



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



Chelsea N. Cook\*, Michael D. Breed<sup>1</sup>

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](mailto:Chelsea.cook@colorado.edu) (C. N. Cook).

<sup>1</sup> E-mail address: [michael.breed@colorado.edu](mailto: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

unit. The bees were allowed to acclimate for 25 min, which was chosen based on the amount of time required in preliminary trials for the activity level of the bees to stabilize. After the acclimation period, we began to increase the jar temperature at a rate of 1 °C per minute, starting at room temperature (an average of 28 °C). Temperatures were taken at approximately the centre of the jar using a Cole Parmer high accuracy ( $\pm 0.3$  °C) digital thermometer probe that was fed through a fitted hole through the top of the jar.

Bees were observed continuously during the heating regime. Fanning during the heating regime was characterized as an individual standing still but fanning her wings for at least 10 s; this is the same criterion applied when entrance fanners were collected in the field. We recorded the initial temperature at which any individual bees fanned (hereafter, 'thermal threshold') and the proportion of bees fanning in a treatment group. We used the first temperature at which bees fanned as the threshold because (1) we wanted to focus on the initial response of the bees and (2) typically, once a bee fanned, others either joined in during that initial bout or did not fan during the entire trial.

### Analysis

We used a generalized linear mixed model to analyse both probability of fanning and thermal thresholds. Both models used four task groups and three group sizes (one, three or 10 bees), both categorical factors. Group size and task group were fixed effects, while colony was a random effect. This representation of colonies was important to control for colony-level effects, so colony was included in the statistical analysis as a random effect.

We used a binomial error distribution (logit link) for our probability analysis and we used a two-column response variable of the number of bees that did fan and the number of bees that did not fan in the group. We used a Gaussian error distribution for our temperature threshold analysis, as our response variable was temperature. We started with a full model to examine two-way interactions between treatment group size and task. We used backward selection; therefore, when an interaction was not significant ( $\alpha = 0.05$ ), it was dropped from the model and the model was rerun. To explore the magnitude of the effects of each treatment variable, we performed a type II ANOVA (Wald chi-square tests), and for each of the significant main effects, we performed a post hoc (Tukey) analysis. We used R v.2.15.0 (R Development Core Team 2012) for all data analysis and library lme4 for generalized linear mixed model analysis (Bates et al. 2012).

## RESULTS

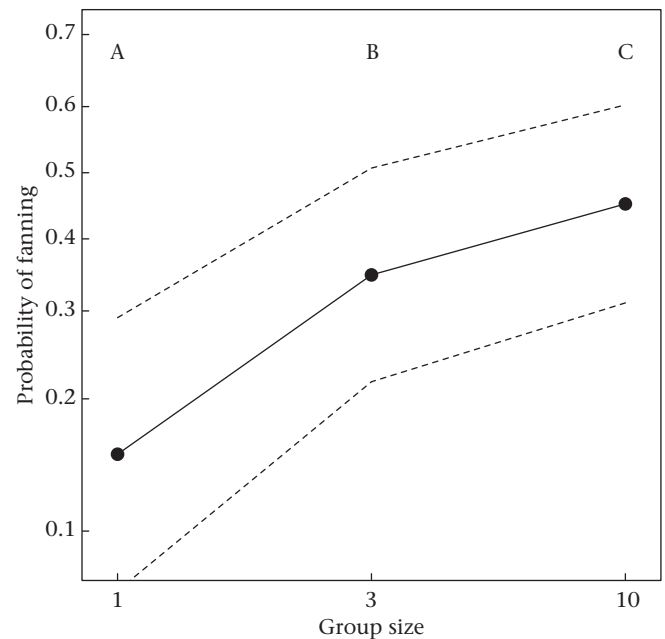
### Hypothesis 1: Probability of Fanning Depends on Group Size

Group size was a significant predictor of probability of fanning (Table 1). Worker honeybees were significantly more likely to fan when assayed in groups of 10 than when assayed singly (Tukey test:  $z = 3.088$ ,  $P = 0.00533$ ; Fig. 1). Fanning was performed by 15 of 80

**Table 1**  
ANOVA (type II Wald chi-square) testing the factors influencing the probability of fanning in honeybees

Model term	$\chi$	df	P
Group size	24.917	2	0.000003885
Caste	44.248	3	0.00000001337
Group size*caste	23.94	6	0.0005357

Probability of fanning was the response variable. There were a total of 240 observations from three group size treatments for four behavioural castes. Hive was controlled for as a random variable. Only significant interactions are shown.



