



Experienced individuals influence the thermoregulatory fanning behaviour in honey bee colonies

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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.

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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, & Deneubourg, 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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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 & Müller, 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, Malesszka, & Oldroyd, 2005; Robinson, 1987, 1992, 2002; Simone-Finstrom, Foo, Tarpy, & Starks, 2014; Su et al., 2007; Withers, Fahrback, & 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

defined as inexperienced bees because they were collected amongst the brood, which indicates that they were young and likely had not fanned as a task yet (Johnson, 2008; Seeley & Kolmes, 1991).

Group Size

Groups of five bees were collected from the same hive and inserted into a mesh cage (cylindrical: 20 × 6 cm) to allow bees to communicate by touching one another and allow continuous airflow. Although a group of five bees is relatively small compared to honey bee colonies, Cook and Breed (2013) illustrated that smaller groups of bees mimic those found in larger groups. However, this study is not focused on the outcome of differently sized groups of bees fanning but the influences within a single group size. Thus, this study used group sizes of five bees. For each sampling event, hives were randomly selected, but collection was distributed uniformly across hives.

Collection of Fanner and Nurse Bees

As described by Cook and Breed (2013), fanners are easily identified from their unique posture and orientation at the entrance. We selected bees that were observed fanning for at least 10 s, as Egley and Breed (2013) suggested that entrance fanners are relatively uniform in age. These identification protocols ensured that we did not collect bees that were Nasanov fanning. Nasanov fanners are distinguished by the straight posture of their abdomen and exposure of the Nasanov gland while fanning (Free, 1967). Cook and Breed (2013) found that pollen foragers were significantly less likely to fan in heating assays, so we avoided 'porch fanners' that had pollen on their corbicula. We selected nurses that were walking on top of brood and inserting their heads into brood comb, as these behaviours are indicative of the nurse task group (Johnson, 2008; Seeley & Kolmes, 1991). To avoid risk of added aggression or disturbance bias by opening the hive, we selected porch fanners before we selected nurses. Nestmates were only used within groups of five bees in a single mesh cage. There were two controls: only fanners and only nurses. There was one treatment: four nurses with one fanner. Bees were collected and brought into the laboratory so that no longer than 15 min elapsed for collection and transportation. During collection, each bee was marked with a unique colour of paint (Sharpie Water-based Paint Marker) to observe both individual and group responses. When sampling, we recorded outside humidity and temperature, date and time of collection, sun or shade over the hive and hive number.

Behavioural Assays

Once transported into the laboratory, groups were acclimated for 20 min within 2-litre glass jars with fitted lids (Specialty Container Inc., Owensboro, KY, U.S.A.). A high-accuracy temperature probe was inserted through the fitted hole of the lid and into the jar. Each container sat on an individual heat stove (Cimarc Digital Hot Plate, Thermo Fisher Scientific, Waltham, MA, U.S.A.). Each group was treated with a 1.0 °C/min temperature increase. We established a 20 min acclimation period and heating assay based on our preliminary tests, which solidified a required protocol of 20 min based on time required for the bees to reach a level of behavioural stability. Each mesh cage was held by wooden skewer stilts within the jar to ensure that the cage was not in contact with the glass jar. We recorded the initial air temperature of the chamber and the trial start time. Although ambient temperature differed across trials because trials were performed at different times of the day and throughout the summer season, the temperatures at which trials

started were consistent, as they were performed in a laboratory setting. Temperatures were taken at approximately the centre of the chamber where bees were restricted in the cage. As with collection, we allowed each individual bee to fan for at least 10 s in order to properly describe the individual as 'fanning'. Trials were concluded when the last bee reached lethal temperature, at which point we recorded the time of trial conclusion and calculated the rate of temperature increase (Cook, Durzi et al., 2016; Cook, Kaspar et al., 2016). We conducted 30 trials per group for a total of 90 trials. Within each trial, we recorded several response variables. Individual response variables consisted of (1) the temperature at which an individual began to fan (hereafter individual thermal response threshold), (2) the initiator and (3) the temperature of each individual's death. Group response variables included (1) the temperature at which the group fanned together (hereafter group thermal response threshold and (2) the proportion of bees that fanned together as a group (hereafter the probability of fanning) (Cook & Breed, 2013; Cook, Durzi et al., 2016; Cook, Kaspar et al., 2016).

Statistical Analysis

Hypotheses 1 and 2: Presence of fanners influences a nurse's individual and group thermal response threshold

To analyse both individual and group thermal response thresholds for each trial group, we used a generalized linear model to conduct an ANOVA using R function `aov()`. When the ANOVA test showed significant difference between means, we conducted multiple comparisons using all pairwise means to determine exactly how they differed through Tukey post hoc test using R function `TukeyHSD`.

