



Social context influences the initiation and threshold of thermoregulatory behaviour in honeybees



Chelsea N. Cook*, Michael D. Breed¹

Ecology and Evolutionary Biology, The University of Colorado Boulder, Boulder, CO, U.S.A.

ARTICLE INFO

Article history:

Received 27 February 2013
Initial acceptance 20 March 2013
Final acceptance 3 May 2013
Available online 19 June 2013
MS. number: A13-00185

Keywords:

Apis mellifera
division of labour
honeybee
social influence
task allocation

Interactions between individuals in a society are the basis of effective task allocation. Division of labour plays a critical role in the ecological efficiency of social insect societies. In this study we tested whether social context, specifically the number of workers present, affects thermoregulatory task performance in honeybees, *Apis mellifera*. We report here that worker bees assayed singly were significantly less likely to initiate fanning behaviour in response to elevated temperature than bees assayed in small groups of three or 10 workers. Bees assayed in groups also showed lower response thresholds than those assayed alone. The likelihood for fanning behaviour varied significantly among behavioural castes, while thermal response thresholds did not. These results suggest that worker task performance depends on the presence of other workers and offer another method by which division of labour in societies is organized. © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

A defining feature of an animal society is the constant interaction among its members. These interactions are crucial to the organization of work and transmission of information within the society. In social insect societies, worker activities are coordinated so that the work is accomplished efficiently (Wilson 1976). The mechanisms underlying this coordination include temporal polyethism, in which worker age determines task specialization (reviewed in: Robinson 1992; Camargo et al. 2007), dominance hierarchies, wherein rank determines task performance (Honk & Hogeweg 1981; Theraulaz et al. 1991; O'Donnell 1998; Powell & Tschinkel 1999), and physical castes, in which worker size and/or shape specialization determines task type (Oster & Wilson 1978; Hölldobler & Wilson 1990). These simple devices are species-level characteristics that provide much of the basic framework for variation in task specialization among individuals in societies. However, these models do not fully explain variation in effort between colonies or variation within colonies of social insects.

In addition to these fundamental factors affecting the division of labour, there are a number of mechanisms that facilitate adjustments in work allocation in response to factors like colony

ontogeny, seasonality and environmental stressors such as low food availability, drought, or pressure from predators and parasites. Key regulatory mechanisms include variation in response thresholds to tasks (Page et al. 1998), information feedback loops (Seeley 1982), 'foraging for work' (Tofts & Franks 1992; Tofts 1993; Pinter-Wollman et al. 2011), genetic variation among workers (Jones et al. 2004) and nutritional status of workers (Toth & Robinson 2005; Toth et al. 2005). Depending on the species in question, several of these factors may interact to predict the behaviour of workers. Variation among workers in response threshold, genetics, nutritional experience and hormonal status may play particularly key roles in driving task specialization in honeybees (Beshers & Fewell 2001; Johnson 2010). Here, we test the novel hypothesis that social context (i.e. the number of conspecifics present) influences the division of labour of thermoregulatory behaviour in honeybees, *Apis mellifera*.

Honeybees maintain a relatively constant temperature of 36 °C within their colonies when rearing brood (Himmer 1927; Lindauer 1954; Fahrenholz et al. 1989). In the winter, when brood is absent, temperature is also regulated (Kronenberg & Heller 1982; Stabentheiner et al. 2002, 2010). Several behaviours contribute to thermal regulation, including fanning to circulate air and remove excess heat (Egley & Breed 2013), heat shielding (Starks & Gilley 1999; Siegel et al. 2005) and foraging for water that is then used for evaporative cooling (Kühnholz & Seeley 1998). In colder ambient temperatures, honeybees shiver to produce thermal

* Correspondence: C. N. Cook, Ecology and Evolutionary Biology, The University of Colorado Boulder, Boulder, CO 80309-0334, U.S.A.

E-mail address: Chelsea.cook@colorado.edu (C. N. Cook).

¹ E-mail address: michael.breed@colorado.edu (M. D. Breed).

energy (Heinrich & Esch 1994; Starks et al. 2005) and will press their abdomens onto the surface of brood comb or even enter cells to distribute the heat more effectively (Kleinhenz et al. 2003). Honeybees also regulate carbon dioxide (Seeley 1974) and humidity (Human et al. 2006). For an overview of social insect thermoregulation see Jones & Oldroyd (2007). The thermoregulatory behaviour on which we focus in this study is fanning (Egley & Breed 2013).

Fanning behaviour is best studied in bumblebees (Heinrich 1993). Recent work by Duong & Dornhaus (2012) in *Bombus impatiens* found that worker responsiveness, in terms of threshold for initiation of fanning behaviour, did not change with age or experience. This differed from the findings of Weidenmüller (2004) and Westhus et al. (2013) in *Bombus terrestris*, in which experience decreased thermal response thresholds. Gardner et al. (2007) studied colony thermoregulation by workers and found that nest climates were more consistently maintained when brood was present. Engels et al. (1995) found a similar mechanism for nest temperature regulation, including fanning, in a stingless bee, *Scaptotrigona postica*. Fine thermoregulatory control is crucial for survival in many social insects, and it is important to understand all mechanisms by which this may be happening.

