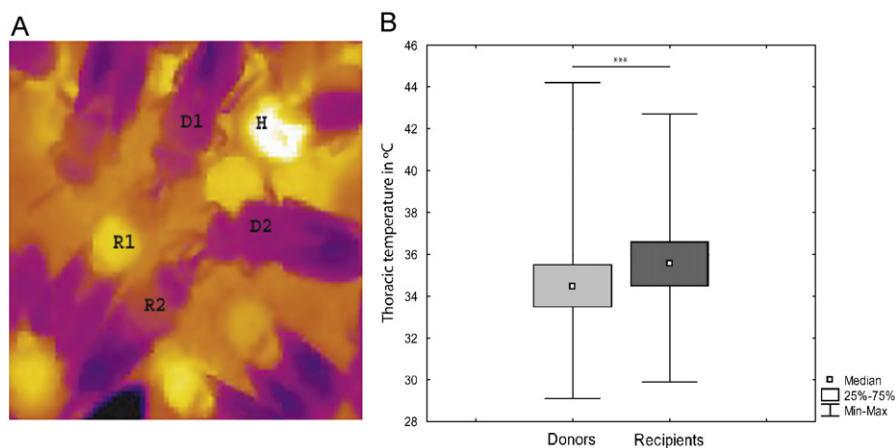


Fig. 2. Connection between thoracic temperature and role in trophallactic contact. (A) Thermal-image detail of trophallactic contacts showing details of feeding contact in the capped brood area: recipients R1 ($T = 37.5^{\circ}\text{C}$) and R2 ($T = 35.8^{\circ}\text{C}$) are fed by donors D1 ($T = 33.8^{\circ}\text{C}$) and D2 ($T = 34.4^{\circ}\text{C}$) while a cell-heating bee H ($T = 40.8^{\circ}\text{C}$) climbs into a cell after a food transfer. The direction of the transmission can be recognised by the way in which the bees manipulate their mouthparts and by the changing colour of the proboscis. The temperature of the transmitted food leads to a change in colour in the thermal image. In this case the transmitted food is cooler than the recipient's mouthparts and they change colour from orange to purple. (B) Differences of thoracic temperatures in donors and recipients at the beginning of a trophallactic contact (see text for details).

Additionally, we calculated correlations between the different behaviours of donors and recipients. Gathering honey and donating food correlate significantly and positively, indicating that the more food donations were registered in an individual, the more time the same individual spent with honey gathering (Spearman coefficient: $R = 0.49$, $n = 150$, $p < 0.05$). Gathering honey and receiving food correlate significantly and negatively, indicating that the more food receptions were registered in an individual, the less time the same individual spent with gathering honey (Spearman coefficient: $R = -0.30$, $n = 150$, $p < 0.05$). Cell-heating and food reception correlate significantly and positively, showing that the more food an individual received, the more time the same individual spent with cell-heating (Spearman coefficient: $R = 0.37$, $n = 150$, $p < 0.05$). Cell-heating and food donation correlate significantly and negatively, meaning that the less time an individual spent with cell-heating, the more time the same individual spent donating food (Spearman coefficient: $R = -0.49$, $n = 150$, $p < 0.05$).

Thoracic temperature and trophallaxis

In 2310 of all 2700 observed feeding contacts (85.5%), the recipients exhibited a higher thoracic temperature than the donors (χ^2 -test: $\chi = 2730.67$, $p < 0.001$). The thoracic temperatures of the recipients (median temperature 35.6°C) were significantly higher than those of the donors (median temperature 34.6°C) at the initiation of a trophallactic contact (Fig. 2B), meaning that generally hotter bees received food from cooler donors

(Mann–Whitney U -test: donors ($N = 2700$), recipients ($N = 2700$), $U = 2249949$, $Z = -24.3545$, $p < 0.001$).

The duration of the contacts varied from a few seconds to over 3 min. Most contacts (55%) lasted 3 s or less. The longer the duration of the interaction, the less often such an interaction was observed (Fig. 5).