**Figure 1.** Probability of fanning in honeybees as related to group size. Points are averaged probabilities; dotted lines are 95% confidence limits. Letters indicate significance as analysed in a post hoc (Tukey) test.

(18.8%) bees while isolated, 79 of 240 (32.9%) bees in groups of three and 381 of 800 (47.6%) bees in groups of 10. Fanning was observed in 68 of 80 trials of groups of 10, compared with 15 of 80 in isolated bees and 45 of 80 trials in groups of three.

### Hypothesis 2: Thermal Threshold Depends on Group Size

Group size was the only significant predictor for thermal threshold (Table 2). As group size increased, thermal threshold significantly decreased (Fig. 2). Bees in groups of 10 fanned at mean  $\pm$  SE temperature of  $38.92 \pm 0.766$  °C ( $N = 68$ ), a significantly lower temperature than bees in groups of three, which fanned at  $42.56 \pm 0.83$  °C (Tukey test:  $z = -2.951$ ,  $N = 42$ ,  $P = 0.00849$ ). Bees in groups of 10 also fanned at a significantly lower temperature than single bees, which initiated fanning at a mean temperature of  $47.97 \pm 0.524$  °C ( $z = -4.820$ ,  $N = 15$ ,  $P = 0.0001$ ). Additionally, bees in groups of three fanned at a significantly lower temperature than single bees ( $z = -2.699$ ,  $P = 0.01826$ ).

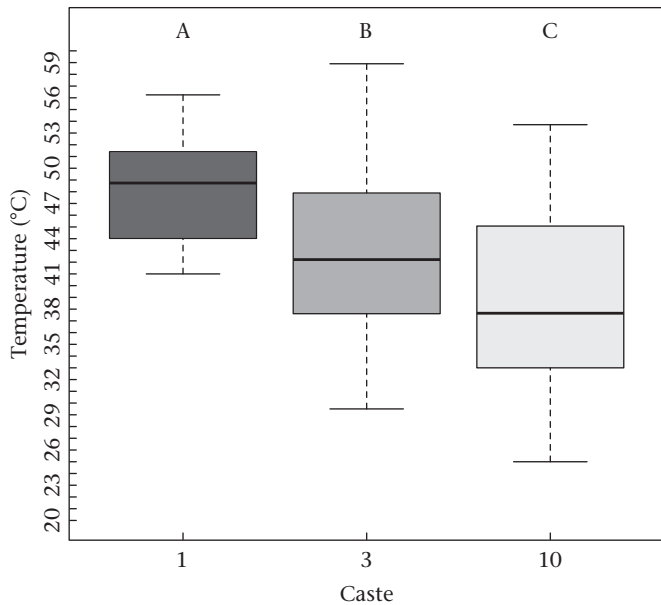
### Hypothesis 3: Probability of Fanning Depends on Caste

Behavioural caste was a significant predictor for fanning probability (Table 1). Across all treatment group sizes, fanners were the most likely to fan (Tukey test:  $z = 3.795$ ,  $N = 60$ ,  $P < 0.001$ ), while foragers were the least likely ( $z = -6.636$ ,  $N = 60$ ,  $P < 0.001$ ; Fig. 3). An ANOVA based on our generalized linear model also showed a

**Table 2**  
ANOVA (type II Wald chi-square) testing the factors affecting thermal threshold for fanning behaviour in honeybees

Model term	$\chi$	df	P
Caste	4.3029	3	0.2306
Group size	27.1107	1	0.00000214

The response variable was thermal threshold (°C). Data were collected from 240 observations, which included three treatment group sizes for four behavioural castes. Hive was controlled for as a random variable. Interactions were tested but were not significant, so they are not included in the final model.