Hypothesis 3: Fanners influence the temperature of the first to fan

To determine the initiator of the group fanning response, it was necessary to analyse each initiator's thermal response threshold between all trial groups. We conducted an ANOVA test using R function `aov()` among the temperatures of fanning (1) for the initiators within the control fanners, (2) if the initiator within the mixed group was a fanner, (3) if the initiator within the mixed group was a nurse and (4) for the initiators within the control nurses. When the test determined significance, we conducted Welch two-sample *t* tests to determine the exact significance between each group using R function `t.test`.

Hypothesis 4: Fanners are more influential on other group members when they fan first

For probability of fanning, we performed a logistic regression with a binomial error distribution (`link = logit`). We did this by using a two-column response variable (number of fanners, number of nonfanners) and performing a generalized linear model using `glm()`. We performed a logistic regression because the response variable was a proportion, and was therefore not normally distributed, using '`family = binomial(link = logit)`'. We initially included hive as a random effect in a mixed model, then compared it to a simpler model without hive as a random effect. The mixed effect model did not have significantly higher predictive power, so we dropped hive as a random effect and used the simpler model. Then, we conducted a post hoc Tukey test to determine the number of bees to fan as a group following an initiator using R function '`TukeyHSD`'.

Ethical Note

A license or certificate was not required through the University of Colorado, Boulder, as our experiments only involved insects.

Even so, we minimized colonial disturbances by only handling individuals during collection periods.

RESULTS

Presence of a Fanner Influences Individual Thermal Response Thresholds

Nurses in the control group had significantly lower individual thermal response thresholds than fanners or the mixed group (ANOVA: $F_{2,207} = 16.39$, $P < 0.0001$, $N = 90$; Fig. 1). There was no significant difference between the individual thermal response thresholds of the control fanners and the mixed group (Tukey: $P = 0.6620$; Fig. 1).

Presence of a Fanner Influences Group Thermal Response Threshold

The group thermal response threshold of nurses was significantly lower than that of the fanners and the mixed group (ANOVA: $F_{2,46} = 5.242$, $P = 0.0089$, $N = 90$; Fig. 2). Additionally, there was no significant difference in the group thermal response thresholds of the fanners and the mixed group (Tukey: $P = 0.934$).

Fanners Influence the Thermal Response Threshold of the First to Fan

The individual thermal response threshold of the nurse initiator was significantly lower in the control nurses than in the mixed group (t test: $t_{39,40} = 2.299$, $P = 0.027$; Fig. 3). The individual thermal response threshold of the fanner initiator in the mixed group did not differ significantly from that of the fanner initiator in the control fanners (t test: $t_{15,40} = 0.580$, $P = 0.569$) but was significantly higher than the nurse initiator in the control nurses (t test: $t_{24,71} = 2.440$, $P = 0.022$). The individual thermal response threshold of the nurse initiator was significantly lower in the control nurses than in both the fanners and the mixed group (ANOVA: $F_{3,73} = 3.036$, $P = 0.034$, $N = 90$; Fig. 3).

Fanners are More Influential When They Fan First

When fanners were the initiators within the mixed group, nurses were significantly more likely to fan as a group (GLM: $Z = 2.219$, $P = 0.026$; Fig. 4). While there was no significant

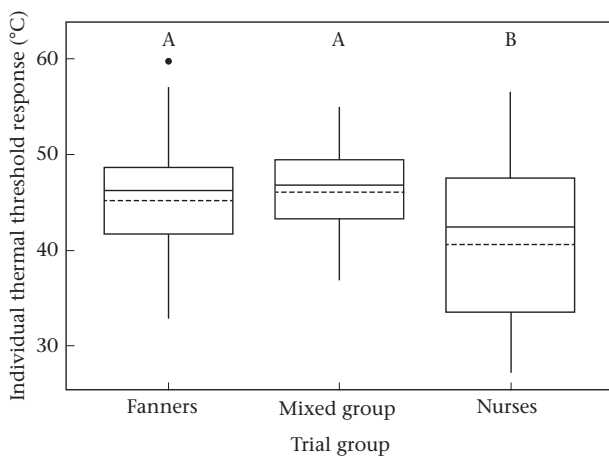


Figure 1. Individual thermal response threshold for control fanners, mixed groups and control nurses. Boxes are 25–75th percentiles, black horizontal lines are medians, red horizontal lines are means, error bars are $1.5 \times IQR$, points are Tukey outliers ($N = 90$). Created using R Package 'ggplot2'. Different letters above plots denote statistically significant differences between trial groups.

