J Insect Behav (2013) 26:238–245
DOI 10.1007/s10905-012-9357-1

The Fanner Honey Bee: Behavioral Variability and Environmental Cues in Workers Performing a Specialized Task

Rachel L. Egley · Michael D. Breed

Revised: 12 September 2012 / Accepted: 21 September 2012 /
Published online: 17 October 2012

Abstract We tested the hypothesis that *Apis mellifera* workers exhibit plasticity in moving from fanning to guarding behavior. Bees marked when fanning are more likely to guard than fan on subsequent days, but guard to fanner reversals were common. Our findings suggest that bees can switch between these tasks, but that their bias between the two tasks changes over time, rather than a strict serial progression of worker tasks. The number of fanning workers is positively correlated with ambient temperature and negatively correlated with humidity; this conclusion gives insight into the environmental triggers for worker behavior.

Keywords Honey bees · task allocation · environmental thresholds · fanning · guarding · eusociality

Introduction

Age and morphological polyethism constitute significant drivers for division of labor in eusocial wasps, bees, ants, and termites (Wilson 1971; Ratnieks and Anderson 1999). In many termites, size and age determine the predominant tasks carried out by each worker (Crosland et al. 1998). In honeybees, workers move with age from specialized tasks within the hive (e.g. cleaning, brood tending, nectar and pollen operations) to tasks performed by middle-aged bees some of which are on the periphery of the colony (e.g. guarding, undertaking) (Winston 1991; Trumbo et al. 1997; Johnson 2008, 2010) and finally to foraging (Seeley and Kolmes 1991). Age determination of task performance in honeybees is well-documented; however, definitive details of the timetable for performance of all tasks are not available, and how

R. L. Egley · M. D. Breed (✉)
Department of Ecology and Evolutionary Biology, The University of Colorado at Boulder, Boulder, CO 80309-0334, USA
e-mail: michael.breed@colorado.edu

the precise sequence from some tasks to other tasks proceeds for individual workers is not well known. This translates into gaps in our knowledge of task duration and succession.

Within a larger collective such as a social insect colony, individuals make decisions about task performance based on both genetic predispositions and environmental factors. Genetics and morphology of the individual can be key to the competency of an individual to perform a given task; external factors such as undone work in a colony, ambient temperature or presence of a parasite or predator provide in-the-moment stimuli for individuals to perform certain tasks (Robinson and Page 1995; Breed et al. 1990). In some cases, the genetic factor may be an inherited threshold level for a particular behavior (Robinson and Page 1988).

External or environmental factors exercise control over a variety of worker tasks such as thermoregulation in honey bees. The temperature of bees individually or the ambient temperature of the hive itself can induce a variety of thermoregulation tactics; some mechanisms for this thermoregulation are well known, as in Lindauer's explication of water-carrying by foragers, while other mechanisms may be more cryptic, as in the shift of workers between guarding and fanning (Winston 1991; Johnson 2002). Other eusocial insects exhibit colonial endothermy as well; bumblebees (*Bombus impatiens* and *B. affinus*) accomplish regulation through wing fanning and brood incubation, while termites (*Macrotermes bellicosus*) plan their nest structure and generate metabolic heat to achieve a temperature-appropriate environment for themselves and the fungi they cultivate (Vogt 1986; Korb and Linsenmair 2000).

Honeybees, like some other eusocial insects, employ passive and active thermoregulatory techniques to maintain relatively static brood temperature inside the hive (Jones and Oldroyd 2006; Stabentheiner et al. 2010). Inside the hive, honeybees increase or decrease their metabolic rate, locomotion or fanning, clustering, and/or evaporative cooling behavior in characteristic ways to maintain a temperature range required for brood growth (Jones and Oldroyd 2006). A variety of thermoregulatory behaviors occur in response to daytime and nighttime temperature change regimes as well as in response to acute changes in ambient air temperature (Kronenberg and Heller 1982; Siegel et al. 2005). Other biophysical properties of the hive interior are also controlled; honeybees regulate carbon dioxide levels and can influence humidity levels within the hive (Seeley 1974; Hannelie et al. 2006). The age of onset of these behaviors, stimulus response thresholds, task partitioning, and task efficiency of thermoregulation is of key importance to the understanding of hive maintenance and eusocial self-organization as a whole (Starks et al. 2005; Yang et al. 2010a, b).