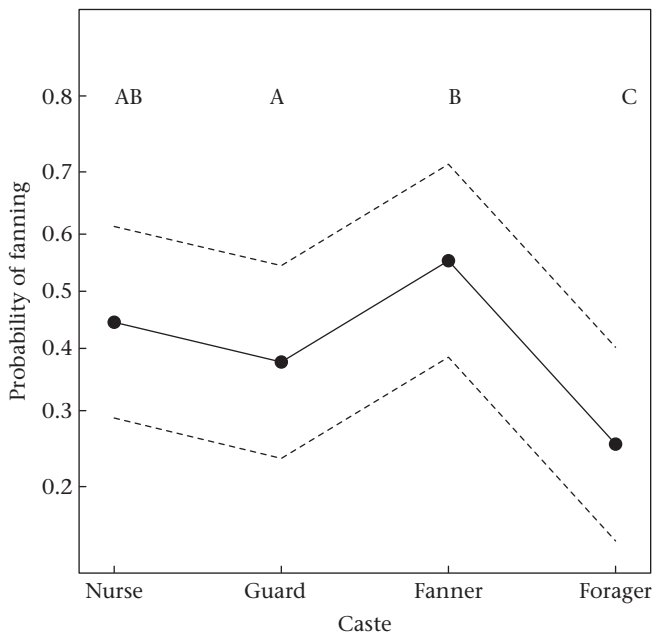


**Figure 2.** Thermal fanning threshold of honeybees by treatment group size. Box plots show median, quartiles and range (there were no outliers). Letters indicate significance as analysed in a post hoc (Tukey) test.

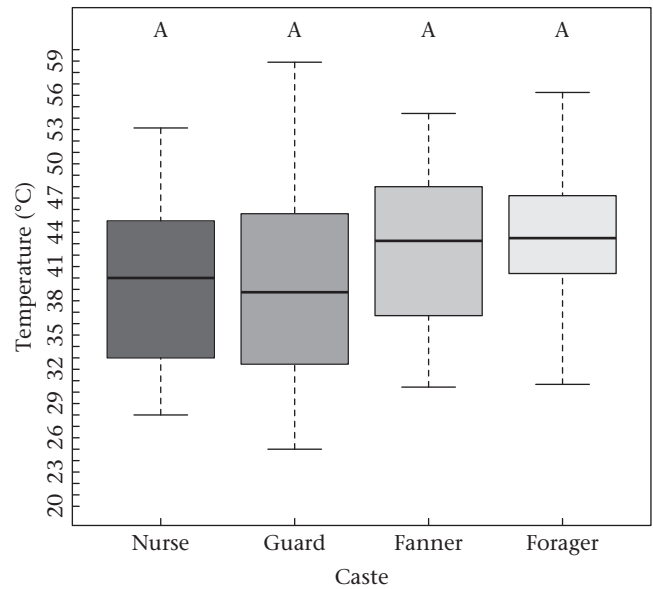
significant interaction between group size and caste (Table 1). This is because foragers did not show increased fanning probability while in the treatment groups of 10 (GLMM:  $z = -2.219$ ,  $P = 0.02652$ ). No other group size–caste pairwise interaction showed a significant effect.

#### Hypothesis 4: Thermal Threshold Depends on Task Group

Although a generalized linear model revealed no significant effect of behavioural caste on thermal threshold, foragers tended to have a higher threshold (Fig. 4). Further analysis of these data, by



**Figure 3.** Probability of fanning as related to honeybee caste. All treatment group sizes are included. Points are averaged probabilities; dotted lines are 95% confidence limits. Letters indicate significance as analysed in a post hoc (Tukey) test.



**Figure 4.** Average thermal fanning thresholds by honeybee caste. Box plots show median, quartiles and range (there were no outliers). Letters indicate significance as analysed in a post hoc (Tukey) test.

isolating the thermal threshold data by caste, revealed no significant effect of caste on thermal threshold. We then analysed only treatment groups of 10 bees (i.e. those for which we had observed the most fanning behaviour). Foragers in groups of 10 fanned at the highest mean temperature,  $42.08 \pm 1.44$  °C ( $N = 16$ ), followed by fanners ( $N = 17$ ) at  $40.02 \pm 1.54$  °C, guards ( $N = 15$ ) at  $37.07 \pm 1.68$  °C and nurses at  $36.84 \pm 1.30$  °C ( $N = 20$ ), but these differences were not significant.

## DISCUSSION

Our results show that social context influences worker bee performance of a critical thermoregulatory behaviour. Honeybees were significantly more likely to initiate fanning when they were in groups than when they were alone. Bees in small groups also showed significantly lower thermal thresholds than isolated bees. While fanners were most likely to fan, foragers were least likely to fan. Effects of probability of fanning within behavioural castes were independent of thermal threshold, as there was no significant effect of caste on fanning threshold. Our results suggest that social context may play a more important role in the division of labour in societies than previously believed.