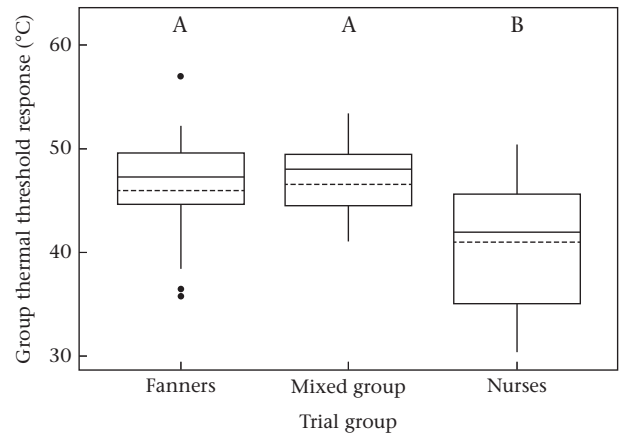


Figure 2. Group thermal response threshold for control fanners, mixed groups and control nurses. Boxes are 25–75th percentiles, black horizontal lines are medians, red horizontal lines are means, error bars are $1.5 \times IQR$, points are Tukey outliers ($N = 90$). Created using R Package 'ggplot2'. Different letters above plots denote statistically significant differences between trial groups.

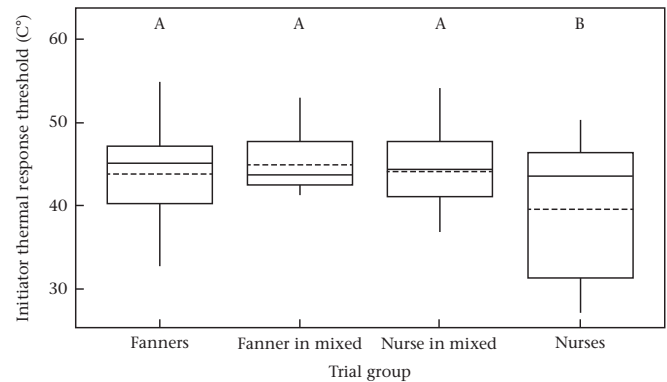


Figure 3. Thermal threshold of initiator for control fanners, fanner initiators within mixed groups, nurse initiators within mixed groups and control nurses. Boxes are 25–75th percentiles, black horizontal lines are medians, red horizontal lines are means, error bars are $1.5 \times IQR$, points are Tukey outliers ($N = 90$). Created using R Package 'ggplot2'. Different letters above plots denote statistically significant differences between trial groups.

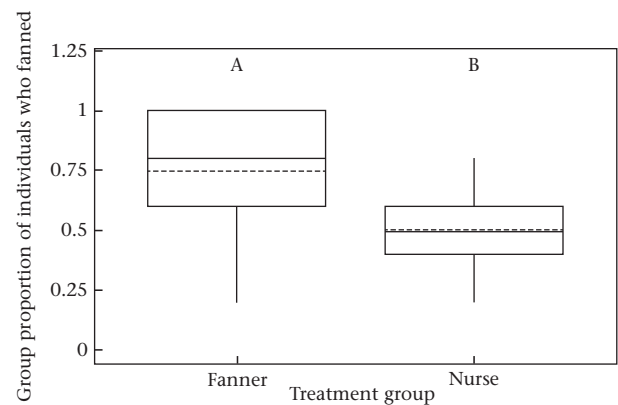


Figure 4. Proportion of bees that fanned after a fanner initiator and after a nurse initiator. Boxes are 25–75th percentiles, black horizontal lines are medians, red horizontal lines are means, error bars are $1.5 \times IQR$, points are Tukey outliers ($N = 30$). Created using R Package 'ggplot2'. Different letters above plots denote statistically significant differences between trial groups.

difference in the probability of a fanner or a nurse performing fanning behaviour across all groups (GLM: $Z = 0.479$, $P > 0.5$; Tukey: $P = 0.379$), the number of individuals fanning significantly increased after the fanner was the initiator compared to when a nurse was the initiator (ANOVA: $F_{2,26} = 10.28$, $P < 0.001$; Tukey: $P < 0.001$). There was no significant difference in the probability of fanning across group types ($Z = 0.25$, $P = 0.64$) or within the mixed trials for fanners and nurses by individual type ($Z = 0.44$, $P = 0.85$).

DISCUSSION

An influential individual can lead other individuals in the performance of coordinated, group-level behavioural responses to changes in ambient conditions. Our results illustrate that certain individuals may influence individual and group thermal response thresholds within honey bee task groups due to differences in temporal caste and experience. Nurses have a lower individual and group thermal response threshold than fanners, however, this is only the case when the group consists of just nurses. In mixed groups of nurses and fanners, when a single fanner was present among nurses, the fanner influenced nurse individual and group behaviour by increasing their thermal response threshold: these mixed groups fanned at higher temperatures. Single nurses had no effect on the individual thermal response threshold of fanners. However, when the single fanner was the initiator within the mixed group, the likelihood of nurses beginning to fan significantly increased. This indicates that fanners play the role of a leader by influencing other individuals and group behavioural response thresholds, and that they are most influential when they are the initiators of the behaviour. Our results suggest that nurses have a lower thermal response threshold than fanners as a consequence of temporal division of labour, and that the presence of a fanner restrains the nurses from fanning at a low temperature threshold. Strikingly, our results also indicate that fanners can recruit younger nurse bees when environmentally stressed.