The frequent feeding activity on the broodcomb supplied this study with a high number of analysed feeding contacts ($n = 2700$). The power analysis shows that the result of the ascertained temperature difference in the trophallactic participants can be

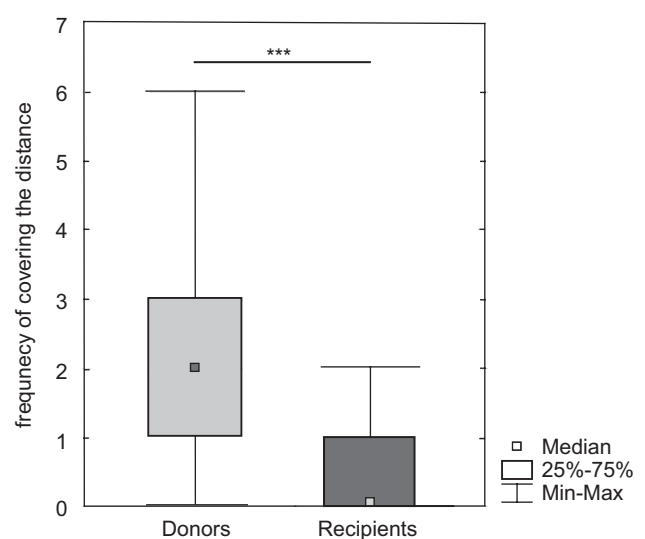


Fig. 3. Number of times (frequency) donors and recipients were bridging the distance between broodcomb and honeycomb. Donors were covering the distance on average two times in one observation.

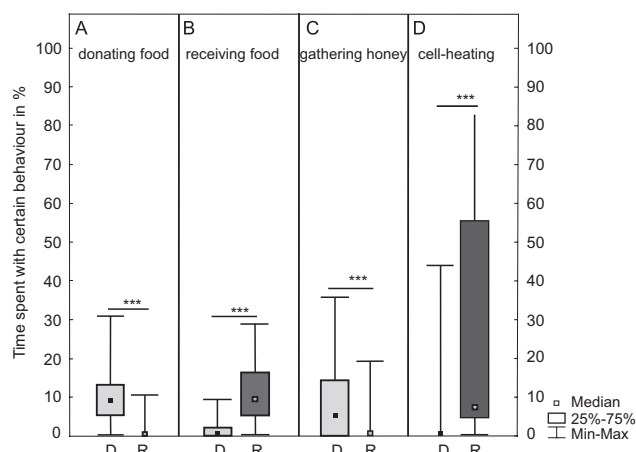


Fig. 4. Behavioural patterns of donors and recipients. Time spent by donors and recipients in percent of total observation time (light grey = donors, D, dark grey = recipients, R). (A) The donors spent significantly more time with the repeated donation of food. (B) The recipients spent significantly more time receiving food. (C) The donors spent significantly more time with the gathering of honey than the recipients. (D) The recipients spent significantly more time heating cells. The donors never showed this behaviour.

regarded as highly reliable (power calculation: Alpha 0.05, Power 1.0).

Discussion

The individual tracking of trophallactic participants showed significant differences in the behaviour of donors and recipients: donors spent significantly more time feeding other bees and sticking their heads into honey cells than recipients (Fig. 4). Recipients performed cell-heating tasks significantly more often than donors. The positive correlation between gathering honey and donating food in all observed bees supports these findings. Therefore, our results show that trophallactic food dispersal and brood heating are linked tasks, although visibly distinct from each other. The behaviour and temperature of the participants in a trophallactic contact are clearly distinguishable and characteristic of the performed tasks.