At the colony level, honeybees show a thermal response threshold at which fanning behaviour commences (Jones et al. 2004). In previously published work, this conclusion was based on observations of bees in entire colonies (Egley & Breed 2013). Our finding that the response threshold for fanning is dependent on the presence of other bees is, to our knowledge, unique in studies of honeybee division of labour. This result suggests that response thresholds for other behavioural tasks should be examined to determine whether expression depends on social context. Furthermore, Pacala et al. (1996) found that, compared to small groups, larger groups are more efficient at tracking changing environments. Our results are consistent with the theme that worker interaction rates are important in division of labour (Gordon 1989; Fewell 2003).

Our results also show that there was a significant difference in probability of fanning across castes. For all treatment group sizes, foragers had the lowest probability of fanning, while fanners had

the highest. Specifically, even foragers in larger groups were less likely to fan than the other groups. While castes differed in their probability of fanning, they did not differ in their thermal response thresholds. In the context of crucial hive behaviours, this makes sense; individuals can vary in the likelihood that they will perform some important behaviour, but to accomplish the task effectively, the ones that perform the behaviour must be coordinated at some level. Given the highly efficient nature of colonial thermoregulation in honeybees, our results provide further evidence of this coordination (Southwick & Moritz 1987). A future direction may be to explore thresholds and probability of fanning in reserve bees that are not seen performing a specific task (Johnson 2002).

Environmental cues, such as temperature and concentration of gasses, play a key role in influencing fanning behaviour (Seeley 1974; Egley & Breed 2013), as indicated by bees fanning before a destructive temperature or CO<sub>2</sub> concentration is reached. However, our results may indicate the ability of worker bees to use the presence of other individuals to evaluate whether and when they should perform a task. Honeybees have an extensive social communication repertoire, including pheromones (Pankiw & Page 2003), vibrations from other bees (Donahoe et al. 2003) and antennal contact with others (Gordon 1989; Cao et al. 2007). Although our results suggest that worker bees utilize both environment and social cues when making behavioural decisions, they leave open the question of what cues elicit fanning, or whether bees actually make an assessment of the number of bees around them.

Other studies have investigated the role that the presence of other individuals has on behaviour. Ruel et al. (2012) found that, below a critical number of workers in the colony, a queen is not likely to be replaced if she is lost. They also found that smaller and larger colonies produce around the same number of queens, but larger colonies have a better chance at rearing a successful new queen (Ruel et al. 2012). Nest size and caste ratio has also been implicated in division of labour among workers. Individual workers are seen doing more specialized tasks in larger colonies, suggesting that a more strict division of labour becomes established as group size increases (Holbrook et al. 2011). Another study also found that, in smaller colonies, foragers spend more time looking for food and eating alone, while workers in larger colonies are more likely to recruit others when they locate a food source (Burkhardt 1998). Alternatively, Sempo & Detrain (2010) found that no significant change in behavioural repertoire or activity level in major workers when minor workers were depleted, although they speculated that regulation of colony function may take place as active workers switch to accomplish tasks important for colony survival. These studies indicate that workers in social groups can alter their behaviours based on the number of individuals around them, and perhaps based on colony need.

Honeybee division of labour appears to be largely structured by age (reviewed in Robinson 1992), response thresholds to stimuli (Robinson et al. 1989) and the physiological state of individual bees (Toth & Robinson 2005; Toth et al. 2005). In these models, task choice depends more on the priming of workers for task performance than on physical proximity to work that needs to be done. In contrast, a 'foraging for work' model for division of labour suggests that workers should engage in tasks that need performing based on their physical proximity to the site of task performance (Tofts & Franks 1992; Tofts 1993; Pinter-Wollman et al. 2011). We found that honeybee workers shared thermal threshold regardless of the task they were performing when collected. Our results suggest that fanning may not be a distinct task for a specialized group of bees and that workers can switch from other tasks to fanning as needed. This fits more closely with a foraging-for-work model for division of labour than the temporal and genetic models often thought to apply to honeybees.

Honeybees perform fanning behaviour in a variety of locations within the nest. A recent study (Egley & Breed 2013) found that fanners at the colony entrance often transition to guarding and that the frequency of fanning is correlated with ambient temperature. While Egley & Breed (2013) treated entrance fanners as a distinct group, fanning in other spatial contexts may not fit this model. Our results indicate that members of tested behavioural castes can perform fanning, although the bees that we behaviourally labelled as fanners were more likely to fan than were the other castes we distinguished. Further experimental tests are needed to understand the specific role that fanning behaviour plays in the division of labour.