Honeybee workers perform several specialized tasks outside the hive near the colony entrance, which we refer to as the porch in our study. Apiarists term the protruding section of the base of a hive as the "porch"; in most beekeeping equipment this is about 10 cm deep and extends the full width of the hive. The hive entrance is a gap between the hive box and the hive base, so that bees entering or leaving the colony often are on the porch. Behavior, such as fanning, on the porch corresponds to behavior exhibited by bees outside the entrance of a colony nesting under natural circumstances, such as an opening in a hollow tree.

Fanning is done primarily in order to regulate conditions on the interior of the hive and, in the case of *A. mellifera capensis*, as an anti-predatory technique (Yang et al. 2010a, b). Little is known about the ontogeny or behavioral variability of this task. Ventilation behavior is reported in bees ranging in age from 1 to 61 days, adult age, with a mean age of 14.7–19 days old (Seeley 1982; Winston and Punnett 1982). Guards may be slightly older than the fanners in mean age and foraging, in turn, succeeds guarding as bees age. It is unclear whether bees proceed from one task to another in a serial manner or if some other program exists for this procession. Additionally, while anecdotal evidence (eg, Southwick and Moritz 1987, which studies gas exchange by colonies in details and mentions fanners as part of this process) exists to suggest that bees tend to fan more on warm days, the current literature does not test this observation.

Here we investigate the plasticity among the specialized tasks of fanning, guarding, and foraging and ask if succession from one task to the next is predictable by age. We hypothesize that honey bees working outside the hive on the porch progress from fanning behavior to guarding behavior. We also investigate the magnitude of the hive's fanning response to daily ambient temperature and relative humidity. We hypothesize that incresed ambient temperature and humidity in the environment will induce a greater number of workers to fan outside the hive.

Materials and Methods

Site Description

The study site was an enclosed bee yard on the University of Colorado at Boulder's East Campus in Boulder County, Colorado. The study was performed on 3 commercial 10-frame hives stationed along the inside perimeter of a security fence. The surroundings include a small open meadow, a moderately dense mixed woodland thicket, and a riparian zone. Bees in this area harvest pollen and nectar from a variety of plants during the growing season including dandelion, crab apple, lilac, maple, and willow. Bees were maintained with standard beekeeping practices. Marking and observation of bees took place from 18 June 2010 through 30 August 2010; all data were collected between 12:00 PM and 5:00 PM MDT daily when activity on the porch was highest.

Behavior Definitions

Behaviors noted during observation were fanning, guarding, and foraging. Fanning was characterized by a bee's stance on the porch with head facing the hive opening and abdomen pointed away from the hive; with the whole body canted downward toward the head, bees would rapidly fan their wings producing a low humming sound. Momentary rests, about 1 s, between sustained bouts of fanning did not constitute two separate fanning events for the purposes of determining length of time spent as a fanner. Breaking from fanning behavior to complete a different task, return inside the hive, fly and exhibit aggression towards the observer, or move about the porch was considered a stop in fanning duration. Guarding was characterized by a bee's stance on the porch facing outward with antennae forward, greeting inbound bees. Often guarding bees would depart the porch to fly toward and aggress the observer or the marking tools; any of these indications would classify a bee as a guard. Foraging was characterized by a bee's return from the surroundings with pollen visibly carried into the hive.

