Animal Behaviour 142 (2018) 69–76

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Experienced individuals influence the thermoregulatory fanning behaviour in honey bee colonies

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ARTICLE INFO

Article history:
Received 25 February 2018
Initial acceptance 4 April 2018
Final acceptance 14 May 2018

MS. number: A18-00153

Keywords:
Apis mellifera L.
fanning behaviour
homeostasis
initiator
leader
social influence
task allocation
thermal response threshold
thermoregulation

The survival of an animal society depends on how individual interactions influence group coordination. Interactions within a group determine coordinated responses to environmental changes. Individuals that are especially influential affect the behavioural responses of other group members. This is exemplified by honey bee worker responses to increasing ambient temperatures by fanning their wings to circulate air through the hive. Groups of workers are more likely to fan than isolated workers, suggesting a coordinated group response. But are some individuals more influential than others in this response? This study tests the hypothesis that an individual influences other group members to perform thermoregulatory fanning behaviour in the western honey bee, *Apis mellifera* L. We show that groups of young nurse bees placed with fanners are more likely to initiate fanning compared to groups of nurses without fanners. Furthermore, we find that groups with young nurse bees have lower response thresholds than groups of just fanners. Our results suggest that individuals have the capability to influence other individuals to follow their fanning response as temperatures increase, and these social dynamics balance probability of fanning with thermal response thresholds. An influential individual may ultimately affect the ability for a society to efficiently respond to environmental fluctuations.

The success of complex societies is facilitated by the division of tasks among individuals (Camazine et al., 2003; Chittka & Muller, 2009; Duffy, Morrison, & Macdonald, 2002; Wilson, 1971). Within a social group, individuals vary in how they respond to environmental stimuli (Beshers & Fewell, 2001; Emerson, 1956; Jeanson & Weidenmüller, 2014; Oster & Wilson, 1978; Pacala, Gordon, & Godfray, 1996; Robinson, 1992; Sih & Watters, 2005; Weidenmüller, 2004). This variation allows an individual to respond to labour demands in a flexible and adaptive manner (Oldroyd & Fewell, 2007; Stabentheiner, Kovac, & Brodschneider, 2010; Theraulaz, Bonabeau, & Denuebourg, 1998). For example, during bouts of social predation in chimpanzee, *Pan troglodytes*, troops the presence of certain individuals with greater hunting motivation increases economic profitability by promoting cooperation (Gilby, Eberly, & Wrangham, 2008). Some studies suggest that individual behavioural variation creates flexibility within group dynamics, which allows for greater robustness in colony responses to environmental perturbations (Duffy et al., 2002; Jones, Myerscough, Graham, & Oldroyd, 2004; Pruitt & Keiser, 2014; Pruitt & Riechert, 2011; Stabentheiner et al., 2010; Vodovotz, An, & Androulakis, 2013). For example, worker bees (middle-aged bees) who perform fanning behaviour (also known as 'fanners') do so more often in groups than as individuals, demonstrating social efficiency during environmental stress (Cook & Breed, 2013; Cook, Durzi, Scheckel, & Breed, 2016; Cook, Kaspar, Flaxman, & Breed, 2016; Weidenmüller, Kleineidam, & Tautz, 2002). While many examples such as these support the idea that individual variation ultimately affects the group response (Bonabeau, Theraulaz, & Deneubourg, 1998; Levin, 1998; Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014; Pruitt & Pinter-Wollman, 2015; Stabentheiner et al., 2010), little experimental work has been conducted to determine individual behaviour and how presence or behaviour of an individual can influence the success of an animal society (Jeanson & Weidenmüller, 2014; Johnstone & Manica, 2011; Sih & Watters, 2005).

Eusocial insect societies, such as honey bees, allow us to explore coordination of individuals within the broad scope of colonial homeostasis (Crespi & Yanega, 1995; Hölldobler & Wilson, 1990; Seeley, 2010; Winston, 1987). Some insect societies, like honey

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https://doi.org/10.1016/j.anbehav.2018.06.004
0003-3472/

bees, coordinate responses by dividing tasks among individuals based on age or sex (Beshers & Fewell, 2001; Beshers & Traniello, 1996; Crespi & Yanega, 1995). Task performance varies among colony members due to genetics and environment (Arathi & Spivak, 2001; Ben-Shahar, Robichon, Sokolowski, & Robinson, 2002; Bonabeau, Theraulaz, & Deneubourg, 1996; Calderone & Page, 1988, 1991; Robinson, 2002; Su et al., 2007). However, many models of division of labour do not fully consider individual behavioural variation because of the difficulty in assessing external effects on individuals (Jeanson & Weidenmüller, 2014; Sokolowski, 2010; Wilson & Hölldobler, 1988). Specifically, the effects of social and environmental modulation are difficult to predict from the standpoint of an individual within a large social insect colony (Chittka & Muller, 2009; Jeanson & Weidenmüller, 2014; Sokolowski, 2010; Wilson & Hölldobler, 1988). Instead, these models assume that all individuals respond to social and environmental modulation with equal likelihood (Camazine et al., 2003; Johnstone & Manica, 2011; Kitano, 2002; Schmickl & Crailsheim, 2004). Thus, these models fail to include components such as the state of the surrounding environment, the degree of coordination among individuals or social influence (Beshers & Fewell, 2001; Cook & Breed, 2013; Johnson, 2010; Mangel, 1995; Pacala et al., 1996; Power et al., 1996). The exclusion of individual variation from group or societal models likely reduces our understanding of coordinated responses (Jeanson & Weidenmüller, 2014), while including this variation will provide more accurate testable hypotheses of these group-level behaviours.