Social interactions between nurses and fanners may influence their group thermoregulatory response thresholds. Previous studies showed that worker bees can switch from other tasks to fanning as needed (Egley & Breed, 2013). Recruitment of young nurses by middle-aged fanners may be one example of Johnson's (2010) push–pull model for colony task allocation. Here, nurses are influenced to fan at higher temperatures if there is only a single fanner in the group. Nurses are more heavily influenced to fan if the initiator is a fanner. A single fanner influences nurses by increasing their thermal response threshold as well as their likelihood of fanning. Our results illustrate that nurses are more likely to fan when they are among fanners. While fanning is not necessarily the primary task of the nurses – they clean cells and feed the brood (Oster & Wilson, 1978) – if the temperature of the hive is not properly regulated, our results suggest that nurses may respond to warming temperatures in the brood area at a lower threshold to ensure the proper development and survival of the brood at an optimal temperature range between 34.5 °C and 36 °C (Groh, Tautz, & Rössler, 2004; Himmer, 1932; Johnson, 2008, 2010; Jones et al., 2005; Kronenberg & Heller, 1982; Seeley & Kolmes, 1991; Tautz, Maier, Groh, Rössler, & Brockmann, 2003; Westhus, Kleineidam, Roces, & Weidenmüller, 2013). Cook, Durzi et al. (2016) found that nurses are more likely to fan when larvae are present, but the nurses must have direct contact with larvae to perform fanning behaviour. Nurses may be especially sensitive to increasing temperatures because the primary role of a nurse is to care for the brood, which are extremely sensitive to temperature fluctuations (Johnson, 2008, 2010; Seeley & Kolmes, 1991). We found that individuals in the nurse control group and the mixed group were able

to survive significantly longer and at higher temperatures than individuals in the fanner control group, but we are unsure as to why this may be the case (Fig. S1). We find this result intriguing because social influence can also be demonstrated during brood heating behaviour: heater bees do not need to sense the temperature by themselves but can be stimulated by other heater bees to do so (Bujok, 2005; Bujok, Kleinhenz, Fuchs, & Tautz, 2002; Tautz & Steen, 2017). In addition, our results suggest social recruitment of nurses to the temporal caste of worker bees, as the probability of nurses to fan only increased when fanners initiated fanning in a group setting. Furthermore, when Su et al. (2007) compared the patriline of the whole colony to different patrilines of workers that performed thermoregulatory fanning, these workers performed thermoregulatory fanning behaviour at different frequencies, suggesting that individual genetic variation can also play a role in fanning behaviour. These studies, including our own, suggest that the performance of fanning behaviour may not be specialized across task groups, but it is likely that the probability of performing this task and its thresholds vary with age as well as among individuals. This makes sense in the context of social insect societies, where the survival of individuals depends on survival of the group.

Individuals can learn from experience, response variation and/or knowledge of the environment and influence a group's collective effort to respond to a variety of situations via social learning (Chittka & Müller, 2009; Reeb, 2000; Sokolowski, 2010; Suboski, 1988). Social learning has been suggested in bumblebees, which also exhibit model thermoregulatory fanning behaviour such as honey bees. Weidenmüller (2004) and Westhus et al. (2013) found that bumblebees, *B. terrestris*, increased their likelihood of fanning and decreased their thermal response thresholds when individuals repeatedly performed fanning behaviour. Inside *Bombus impatiens* nests, Jandt, Huang, and Dornhaus (2009) found no evidence of fanning specialization among task groups, and Duong and Dornhaus (2012) only found high levels of intraindividual variation in response thresholds. Could it be possible that middle-aged 'experienced' fanners exhibit a self-reinforcement model and then influence younger nurse individuals? If so, how do honey bees assess each other's experience levels? Are honey bees capable of individual age detection? Honey bees can recognize one another via pheromones, and there are also many examples of associative self-reinforcement learning found in foraging behaviour, but there are no published studies on social learning for thermoregulation (Bitterman, 1996; Breed, 1998; Couvillon et al., 2015; Free, 1967; Giurfa, et al., 1999; Menzel, 1993). However, social learning can be found in other organisms, such as golden shiner fish, *Notemigonus crysoleucas*, where experienced individuals led naïve individuals to certain areas of a tank where food was anticipated at certain times of the day, demonstrating that experienced individuals facilitate group events (Reeb, 2000; Suboski, 1988). Unlike bumblebees, we suggest that honey bee fanners may have previously fanned and are more accustomed to higher temperatures as a result of their age (Cook & Breed, 2013; Cook, Durzi et al., 2016; Cook, Kaspar et al., 2016; Westhus et al., 2013). Here, our results show that experienced fanners lead inexperienced nurses to fan at a higher thermal threshold, initiating nurses to help facilitate cooling of warming environments. Thermoregulatory experience within a temporal task group may have an influence on social learning between individuals, but our experiments did not directly test social learning. Further investigation into experience recognition in honey bees would greatly benefit our understanding of social learning.