Capture and Marking

On each of 14 consecutive days for each hive, 20 fanning bees were individually captured and marked with a dot of enamel modeling paint in a color corresponding to the day of observation (n=20 per day per hive; 840 total). Bees were randomly selected from the group of fanners present on the porch until 20 fanning bees were marked. Observation and capture took place at each hive on a given day until 20 total bees were marked, or for a period of not less than 90 min. On each subsequent day, the number of bees in a colored cohort observed fanning, guarding, and/or foraging was recorded. Bees marked on a previous day as fanners were among those randomly chosen for marking on a subsequent day, but were not selectively targeted for marking.

Environmental Conditions

The minimum and maximum number of bees fanning at one time over a 90 min observation period was recorded for each day for each of three hives, and the temperature and humidity during the observation period were recorded. These daily minima and maxima were averaged for each hive to give the mean number of fanners present on the porch at a given time for that observation period. Each observation period was treated as a single data point, and between-hive variation was tested in the final analysis. Data were collected over 16 days for hive 11 (primarily during the month of June), over 42 days for hive 4 (primarily during the months of July and August), and over 36 days for hive 13 (primarily during the months of July and August); totaling 94 total hive-days. Each hive was assessed once each day, so that measures were not repeatedly taken of the same bees fanning on the same day. In July, seasonal afternoon thunderstorms began occurring regularly; from June to August, each month became progressively warmer and drier.

Statistical Tests

A data matrix was constructed consisting of day, time of day, hive identity, temperature, relative humidity, and the mean number of bees fanning during the observation period that day. This matrix was imported into JMP (2010 SAS Institute Inc.) and analyzed using the standard least squares method of model fitting. Fanning was used as the Y (response) variable and temperature, humidity and hive were X (model effects) variables. In addition to the main effects of temperature, humidity and hive, interactions among these three variables were included in the analysis. Repeated measures analysis in JMP was employed in the test of change of behavior of bees across days.

Results

Marked bees decreased in fanning persistence over 14 days of observation (Fig. 1); of those observed fanning the first day, a greater percentage was found to guard than to fan on any subsequent day. Some immediate flexibility in fanning and guarding was also observed, as 9 % of bees marked as fanners on day one also guarded on the same day. Guarding on day one did not appear to be a response to interaction with the researcher; marked bees returned to fanning for a period of at least 5 min before beginning guarding behavior.

Thirty of the marked bees could be uniquely recognized from day to day during the sampling. The activity of each of these bees was sampled 20 times daily for 5 days. All of these bees were predominately fanning when initially marked. These bees were progressively more likely to guard and less likely to fan over subsequent days. To account for repeated measures of bees, paired *t*-tests between day 1 and day 2 of the experiment were performed for fanning and guarding activity. Bees were significantly less likely to fan on the second day than the first day (t=57.44, p<0.0001, df=29) and significantly more likely to guard on the second day than the first day (t=4.39, p<0.0001, df=29). ANOVAs, of bees over five days of obseration show significant