Individual honey bee workers use both internal social interactions and external conditions as cues for initiation of thermoregulatory fanning behaviour (Cook & Breed, 2013; Egley & Breed, 2013; Huang & Robinson, 1992). Each individual honey bee differs in their likelihood to respond to increasing temperatures due to age, genetic variation, morphological characteristics, or environmental experience (Breed, Williams, & Queral, 2002; Calderone, 1995; Calderone & Page, 1991; Huang & Robinson, 1996; Johnson, 2008; Jones, Helliwell, Beekman, Maleszka, & Oldroyd, 2005; Robinson, 1987, 1992, 2002; Simone-Finstrom, Foo, Tarpy, & Starks, 2014; Su et al., 2007; Withers, Fahrbach, & Robinson, 1993). Worker bees (middle-aged bees) are significantly more likely to perform the task of fanning than any other temporal caste, but genetic variation can also affect the frequency of the performance of fanning among subsets of workers (Cook & Breed, 2013; Su et al., 2007). However, worker bees can also be described in other behavioural castes, such as guarding the hive or removal of dead bees (Breed et al., 2002; Egley & Breed, 2013). Specifically, middle-aged bees can be pulled from their caste to develop into foragers (oldest bees) if the hive needs more resources and nurses (young bees) can be pushed from their caste depending on the status of the development of the brood (Calderone, 1995; Calderone & Page, 1996; Johnson, 2010; Johnson & Frost, 2012). The differences in response among behavioural and temporal task groups as well as the increased likelihood for individuals within a group to respond suggest that the interactions between nestmates enable individuals to cue in on environmental stress (Cook & Breed, 2013; Cook, Durzi et al., 2016; Cook, Kaspar et al., 2016; Pacala et al., 1996).

Honey bees interact individually to exchange information for proper task coordination to maintain colony homeostasis. These interactions within groups may ultimately have strong influences on the behavioural response of an individual (Calderone & Page, 1991; Cook & Breed, 2013; Schmickl & Crailsheim, 2004). But, it is still largely unclear whether certain individuals have the ability to influence the social processes of the coordination of various worker bees to organize into groups for a synergetic response (Bonabeau et al., 1998; Camazine et al., 2003; Jeanson & Weidenmüller, 2014; Jones et al., 2004; Levin, 1998; Modlmeier et al., 2014; Pruitt & Pinter-Wollman, 2015; Stabentheiner et al., 2010). Similar to Weidenmüller's observations (2004) in bumblebees, *Bombus terrestris*, we observed that other individuals influenced the fanning behaviour of an individual honey bee (Cook & Breed, 2013). Therefore, we were curious if the behaviour of an experienced individual influenced the behaviour of other individuals as well as the group response in European honey bees.

Here, we ask whether the presence of an experienced individual influences other inexperienced honey bees within the collective group fanning response. We explored this question by manipulating the social environment of honey bees by including a single fanner into a group of nurses. Fanners are older, experienced bees collected while fanning at the entrance of the colony. Nurses, in contrast, are young and active in caring for the brood, and thus likely have not fanned as a task yet (Seeley & Kolmes, 1991). First, we hypothesized that the presence of a fanner would influence the individual fanning response threshold of a nurse. We define the temperature at which an individual begins to fan as the 'individual thermal response threshold'. Specifically, we predicted that the presence of a fanner would alter the temperature at which a nurse began to fan to be similar to the individual thermal response threshold of a fanner. Second, we hypothesized that the presence of a fanner would influence the temperature at which nurses would fan together as a group. We define the temperature at which the group begins to fan together, or the temperature at which the last member of the group begins to fan, as the 'group thermal response threshold'. Third, we hypothesized that the presence of a fanner would influence the temperature at which the first bee fanned. We define the first bee to fan as the 'initiator' in the collective group fanning response. Fourth, contingent upon support of our previous predictions, we hypothesized that a fanner would be most influential if the fanner was the initiator in the group; the probability of bees to fan together as a group would be higher than if a nurse was initiator. Testing these hypotheses illuminates the importance of individual roles in the coordinated fanning response.

METHODS

Twelve *Apis mellifera* colonies on University of Colorado's East Campus were used for this experiment. Colonies were maintained in 10-frame wooden Langstroth hives with plastic or wood frames. Bees were supplemented with 1 M sucrose or pollen patties (Mann Lake, Hackensack, MN, U.S.A.) as needed. All experiments were conducted during June–September 2015 for a total of 90 trials. Data were recorded in a notebook and entered into a Microsoft Excel sheet and backed up on Google Drive. Microsoft Excel sheet was converted to CSV to be used in R and RStudio, version 0.99.486 (R Foundation for Statistical Computing, Vienna, Austria).

Experimental Design

To test an individual's influence on the response of fanning behaviour, we applied Weidenmüller's (2004) 'influence of experience' experiment. Rather than looking for a change of individual response threshold over time, we were interested in how an individual's response threshold was influenced by another individual. We tested the influence of a single fanner (middle-aged 'experienced' task group) within a group of nurses (youngest 'inexperienced' task group). There were two controls; a group composed only of fanners and a group composed only of nurses. There was a treatment group (hereafter 'mixed group') composed of a single fanner and four nurses. Fanners were defined as experienced bees because we collected them as they were experiencing the task of fanning at the entrance of the colony. Unlike fanners, nurses were