Gathering honey in one part of the hive and redistributing it elsewhere cannot be considered random, especially since donor bees cover the distance bidirectionally, i.e. they donate food in the brood area, take up food on the honeycomb, then return to the brood area and donate food again, while recipients stay on the broodcomb (Figs. 1 and 3). Some donors were observed to shuttle six times between brood and food during observation period of 20 min. The idea that donor bees are nurse bees who feed workers as a by-product on their way to their “real” task of larvae

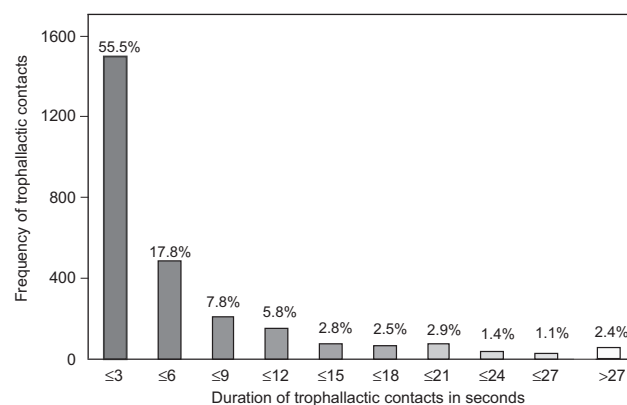


Fig. 5. Feeding contact frequency and duration. Observed feeding contacts sorted by their duration. Most of the 2700 observed contacts lasted up to 3 s (55.5%). The median of all contacts is 3 s.

feeding is not supported by these observations. The insertion of the head into a larva-containing cell, which is the basic criterion of larvae feeding was not performed more often or for a longer period of time by donors than by recipients. In addition, trophallactic contacts which distinguish donors and recipients were only observed in the capped brood area and not in the open brood area, where nurse bees are usually active (Rösch, 1925; Lindauer, 1952).

Recipients, on the other hand, spent significantly more time getting fed and heating cells (Fig. 4). The positive correlation between cell-heating and receiving food supports these findings. Therefore, food ingestion by trophallaxis in the brood area is significantly coupled to cell-heating behaviour. The difference in thoracic temperatures of donors and recipients confirms this interrelation between feeding and heating.

Brief feeding contacts often lead to discussions as to whether they can be counted as real trophallactic transmissions or not (Farina and Wainelboim, 2001a). Here, feeding was only counted as trophallaxis if the direction of the transmission could be detected by the way the bees manipulated their mouthparts (Free, 1956) and if there was a detectable food transmission. Farina and Wainelboim (2005) used the same technique to demonstrate that there are food transmissions even during brief trophallactic contacts.

The thermal imaging data supports the behavioural data by giving information about the thoracic temperatures of the participants at the starting point of the behavioural observation, when food is exchanged on the broodcomb. The food intake before and in-between heat production sequences fuels the heating activity of the recipients. Especially the in-cell-heating performance is limited by the sugar fuel the bee was loaded with shortly before for two reasons: Firstly, there cannot be any trophallactic contacts with a bee that has climbed head first into an empty cell and usually there is no food

deposited in these empty cells. Secondly, only very small amounts of glycogen can be stored in the flight muscle (Neukirch, 1982; Panzenböck and Crailsheim, 1997). Heat production in the honeybee is subject to strict physiological conditions: the glycogen that is required for the metabolic efficiency of the flight muscle can be transferred only by passing the ventriculus and entering the midgut, i.e. sugar that is stored in the crop cannot enter the bloodstream directly (Crailsheim, 1988). Honeybees almost exclusively depend on intestinal and haemolymph energy supplies for energetically demanding activities like heating or flying, because, in contrast to vertebrates, fat or protein can only be metabolised to a very small amount in order to increase the blood sugar level (John, 1958; Panzenböck and Crailsheim, 1997; Micheu et al., 2000; Blatt and Roces, 2001).

Younger bees which are usually performing the in-hive tasks including brood care (Rösch, 1925; Lindauer, 1952), have an extremely high level of glycogen, which can be stored in the flight muscle only in limited amounts (Neukirch, 1982; Panzenböck and Crailsheim, 1997). Therefore, the need of heating bees to refuel follows from their activity that requires a lot of energy and the limited opportunities of increasing the blood sugar level in honeybees. The physiological limits of the flight muscle, its low energy capacity and high metabolism could be the reason behind the honeybees' consistent behaviour of donating and receiving food in small doses and quick succession as described in our behavioural data.