Studies have not explored the effect of learning in honeybee thermoregulation, although this has been explored in different species of bumblebees. Duong & Dornhaus (2012) found that *B. impatiens* workers showed no change in temperature threshold if they had previously fanned, indicating that they do not use a self-reinforcement model for thermal threshold. However, the authors concluded that the differences in observed response thresholds could be due to an increased probability of performing a given task, instead of an exhibited variation in perceived thermal threshold for a perceived stimulus (Duong & Dornhaus 2012). The large variation in fanning threshold among bees probably allows the colony to thermoregulate more efficiently than if there were little variation among fanners (Jones et al. 2004; Jones & Oldroyd 2007). Additionally, O'Donnell & Foster (2001) found that although *Bombus bifarius nearcticus* workers differ in their thresholds, they do not seem to specialize in thermoregulation.

Furthermore, while social learning has been extensively studied in social animals (reviewed in Galef & Laland 2005), social influence has not. Social influence is when behaviour is altered by the presence of conspecifics (Whiten & Ham 1992). While task specialization can be socially induced in solitary bees (Jeanson et al. 2008), the increase in efficiency of a particular task based on the interaction of nestmates has not been explored in the context of social influence. Webster & Fiorito (2001) further parsed out social influence into several more specific categories, including social facilitation and social support. Social facilitation involves the initiation of a behaviour based on a conspecific performing the behaviour, while social support posits a situation where simply the presence of another individual is enough stimuli to trigger a change in its motivational state (Whiten & Ham 1992; Webster & Fiorito 2001). Further experiments are needed to explore whether the initiation of fanning is being induced because of social support or because of social facilitation.

The bees used in this study were removed from their normal nest environment, a procedure that could affect their behaviour. Removals in this way are very much a part of the experimental procedures used in studies of behavioural thresholds, with a large literature having developed around assays of sucrose response thresholds (integrated sometimes with olfactory thresholds) in single harnessed bees (Pankiw & Page 1999; Scheiner et al. 2004). The behaviour of bees in our assays corresponded well to the observed behaviour of fanning bees in colonies, with the typical thermal thresholds in our assays corresponding to thermal responses of fanners at colony entrances documented by Egley & Breed (2013).

If response thresholds are being considered as organizing features, or factors that drive self-organization in societies, then the social context in which the threshold is measured must be considered. For fanning by worker honeybees, our results show that shifting thermal threshold and group size effects could have nonlinear outcomes in models of labour allocation. A number of studies have addressed how the rate of social interactions affect behaviour and task performance in social insects (Cole & Cheshire

1996; Pinter-Wollman et al. 2011). Our study differs in that we explore how social context can alter the methods by which individuals respond to environmental stimuli. While it is unclear what social cues operate in our system, the social modulation of response thresholds should be explored in other behavioural contexts and in other social insect species. Our results also provide insight into how analogies might be drawn between social insect societies and the importance of social awareness in other animal societies.

## Acknowledgments

We thank the Graduate Research Fund of the Department of Ecology and Evolutionary Biology, the University of Colorado Graduate School, and the Beverly Sears grant for financial support, as well as the Science Discovery Program for the use of laboratory space. Thank you to the Breed lab and others in the EBIO department for edits and suggestions, as well as T. Tuff, T. Farkas and J. Tarsi for experimental design and statistical advice. We also thank the two anonymous referees and the editor for wonderful suggestions.