In societies, certain individuals may be more influential than others to effectively organize difficult tasks and can be often denoted as 'leaders'. Why might these influential individuals

emerge? Individuals may be persistent leaders, such as in elephants and dogs, as a result of being the oldest individual in the group and possessing the most experience, thereby influencing the social knowledge of their entire group due to their reliability (Bonanni, Cafazzo, Valsecchi, & Natoli, 2010; McComb et al., 2011; Payne, 2003). Furthermore, when group survival depends on a particularly influential individual, consequences may arise when these influential individuals are removed from their societies (Gilby et al., 2008; Lewis, Wartzok, & Heithaus, 2011; McComb et al., 2011; Pruitt & Keiser, 2014; Pruitt & Pinter-Wollman, 2015). However, in honey bees, rather than hierarchical informational flow, colonies have distributed patterns of dissemination, making it unlikely that honey bees exhibit keystone individuals or dominance hierarchies in social regulation (Boes, 2010; Bonabeau et al., 1998; Hrassnigg & Craisheim, 2005; Huang & Robinson, 1996; King, Douglas, Huchard, Isaac, & Cowlishaw, 2008; Schmickl & Craisheim, 2004; Sih, Hanser, & McHugh, 2009; Sih & Watters, 2005). Due to biological constraints, we did not test whether specific individuals were consistent leaders and whether their influence persisted after removal from the group in honey bees. But, social dynamics within collective group efforts can be plastic, and leaders within a group may not be consistently the same individual and may arise due to other individual variations. Such as in caterpillars (*Malacosoma disstria*), only the hungriest individuals initiate successful collective group foraging bouts (McClure, Ralph, & Despland, 2011). Some experienced leaders will maintain their roles only if they are familiar with the environment or else group members select other leaders, such as is found in social sawfly, *Perga affinis* (Hodgkin, Symonds, & Elgar, 2017). Others argue that there is no need for individual variation to have influential individuals spontaneously emerge in populations to influence followers (Johnstone & Manica, 2011). Yet, the persistent relationship between leaders and followers across a wide scope of biological societies suggests that individual variation is indeed beneficial (King, Johnson, & Van Vugt, 2009). Exploitation of individual knowledge fosters social coordination to support the maintenance of leaders and followers within a group, ultimately benefiting a society (Hodgkin et al., 2017; Sokolowski, 2010). Our study with honey bees demonstrates that not only do middle-aged fanners and younger nurses have different thermal response thresholds, but fanners are exceptionally influential individuals when they are the initiators of fanning among nurses, suggesting that nurses follow a fanner's behaviour to help lower the temperature of the surrounding environment. Our results provide further evidence that honey bee workers show individual variation in temporal tasks and that this variation likely affects colony survival – but how individuals emerge to be socially influential remains to be explored (Breed et al., 2002; Page & Robinson, 1991).

Our results suggest that an influential experienced individual may ultimately affect the ability of a society to efficiently respond to environmental fluctuations. The emergence of an influential leader for a task within a honey bee colony may occur due a variety of influences such as the task and age differences within temporal task groups, prior fanning behaviour experience or prior exposure to stimuli related to increasing temperatures, indirect social interactions and individual behavioural or genetic variation (Beshers & Fewell, 2001; Robinson, 2002; Seeley, 2010; Su et al., 2007). While we do not understand the precise social mechanisms by which one bee influences the behaviour of other bees, both indirect and direct interactions can result in increased efficiency of response to environmental stimuli (Calderone & Page, 1991; Camazine, 1993; Kühnholz & Seeley, 1997). Social thermoregulatory fanning behaviour in honey bees furthers our understanding of how individual variance influences a synchronous homeostatic response to environmental stressors.

Declaration of Interest

None.