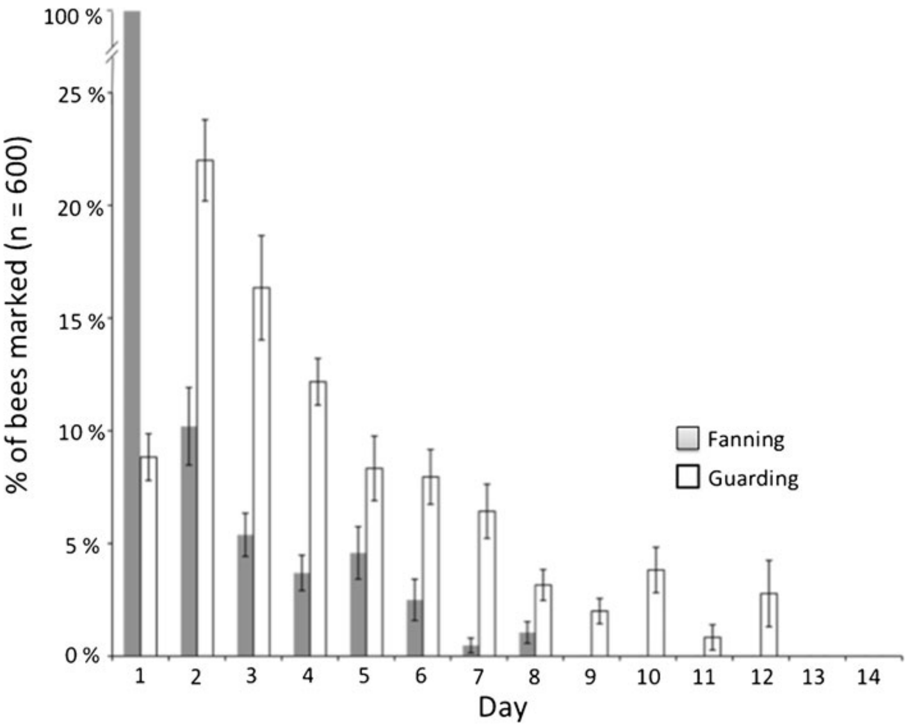

Fig. 1 Fanning persistence; percentage of all marked bees (n=600) observed fanning or guarding over 14 sequential days. Bees were collected when fanning, so 100 % of the marked bees exhibited fanning on day one. Of these, 9 % proceeded immediately to guarding on the same day. On each subsequent day, fewer marked bees were observed, and those observed were more likely to exhibit guarding behavior than fanning behavior

effects of day on fanning behavior (F=13.78, df=2, 149, p<0.0001) and on guarding (F=3.52, df=2, 149, p=0.032). In both cases there was a significant effect of day (fanning, p<0.0001; guarding, p=0.02), but not of bee (fanning, p=0.72; guarding, p=0.22)

An additional, opportunistic observation was that 4 fanners were observed either fanning with pollen on their legs or departing with other foragers immediately following a bout of fanning.

The mean number of bees fanning increased with temperature (Fig. 2) and decreased with humidity. For all hives, temperature was a significant correlate for number of fanning bees; however, humidity, hive, and crossed factors of each were not significant correlates (Table 1).

Discussion

The number of fanning bees increases outside the hive in response to ambient temperature; hotter temperatures will drive more bees to fan in order to thermoregulate the hive. There also appears to be a downward trend in number of bees fanning as relative humidity increases; this may be influenced by the availability of water outside the hive. Our data suggest that bees collected when fanning are statistically likely to shift their bias in behavior from fanning to guarding. While the probabilities of task performance suggest that fanning bees progress to higher levels of guarding in