Our findings that heating bees on the broodcomb are fed with honey correspond with Nixon and Ribbands' (1952) data which showed that honeybees in the brood area are least often fed with freshly collected nectar. The radioactive nectar foragers collected in their study was distributed all over the hive to a certain extent, but the bees on the broodcomb had the lowest radioactive load, which leads to the conclusion that if they are not fed with freshly collected nectar, it must be stored honey they are supplied with. Assuming that stored honey has a higher sugar content than freshly collected nectar, the short trophallactic contacts of the donor bees with many different recipients on the broodcomb might be intended to provide many heat-producing bees with small doses of high performance fuel. The fact that most trophallactic contacts on the capped brood were brief and the couples on the capped brood consisted of a donor with a lower thoracic temperature and a recipient with a higher thoracic temperature speaks well for this conclusion (Fig. 2).

The ingestion of food, which is high in sugar content might even have a direct influence on the thoracic temperature of the recipients. The connection between sugar content and thoracic temperature was described by Stabentheiner and Schmaranzer (1987). They found a positive correlation between sugar content of food with

an increase of thoracic temperature for ingestion at the feeding place outside the hive. Stabentheiner (1996) confirmed that the increase in thoracic temperature, depending on the food source, correlated with dancing, walking and trophallaxis, but he did not specify the area in the hive where the feeding contacts took place nor did he differentiate between donating and receiving a food transmission.

A different correlation for behaviour and thoracic temperature was described by Farina and Wainseboim (2001b). They reported a higher thoracic temperature in returning nectar foragers and a cooler thoracic temperature in nectar-receiving bees at the beginning of a trophallactic contact ($N = 69$). Our observation, on the other hand, showed a contrary effect in thoracic temperature concerning donors and recipients in trophallactic contacts on the broodcomb in 2390 out of 2700 cases (Fig. 2A and B). This is not surprising as the higher thoracic temperature at the beginning of the trophallactic contact measured by Farina and Wainseboim (2001b) probably was a side effect of the flying action of the returning nectar forager. As mentioned before, our observations with the thermal imaging camera were restricted to the broodcomb, which is not identical with the hive entrance where the nectar transfer between returning foragers and nectar-receiving bees usually takes place (Seeley, 1989). The donors in our behavioural observations shuttled between honeycomb and broodcomb, and are therefore not very likely to be returning nectar foragers.

Cooler bees that are engaged in supplying and regurgitating food with high sugar content and hotter bees that are engaged in cell-heating demonstrate a clear task-sharing which is beneficial for the whole colony. The fact that donor bees distribute small doses of high performance fuel to many heat-emitting bees, instead of loading bees randomly on their way across the hive increases the efficiency of the feeding task and of the heating bees.

It is an established fact that bringing nourishment to the active heaters whose energy capacity is low and so avoiding down time increases brood rearing efficiency (Scholze et al., 1964; Southwick and Heldmaier, 1987; Crailsheim, 1988). In addition, keeping the cluster together on the broodcomb improves the efficiency of insulation against heat loss (Sacktor, 1970; Kronenberg and Heller, 1982; Southwick and Heldmaier, 1987). Why heating bees stay and continue their energy-consuming task which is very likely to reduce their life span (Neukirch, 1982) instead of interrupting it is unknown.

This task partitioning system, which provides heat-producing workers with small doses of high performance fuel, contributes to a highly economical resource management that is in line with the physiological conditions of the bees and the ecological requirements

of the hive. Moreover, in contrast to bumblebees where trophallaxis between workers is lacking (Dornhaus et al., 1998), this trophallactic behaviour might be the underlying mechanism to develop such a sophisticated task partitioning. The resulting economical resource management might be one of the factors favouring the evolution of perennial bee colonies in temperate regions.

Acknowledgements

R.B. has been supported by grants from the Deutsche Forschungsgemeinschaft (SFB 554). Financial support to CWWP was provided by a Claude Leon Fellowship. We would like to thank H. Tichy for his recommendations on literature, T. Seeley for his helpful remarks, and H.R. Hepburn for proof reading and valuable comments.

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