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Supplementary Material

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References

- Arathi, H. S., & Spivak, M. (2001). Influence of colony genotypic composition on the performance of hygienic behaviour in the honeybee, *Apis mellifera* L. *Animal Behaviour*, 62, 57–66.
- Ben-Shahar, Y., Robichon, A., Sokolowski, M. B., & Robinson, G. E. (2002). Influence of gene action across different time scales on behavior. *Science*, 296(5568), 741–744.
- Beshers, S. N., & Fewell, J. H. (2001). Models of division of labor in social insects. *Annual Review of Entomology*, 46(1), 413–440.
- Beshers, S. N., & Traniello, J. F. A. (1996). Polyethism and the adaptiveness of worker size variation in the attine ant *Trachymyrmex septentrionalis*. *Journal of Insect Behavior*, 9(1), 6183.
- Bitterman, M. E. (1996). Comparative analysis of learning in honeybees. *Animal Learning & Behavior*, 24(2), 123–141.
- Boes, K. E. (2010). Honeybee colony drone production and maintenance in accordance with environmental factors: An interplay of queen and worker decisions. *Insectes Sociaux*, 57, 1–9.
- Bonabeau, E., Theraulaz, G., & Deneubourg, J. L. (1996). Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proceedings of the Royal Society B: Biological Sciences*, 263(1376), 1565–1569.
- Bonabeau, E., Theraulaz, G., & Deneubourg, J. L. (1998). Group and mass recruitment in ant colonies: The influence of contact rates. *Journal of Theoretical Biology*, 195(2), 157–166.
- Bonanni, R., Cafazzo, S., Valsecchi, P., & Natoli, E. (2010). Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs. *Animal Behaviour*, 79, 981–991.
- Breed, M. D. (1998). Recognition pheromones of the honey bee. *BioScience*, 48(6), 463–470.
- Breed, M. D., Williams, D. B., & Queral, A. (2002). Demand for task performance and workforce replacement: Undertakers in honeybee, *Apis mellifera*, colonies. *Journal of Insect Behavior*, 15(3), 319–329.
- Bujok, B. (2005). *Thermoregulation in the brood region of honeybees (Apis mellifera carnica)* (Doctoral thesis). Würzburg, Germany: Universität Würzburg. Retrieved from: <https://opus.bibliothek.uni-wuerzburg.de/frontdoor/index/year/2005/docId/1364>.
- Bujok, B., Kleinhenz, M., Fuchs, S., & Tautz, J. (2002). Hot spots in the bee hive. *Naturwissenschaften*, 89(7), 299–301.
- Calderone, N. W. (1995). Temporal division of labor in the honey bee, *Apis mellifera*: Developmental process or the result of environmental influences? *Canadian Journal of Zoology*, 73, 1410–1416.
- Calderone, N. W., & Page, R. E., Jr. (1988). Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology*, 22, 17–25.
- Calderone, N. W., & Page, R. E., Jr. (1991). Evolutionary genetics of division of labor in colonies of the honey bee (*Apis mellifera*). *American Naturalist*, 138(1), 69–92.
- Calderone, N. W., & Page, R. E., Jr. (1996). Temporal polyethism and behavioural canalization in the honey bee, *Apis mellifera*. *Animal Behaviour*, 51, 631–643.
- Camazine, S. (1993). The regulation of pollen foraging by honey bees: How foragers assess the colony's need for pollen. *Behavioral Ecology and Sociobiology*, 32(4), 265–272.
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Bonabeau, E., & Theraulaz, G. (2003). *Self-organization in biological systems*. Princeton, NJ: Princeton University Press.
- Chittka, L., & Müller, H. (2009). Learning, specialization, efficiency and task allocation in social insects. *Communicative and Integrative Biology*, 2(2), 151–154.
- Cook, C. N., & Breed, M. D. (2013). Social context influences the initiation and threshold of thermoregulatory behaviour in honeybees. *Animal Behaviour*, 86, 323–329.