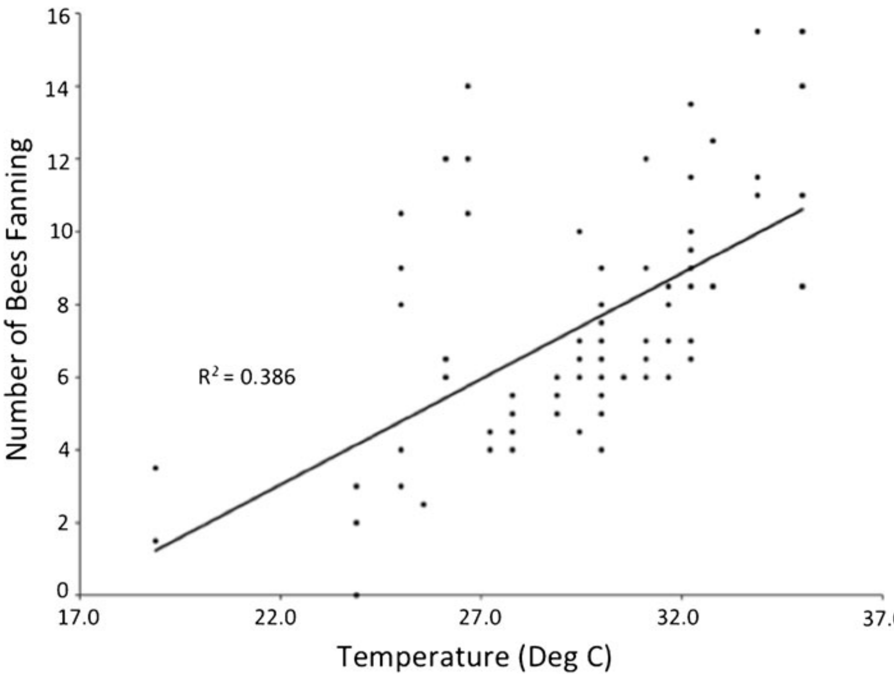

Fig. 2 Number of bees fanning and temperature during observational periods. As ambient temperature increased, fanners were present in greater numbers

Table 1 Standard least squares model fit effect tests for temperature, humidity, hive, and the interaction of temperature and humidity on the number of bees fanning. Total df=67, which are partitioned into 7 model df and 60 error df. For each effect and interaction F value, df=1, 60. Non-significant interactions are not reported in the table

	F	Probability
Overall ANOVA	6.67	<0.0001
Temperature	36.45	<0.0001
Humidity	3.10	0.0836
Hive	1.89	0.1742
Temp x Humidity	5.92	0.0180

successive days, there is more plasticity in the allocation between these tasks than we originally hypothesized. Instead of direct serial progression from one task to the next over the course of several days, it may be better to conceptually view fanning and guarding tasks with overlapping response thresholds, so that to a certain extent bees perform these tasks in parallel rather than in sequence. If this is the case, this raises the question of whether may also be other tasks that are performed in this parallel task partitioning scheme rather than in a stepwise serial fashion.

The idea that bees may act as pools of workers from which to be drawn for a given task also raises the idea of potential environmental triggers or thresholds that might change the daily relative composition of workers. It is well known that the defensive response of honeybee colonies changes seasonally and also as a response to a history of disturbances for the colony (Couvillon et al. 2008). The potential advantage of such flexibility in task partitioning remains to be seen. The concept of a worker pool and parallel task organization merits future study.

Our findings fit well with other studies, such as that of Southwick and Moritz (1987) in which bees were observed fanning a colony entrances. Water carrying and production of heat during have been the central foci of work on thermoregulation in honeybees (Kühnholz and Seeley 1998; Jones and Oldroyd 2006), while fanning has received less attention. Water carrying and fanning are both essential to the down-regulation of the thermal load on colonies

Fanning, like guarding (Breed et al. 1990) and undertaking (Robinson and Page 1988) is a relatively rare behavior (compared to nursing or foraging) and is unlikely to be exhibited by a meaningful number of bees in studies of marked cohorts (Johnson 2008). While the hypothesis that any bee may exhibit fanning above a temperature threshold should be considered, the stimulus threshold for virtually all behaviors in honeybee colonies is regulated by the age, physiological state, and genetics of individual bees. There is no data-based evidence for the assumption that fanning does not fit this general pattern, although as we suggest that some bees may be responsive to more than one stimulus, such as the need for guarding and the need for temperature regulation.

Acknowledgements We thank the University of Colorado at Boulder for housing the bee colonies used in this study. We are also grateful to M. Ochomogo Krasnec, C. Cook, and L. Sanchez for comments on the manuscript. R.E. was supported by the U.S. Air Force Institute of Technology's Civilian Institutions Program.