## References

- Bates, D. M., Maechler, M. & Bolker, B. 2012. *lme4: Linear Mixed-Effects Models Using Eigen and S4*. R Package version 0.999999-0. Vienna: R Foundation for Statistical Computing. Published online 13 June 2012. <http://lme4.r-forge.r-project.org/>.
- Beshers, S. N. & Fewell, J. H. 2001. Models of division of labor in social insects. *Annual Review of Entomology*, **46**, 413–440.
- Breed, M. D., Guzman-Novoa, E. & Hunt, G. J. 2004. Defensive behaviour of honey bees: organization, genetics, and comparisons with other bees. *Annual Review of Entomology*, **49**, 271–298.
- Burkhardt, J. F. 1998. Individual flexibility and tempo in the ant, *Pheidole dentata*, the influence of group size. *Journal of Insect Behavior*, **11**, 493–505.
- Camargo, R. S., Forti, L. C., Lopes, J. F. S., Andrade, A. P. P. & Ottati, A. L. T. 2007. Age polyethism in the leaf-cutting ant *Acromyrmex subterraneus brunneus* Forel, 1911 (Hymenoptera, Formicidae). *Journal of Applied Entomology*, **131**, 139–145.
- Cao, T. T., Hyland, K. M., Malechuk, A., Lewis, L. A. & Schneider, S. S. 2007. The influence of the vibration signal on worker interactions with the nest and nest mates in established and newly founded colonies of the honeybee, *Apis mellifera*. *Insectes Sociaux*, **54**, 144–149.
- Cole, B. J. & Cheshire, D. 1996. Mobile cellular automata models of ant behavior: movement activity of *Leptothorax allardyei*. *American Naturalist*, **148**, 1–15.
- Donahoe, K., Lewis, L. A. & Schneider, S. S. 2003. The role of the vibration signal in the house-hunting process of honeybee (*Apis mellifera*) swarms. *Behavioral Ecology and Sociobiology*, **54**, 593–600.
- Downs, S. G. & Ratnieks, F. L. W. 2000. Adaptive shifts in honey bee (*Apis mellifera* L.) guarding behavior support predictions of the acceptance model threshold. *Behavioral Ecology*, **11**, 326–333.
- Duong, N. & Dornhaus, A. 2012. Ventilation response thresholds do not change with age or self-reinforcement in workers of the bumble bee *Bombus impatiens*. *Insectes Sociaux*, **59**, 25–32.
- Egley, R. L. & Breed, M. D. 2013. The fanner honey bee: behavioral variability and environmental cues in workers performing a specialized task. *Journal of Insect Behavior*, **26**, 238–245.
- Engels, W., Rosenkranz, P. & Engels, E. 1995. Thermoregulation in the nest of the neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees. *Studies on Neotropical Fauna and Environment*, **30**, 193–205.
- Fahrenholz, L., Lamprecht, I. & Schrick, B. 1989. Thermal investigations of a honey bee colony: thermoregulation of the hive during summer and winter and heat production of members of different bee castes. *Journal of Comparative Physiology B*, **159**, 551–560.
- Fewell, J. H. 2003. Social insect networks. *Science*, **301**, 1867–1870.
- Free, J. B. 1987. *Pheromones of Social Bees*. Ithaca, New York: Cornell University Press.
- Galef, B. G., Jr. & Laland, K. N. 2005. Social learning in animals: empirical studies and theoretical models. *BioScience*, **5**, 489–499.
- Gardner, K. E., Foster, R. L. & O'Donnell, S. 2007. Experimental analysis of worker division of labor in bumblebee nest thermoregulation (*Bombus huntii*, Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology*, **61**, 783–792.
- Gordon, D. 1989. Dynamics of task switching in harvester ants. *Animal Behaviour*, **38**, 194–204.
- Heinrich, B. 1993. *The Hot-blooded Insects: Strategies and Mechanisms of Thermoregulation*. Cambridge, Massachusetts: Harvard University Press.
- Heinrich, B. & Esch, H. 1994. Thermoregulation in bees. *American Scientist*, **82**, 164–170.
- Himmer, A. 1927. Ein Beitrag zur Kenntnis des Wärmeschaltungs im Nestbau sozialer Hautflügler. *Zeitschrift für Vergleichende Physiologie*, **5**, 375–389.
- Holbrook, C. T., Barden, P. M. & Fewell, J. H. 2011. Division of labor increases with colony size in the harvester ant *Pogonomyrmex californicus*. *Behavioral Ecology*, **22**, 960–966.
- Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.
- Honk, C. J. G. & Hogeweg, P. 1981. The ontogeny of the social structure in a captive *Bombus terrestris* colony. *Behavioral Ecology Sociobiology*, **9**, 111–119.
- Human, H., Nicolson, S. W. & Diemann, V. 2006. Do honeybees, *Apis mellifera*, regulate humidity in their nest? *Naturwissenschaften*, **93**, 397–401.
- Huang, Z. Y., Robinson, G. E. & Borst, D. W. 1994. Physiological correlates of division of labor among similarly aged honey bees. *Journal of Comparative Physiology A*, **174**, 731–739.
- Hunt, G. J., Amdam, G. V., Schlipalius, D., Emore, C., Sardesai, N., Williams, C. E., Rueppell, O., Guzman-Novoa, E., Arechavala-Velasco, M., Chandra, S., et al. 2007. Behavioral genomics of honeybee foraging and nest defense. *Naturwissenschaften*, **94**, 247–267.