- Cook, C. N., Durzi, S., Scheckel, K. J., & Breed, M. D. (2016). Larvae influence thermoregulatory fanning behavior in honeybees (*Apis mellifera* L.). *Insectes Sociaux*, 63(2), 271–278.
- Cook, C. N., Kaspar, R. E., Flaxman, S. M., & Breed, M. D. (2016). Rapidly changing environment modulates the thermoregulatory fanning response in honeybee groups. *Animal Behaviour*, 115, 237–243.
- Couvillon, M. J., Al Toufaïlia, H., Butterfield, T. M., Schrell, F., Ratnieks, F. L., & Schürch, R. (2015). Caffeinated forage tricks honeybees into increasing foraging and recruitment behaviors. *Current Biology*, 25(21), 2815–2818.
- Crespi, B. J., & Yanega, D. (1995). The definition of eusociality. *Behavioral Ecology*, 6(1), 109–115.
- Duffy, E. J., Morrison, C. L., & Macdonald, K. S. (2002). Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. *Behavioral Ecology and Sociobiology*, 51(5), 488–495.
- 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(1), 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.
- Emerson, A. E. (1956). Regenerate behavior and social homeostasis of termites. *Ecology*, 37(2), 248–258.
- Free, J. B. (1967). Factors determining the collection of pollen by honeybee foragers. *Animal Behaviour*, 15, 134–144.
- Gilby, I. C., Eberly, L. E., & Wrangham, R. W. (2008). Economic profitability of social predation among wild chimpanzees: Individual variation promotes cooperation. *Animal Behaviour*, 75, 351–360.
- Giurfa, M., Hammer, M., Stach, S., Stollhoff, N., Müller-Deisig, N., & Mizrycki, C. (1999). Pattern learning by honeybees: Conditioning procedure and recognition strategy. *Animal Behaviour*, 57, 315–324.
- Groh, C., Tautz, J., & Rössler, W. (2004). Synaptic organization in the adult honey bee brain is influenced by brood-temperature control during pupal development. *Proceedings of the National Academy of Sciences of the United States of America*, 101(12), 4268–4273.
- Himmer, A. (1932). Die Temperaturverhältnisse bei den sozialen Hymenopteren. *Biological Reviews*, 7(3), 224–253.
- Hodgkin, L. K., Symonds, M. R., & Elgar, M. A. (2017). Leadership through knowledge and experience in a social sawfly. *Animal Behaviour*, 134, 177–181.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Harvard University Press.
- Hrassnigg, N., & Crailsheim, K. (2005). Differences in drone and worker physiology in honeybees (*Apis mellifera*). *Apidologie*, 36(2), 255–277.
- Huang, Z. Y., & Robinson, G. E. (1992). Honeybee colony integration: Worker–worker interactions mediate hormonally regulated plasticity in division of labor. *Proceedings of the National Academy of Sciences of the United States of America*, 89(24), 11726–11729.
- Huang, Z. Y., & Robinson, G. E. (1996). Regulation of honey bee division of labor by colony age demography. *Behavioral Ecology and Sociobiology*, 39(3), 147–158.
- Jandt, J. M., Huang, E., & Dornhaus, A. (2009). Weak specialization of workers inside a bumble bee (*Bombus impatiens*) nest. *Behavioral Ecology and Sociobiology*, 63(12), 1829–1836.
- Jeanson, R., & Weidenmüller, A. (2014). Interindividual variability in social insects: Proximate causes and ultimate consequences. *Biological Reviews*, 89(3), 671–687.
- Johnson, B. R. (2008). Within-nest temporal polyethism in the honey bee. *Behavioral Ecology and Sociobiology*, 62, 777–784.
- Johnson, B. R. (2010). Division of labor in honeybees: Form, function, and proximate mechanisms. *Behavioral Ecology and Sociobiology*, 64(3), 305–316.
- Johnson, B. R., & Frost, E. (2012). Individual-level patterns of division of labor in honeybees highlight flexibility in colony-level developmental mechanisms. *Behavioral Ecology and Sociobiology*, 66(6), 923–930.
- Johnstone, R. A., & Manica, A. (2011). Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences of the United States of America*, 108(20), 8373–8378.
- Jones, J. C., Helliwell, P., Beekman, M., Maleszka, R., & Oldroyd, B. P. (2005). The effects of rearing temperature on developmental stability and learning and memory in the honey bee, *Apis mellifera*. *Journal of Comparative Physiology A*, 191(12), 1121–1129.
- Jones, J. C., Myerscough, M. R., Graham, S., & Oldroyd, B. P. (2004). Honey bee nest thermoregulation: Diversity promotes stability. *Science*, 305(5682), 402–404.
- King, A. J., Douglas, C. M., Huchard, E., Isaac, N. J., & Cowlishaw, G. (2008). Dominance and affiliation mediate despotism in a social primate. *Current Biology*, 18(23), 1833–1838.
- King, A. J., Johnson, D. D., & Van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology*, 19(19), R911–R916.
- Kitano, H. (2002). Computational systems biology. *Nature*, 420, 206–210.
- 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. (1997). The control of water collection in honey bee colonies. *Behavioral Ecology and Sociobiology*, 41(6), 407–422.
- Levin, S. A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, 1, 431–436.
- Lewis, J. S., Wartzok, D., & Heithaus, M. R. (2011). Highly dynamic fission–fusion species can exhibit leadership when traveling. *Behavioral Ecology and Sociobiology*, 65(5), 1061–1069.
- Mangel, M. (1995). Social interactions, nonlinear dynamics and task allocation in groups. *Trends in Ecology & Evolution*, 10(9), 347.