References

Breed MD, Robinson GE, Page RE (1990) Division of labour during honey-bee colony defense. Behav Ecol Sociobiol 27:395–401

Couvillon MJ, Robinson EJH, Atkinson B, Child L, Dent KR, Ratnieks FLW (2008) En garde: rapid shifts in honeybee, *Apis mellifera*, guarding behaviour are triggered by onslaught of conspecific intruders. Anim Behav 76:1653–1658

Crosland MWJ, Ren SX, Traniello JFA (1998) Division of labour among workers in the termite, *Reticulitermes fukienensis* (Isoptera: Rhinotermitidae). Ethol 104:57–67

Hannelie H, Nicolson SW, Dietemann V (2006) Do honeybees, *Apis mellifera scutellata*, regulate humidity in their nest? Naturwiss 93:397–401

Johnson BR (2002) Reallocation of labor in honeybee colonies during heat stress: the relative roles of task switching and the activation of reserve labor. Behav Ecol Sociobiol 51:188–196

Johnson BR (2008) Within-nest temporal polyethism in the honey bee. Behav Ecol Sociobiol 62:777–784

Johnson BR (2010) Division of labor in honeybees: form, function, and proximate mechanisms. Behav Ecol Sociobiol 64:305–316

Jones JC, Oldroyd BP (2006) Nest thermoregulation in social insects. Adv Insect Physiol 33:153–191

Korb J, Linsenmair KE (2000) Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? Insectes Sociaux 47:357–363

Kronenberg F, Heller HC (1982) Colonial thermoregulation in honey bees (*Apis mellifera*). J Comp Physiol 148:65–76

Kühnholz S, Seeley TD (1998) The control of water collection in honey bee colonies. Behav Ecol Sociobiol 41:407–422

Ratnieks FLW, Anderson C (1999) Task partitioning in insect societies. Insectes Sociaux 46:95–108

Robinson GE, Page RE (1988) Genetic determination of guarding and undertaking in honey-bee colonies. Nature 333:356–358

Robinson GE, Page RE (1995) Genotypic constraints on plasticity for corpse removal in honey-bee colonies. Anim Behav 49:867–876

Seeley TD (1974) Atmospheric carbon dioxide regulation in honey-bee (*Apis mellifera*) colonies. J Insect Physiol 20:2301–2305

Seeley TD (1982) Adaptive significance of the age polyethism schedule in honeybee colonies. Behav Ecol Sociobiol 11:287–293

Seeley TD, Kolmes SA (1991) Age polyethism for hive duties in honey bees—illusion or reality? Ethology 87:284–297

Siegel AJ, Hui J, Johnson RN, Starks PT (2005) Honey bee workers as mobile insulating units. Insectes Sociaux 52:242–246

Southwick EE, Moritz RFA (1987) Social control of air ventilation in colonies of honey bees, *Apis mellifera*. J Insect Physiol 33:623–626

Stabentheiner A, Kovac H, Brodschneider R (2010) Honeybee colony thermoregulation—regulatory mechanisms and contribution of individuals in dependence on age, location and thermal stress. Public Libr Sci One 5:e8967

Starks PT, Johnson RN, Siegel AJ, Decelle MM (2005) Heat shielding: a task for youngsters. Behav Ecol 16:128–132

Trumbo ST, Huang Z-Y, Robinson GE (1997) Division of labor between undertaker specialists and other middle-age honey bees. Behav Ecol Sociobiol 41:151–163

Vogt FD (1986) Thermoregulation in bumblebee colonies. I. Thermoregulatory versus brood-maintenance behaviors during acute changes in ambient temperature. Physiol Zool 59:55–59

Wilson EO (1971) The insect societies. Harvard University Press, Massachusetts

Winston ML (1991) The biology of the honey bee. Harvard University Press, London

Winston ML, Punnett EN (1982) Factors determining temporal division of labor in honeybees. Can J Zool 60:2947–2952

Yang MX, Radloff S, Tan K, Hepburn R (2010a) Anti-predator fan-blowing in guard bees, *Apis mellifera capensis* Esch. J Insect Behav 23:12–18

Yang MX, Wang ZW, Li H, Zhang ZY, Tan K, Radloff SE, Hepburn HR (2010b) Thermoregulation in mixed-species colonies of honeybees (*Apis cerana* and *Apis mellifera*). J Insect Physiol 56:706–709