- Jeanson, R., Clark, R., Holbrook, C., Bertram, S., Fewell, J. & Kukul, P. 2008. Division of labor and socially induced changes in response thresholds in associations of solitary halictine bees. *Animal Behaviour*, **76**, 593–602.
- Johnson, B. R. 2002. Reallocation of labor in honeybee colonies during heat stress: the relative roles of task switching and the activation of reserve labor. *Behavioral Ecology and Sociobiology*, **51**, 188–196.
- Johnson, B. R. 2010. Division of labor in honeybees: form, function, and proximate mechanisms. *Behavioral Ecology and Sociobiology*, **64**, 305–316.
- Jones, J. & Oldroyd, B. P. 2007. Nest thermoregulation in social insects. *Advances in Insect Physiology*, **33**, 153–191.
- Jones, J. C., Myerscough, M., Graham, S. & Oldroyd, B. 2004. Honey bee nest thermoregulation: diversity promotes stability. *Science*, **305**, 402–404.
- Kleinhenz, M., Bujok, B., Fuchs, S. & Tautz, J. 2003. Hot bees in empty broodnest cells: heating from within. *Journal of Experimental Biology*, **206**, 4217–4231.
- Kronenberg, F. & Heller, H. C. 1982. Colonial thermoregulation in honey bees (*Apis mellifera*). *Journal of Comparative Physiology B*, **148**, 65–76.
- Kühnholz, S. & Seeley, T. D. 1998. The control of water collection in honey bee colonies. *Behavioral Ecology and Sociobiology*, **41**, 407–422.
- Lindauer, M. 1954. Temperaturregulierung und Wasserhaushalt im Bienenstaat. *Zeitschrift für vergleichende Physiologie*, **36**, 391–432.
- Moore, A. J., Breed, M. D. & Moor, M. J. 1987. The guard honeybee: ontogeny and behavioural variability of workers performing a specialized task. *Animal Behaviour*, **35**, 1159–1167.
- O'Donnell, S. 1998. Dominance and polyethism in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, **43**, 327–331.
- O'Donnell, S. & Foster, R. L. 2001. Threshold of response in nest thermoregulation by worker bumble bee, *Bombus bifarius nearcticus* (Hymenoptera: Apidae). *Ethology*, **107**, 387–399.
- Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects*. Princeton, New Jersey: Princeton University Press.
- Pacala, S. W., Gordon, D. M. & Godfray, H. C. J. 1996. Effects of social group size on information transfer. *Evolutionary Ecology*, **10**, 127–165.
- Pacheco, J. & Breed, M. D. 2008. Sucrose response thresholds and the expression of behavioural tasks by middle-aged honeybee workers. *Animal Behaviour*, **76**, 1641–1646.
- Page, R. E., Erber, J. & Fondrk, M. K. 1998. The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). *Journal of Comparative Physiology A*, **182**, 489–500.
- Pankiw, T. & Page, R. E. 1999. The effect of genotype, age, sex, and caste on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). *Journal of Comparative Physiology A*, **185**, 207–213.
- Pankiw, T. & Page, R. E. 2001. Genotype and colony environment affect honeybee (*Apis mellifera* L.) development and foraging behavior. *Behavioral Ecology and Sociobiology*, **51**, 87–94.
- Pankiw, T. & Page, R. E. 2003. Effect of pheromones, hormones, and handling on sucrose response thresholds of honey bees (*Apis mellifera* L.). *Journal of Comparative Physiology A*, **189**, 675–684.
- Pinter-Wollman, N., Wollman, R., Guetz, A., Holmes, S. & Gordon, D. M. 2011. The effect of individual variation on the structure and function of interaction networks in harvester ants. *Journal of the Royal Society Interface*, **8**, 1562–1573.
- Powell, S. & Tschinkel, W. R. 1999. Ritualized conflict in *Odontomachus brunneus* and the generation of interaction-based task allocation: a new organizational mechanism in ants. *Animal Behaviour*, **58**, 965–972.
- R Development Core Team 2012. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Robinson, G. E. 1992. Regulation of division of labor in insect societies. *Annual Review of Entomology*, **37**, 637–665.
- Robinson, G. E., Page, R. E., Strambi, C. & Strambi, A. 1989. Hormonal and genetic control of behavioral integration in honey bee colonies. *Science*, **246**, 109–111.
- Ruel, C., Cerda, X. & Boulay, R. 2012. Behaviour-mediated group size effect constrains reproductive decisions in a social insect. *Animal Behaviour*, **84**, 853–860.
- Sakagami, S. F. 1953. Untersuchungen über die Arbeitsteilung im einem Zwergvolk der Honigbiene. Beiträge zur Biologie des Bienenvolkes, *Apis mellifera* L. I. *Japanese Journal of Zoology*, **11**, 117–185.
- Scheiner, R., Page, R. E. & Erber, J. 2004. Sucrose responsiveness and behavioral plasticity in honey bees (*Apis mellifera*). *Apidologie*, **35**, 133–142.