We first tested the hypothesis that honeybees respond to a thermal threshold to commence fanning behaviour. We then tested the hypothesis that bees are more likely to fan when in groups than when solitary. We also tested whether the thermal fanning threshold decreases as group size increases. Because we could identify distinct behavioural task groups among honeybee workers (nurses, guards, entrance fanners and foragers), our final experiment tested whether these task groups differ in their probability of fanning and thermal thresholds. Taken together, the results from this study address how individual behavioural thresholds can interact with social context to shape division of labour in social insects, as well as in animal societies in general.

METHODS

General

Ten *Apis mellifera* L., 'Italian' colonies on University of Colorado campus were used for these experiments. Colonies were maintained in 10-frame wooden hive bodies with plastic frames. Supplemental feeding of a 1M sucrose solution was performed at the beginning of the season due to dry conditions. All experiments were conducted between 1 May and 1 October 2012.

Collection

Task groups

These experiments required bees from four distinct task groups (nurses, guards, fanners and pollen foragers), which were defined using established behavioural criteria, described below. Our focus was on behavioural role, rather than chronological age of the bees. Behavioural castes were determined by observing the behaviour of bees in colonies.

Nurses. We identified a nurse as a bee seen with her head in a brood comb cell. This method follows the methods of Sakagami (1953), Huang et al. (1994) and Wagener-Hulme et al. (1999). While it is possible that not all bees we categorized as nurses were providing care, for the purpose of identifying nurses we felt this method was reasonable.

Guards. We identified guards as a subset of the bees on the entrance landing board. Guards show a distinctive posture with

their wings spread and their abdomen slightly tilted upward. They are also active in examining incoming bees. This method of identifying guards has been used extensively in studies of this task group. Moore et al. (1987) gave a detailed description of guard behaviour and subsequent studies include Downs & Ratnieks (2000), Hunt et al. (2007) and Pacheco & Breed (2008). Breed et al. (2004) reviewed defensive behaviour of honeybees and give an overview of the role of guards in honeybee colony defence.

Fanners. Fanners were also a subset of the bees collected on the entrance landing board. These bees fan their wings to ventilate the colony. Their distinctive posture and orientation relative to the entrance allowed us to distinguish fanners from foragers that briefly fanned before departing, or from other bees that signalled using their Nasanov gland (Free 1987) or other defensive behaviours, as occurs in the presence of intruders (Yang et al. 2010). Egley & Breed (2013) recently described entrance fanning for ventilation in honeybees. For this study we identified a bee as a fanner only after it had performed fanning behaviour for at least 10 s. We recognize that bees in other locations in the colony may also perform fanning for ventilation purposes, but we focused on entrance fanners because they were easily collected in a field context and because Egley & Breed (2013) suggested that entrance fanners are relatively uniform in age.

Pollen foragers. We used one type of forager, pollen foragers, in this study. Pollen foragers are easily identified because they fly back to the nest with corbiculae (pollen sacs) full of pollen (Huang et al. 1994; Wagener-Hulme et al. 1999; Pankiw & Page 2001). Excluding other forager types reduced task variance among bees in our experiment, as nectar foragers may represent a broader range of ages than pollen foragers (Pankiw & Page 2001). Also, nectar foragers are difficult to identify without expressing the crop contents, a method that may disrupt subsequent behaviour. Bees returning to the colony without pollen loads include nectar foragers, water foragers, guards that have made short flights and younger bees on orientation flights. To collect pollen foragers, we used steel mesh placed over the colony entrance to keep bees from entering the colony. Pollen foragers were then easily identified and collected.

Treatment Groups

Our experiments required isolation of one, three or 10 bees for testing in the laboratory. For any given replicate, each isolated individual or group came from the same task group and hive. Thus, we had, for example, single isolated guards, guards in groups of three and guards in groups of 10. We collected bees opportunistically, as we observed a bee performing one of the focal tasks.

We collected bees from a chosen task group one at a time using forceps and placed them into a mesh cage (4 × 4 × 4 cm). During collection, we randomly placed bees into the three treatment groups of individuals, three or 10 bees. We then transported them back to the laboratory. Time and date of collection were recorded at this time. Our sample size was 20 of each of the treatment group sizes for each task group, and we attempted to maintain approximately equal colony representation across task group and treatment group size. The overall sample size was 240 treatment groups.

Temperature Regime and Behavioural Assay

The overall experimental design assessed the frequency of fanning and the temperature at which fanning was initiated in our treatment groups. The mesh cage containing the bees was placed into a 2-litre glass container (9 × 24 cm), which sat on a heating

Download English Version:

<https://daneshyari.com/en/article/2416597>

Download Persian Version:

<https://daneshyari.com/article/2416597>

[Daneshyari.com](https://daneshyari.com)