- Seeley, T. D.** 1974. Atmospheric carbon dioxide regulation in honey-bee (*Apis mellifera*) colonies. *Journal of Insect Physiology*, **20**, 2301–2305.
- Seeley, T. D.** 1982. Adaptive significance of the age polyethism schedule in honey-bee colonies. *Behavioral Ecology and Sociobiology*, **11**, 287.
- Sempo, G. & Detrain, C.** 2010. Social task regulation in the dimorphic ant, *Pheidole pallidula*: the influence of caste ratio. *Journal of Insect Science*, **10**, 1–16.
- Siegel, A. J., Hui, J., Johnson, R. N. & Starks, P. T.** 2005. Honey bee workers as mobile insulating units. *Insectes Sociaux*, **52**, 242–246.
- Southwick, E. E. & Moritz, R. F. A.** 1987. Social control of air ventilation in colonies of honey bees, *Apis mellifera*. *Journal of Insect Physiology*, **33**, 623–626.
- Stabentheiner, A., Pressi, H., Papst, T., Hrassing, N. & Crailsheim, K.** 2002. Endothermic heat production in honeybee winter clusters. *Journal of Experimental Biology*, **206**, 353–358.
- Stabentheiner, A., Kovac, H. & Brodschneider, R.** 2010. Honeybee colony thermoregulation: regulatory mechanisms and contribution of individuals in dependence on age, location and thermal stress. *PLoS One*, **5**, e8967.
- Starks, P. T. & Gilley, D. C.** 1999. Heat shielding: a novel method of colonial thermoregulation in honeybees. *Naturwissenschaften*, **86**, 438–440.
- Starks, P. T., Johnson, R. N., Siegel, A. J. & Decelle, M. M.** 2005. Heat shielding: a task for youngsters. *Behavioral Ecology*, **16**, 128–132.
- Theraulaz, G., Gervet, J. & Tian-Chanski, S. S.** 1991. Social regulation of foraging activities in *Polistes dominulus* Christ: a systematic approach to behavioural organization. *Behaviour*, **116**, 292–320.
- Tofts, C.** 1993. Algorithms for task allocation in ants (a study of temporal polyethism: theory). *Bulletin of Mathematical Biology*, **55**, 891–918.
- Tofts, C. & Franks, N. R.** 1992. Doing the right thing: ants, honeybees and naked mole-rats. *Trends in Ecology & Evolution*, **7**, 346–349.
- Toth, A. L. & Robinson, G. E.** 2005. Worker nutrition and division of labour in honeybees. *Animal Behaviour*, **69**, 427–435.
- Toth, A. L., Kantarovich, S., Meisel, A. F. & Robinson, G. E.** 2005. Nutritional status influences socially regulated foraging ontogeny in honey bees. *Journal of Experimental Biology*, **208**, 4641–4649.
- Wagener-Hulme, C., Kuehn, J. C., Schulz, D. J. & Robinson, G. E.** 1999. Biogenic amines and division of labor in honey bee colonies. *Journal of Comparative Physiology*, **184**, 471–479.
- Webster, S. & Fiorito, G.** 2001. Socially guided behavior in non-insect vertebrates. *Animal Cognition*, **4**, 69–79.
- Weidenmuller, A.** 2004. The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self reinforcement in fanning response. *Behavioral Ecology*, **15**, 120–128.
- Westhus, C., Kleineidam, C. J., Roces, F. & Weidenmüller, A.** 2013. Behavioral plasticity in the fanning response of bumblebee workers: impact of experience and rate of temperature change. *Animal Behaviour*, **85**, 27–34.
- Whiten, A. & Ham, R.** 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, **21**, 239–283.
- Wilson, E. O.** 1976. Behavioral discretization and number of castes in an ant species. *Behavioral Ecology and Sociobiology*, **1**, 141–154.
- Yang, M. X., Radloff, S., Tan, K. & Hepburn, R.** 2010. Anti-predator fan-blowing in guard bees, *Apis mellifera capensis* Esch. *Journal of Insect Behavior*, **23**, 12–18.