- McClure, M., Ralph, M., & Despland, E. (2011). Group leadership depends on energetic state in a nomadic collective foraging caterpillar. *Behavioral Ecology and Sociobiology*, 65(8), 1573–1579.
- McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., et al. (2011). Leadership in elephants: The adaptive value of age. *Proceedings of the Royal Society B: Biological Sciences*, 278(1722), 3270–3276. <https://doi.org/10.1098/rspb.2011.0168>.
- Menzel, R. (1993). Associative learning in honey bees. *Apidologie*, 24, 157–168.
- Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: An ecological and evolutionary overview. *Animal Behaviour*, 89, 53–62.
- Oldroyd, B. P., & Fewell, J. H. (2007). Genetic diversity promotes homeostasis in insect colonies. *Trends in Ecology & Evolution*, 22(8), 408–413.
- Oster, G. F., & Wilson, E. O. (1978). *Caste and ecology in the social insects*. Princeton, NJ: Princeton University Press.
- Pacala, S. W., Gordon, D. M., & Godfray, H. C. J. (1996). Effects of social group size on information transfer and task allocation. *Evolutionary Ecology*, 10, 127–165.
- Page, R. E., & Robinson, G. E. (1991). The genetics of division of labour in honey bee colonies. In P. D. Evans (Ed.), *Advances in insect physiology* (Vol. 23, pp. 117–169). London, U.K.: Academic Press.
- Payne, K. (2003). Sources of social complexity in the three elephant species. In F. B. M. de Waal, & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 57–85). Cambridge, MA: Harvard University Press.
- Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., et al. (1996). Challenges in the quest for keystones. *BioScience*, 46(8), 609–620.
- Pruitt, J. N. J., & Keiser, C. N. (2014). The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Animal Behaviour*, 93, 87–95.
- Pruitt, J. N. J., & Pinter-Wollman, N. (2015). The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151766. <https://doi.org/10.1098/rspb.2015.1766>.
- Pruitt, J. N. J., & Riechert, S. S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B: Biological Sciences*, 278(1709), 1209–1215.
- Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour*, 59, 403–409.
- Robinson, G. E. (1987). Regulation of honey bee age polyethism by juvenile hormone. *Behavioral Ecology and Sociobiology*, 20(5), 329–338.
- Robinson, G. E. (1992). Regulation of division of labor in insect societies. *Annual Review of Entomology*, 37(1), 637–665.
- Robinson, G. E. (2002). Genomics and integrative analyses of division of labor in honeybee colonies. *American Naturalist*, 160(Suppl. 6), S160–S172.
- Schmickl, T., & Crailsheim, K. (2004). Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply. *Apidologie*, 35(3), 249–263.
- Seeley, T. D. (2010). *Honeybee democracy*. Princeton, NJ: Princeton University Press.
- Seeley, T. D., & Kolmes, S. A. (1991). Age polyethism for hive duties in honey bees: Illusion or reality? *Ethology*, 87(3–4), 284–297.
- Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63(7), 975–988.
- Sih, A., & Watters, J. V. (2005). The mix matters: Behavioural types and group dynamics in water striders. *Behaviour*, 142(9–10), 1417–1431.
- Simone-Finstrom, M., Foo, B., Tarry, D. R., & Starks, P. T. (2014). Impact of food availability, pathogen exposure, and genetic diversity on thermoregulation in honey bees (*Apis mellifera*). *Journal of Insect Behavior*, 27, 527–539.
- Sokolowski, M. B. (2010). Social interactions in 'simple' model systems. *Neuron*, 65(6), 780–794.
- 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(1), e8967. <https://doi.org/10.1371/journal.pone.0008967>.
- Su, S., Albert, S., Zhang, S., Maier, S., Chen, S., Du, H., et al. (2007). Non-destructive genotyping and genetic variation of fanning in a honey bee colony. *Journal of Insect Physiology*, 53(5), 411–417.
- Suboski, M. D. (1988). Acquisition and social communication of stimulus recognition by fish. *Behavioural Processes*, 16(3), 213–244.
- Tautz, J., Maier, S., Groh, C., Rössler, W., & Brockmann, A. (2003). Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development. *Proceedings of the National Academy of Sciences of the United States of America*, 100(12), 7343–7347.
- Tautz, J., & Steen, D. (2017). *Die Honigfabrik: Die Wunderwelt der Bienen – Eine Betriebsbesichtigung*. Gütersloh, Germany: Gütersloher Verlagshaus.
- Theraulaz, G., Bonabeau, E., & Deneubourg, J. N. (1998). Response threshold reinforcements and division of labour in insect societies. *Proceedings of the Royal Society B: Biological Sciences*, 265(1393), 327–332.
- Vodovotz, Y., An, G., & Androulakis, I. P. (2013). A systems engineering perspective on homeostasis and disease. *Frontiers in Bioengineering and Biotechnology*, 1, 6. <https://doi.org/10.3389/fbioe.2013.00006>.
- Weidenmüller, A. (2004). The control of nest climate in bumblebee (*Bombus terrestris*) colonies: Interindividual variability and self reinforcement in fanning response. *Behavioral Ecology*, 15(1), 120–128.

- Weidenmüller, A., Kleineidam, C., & Tautz, J. (2002). Collective control of nest climate parameters in bumblebee colonies. *Animal Behaviour*, *63*, 1065–1071.
- Westhus, C., Kleineidam, C. J., Roces, F., & Weidenmüller, A. (2013). Behavioural plasticity in the fanning response of bumblebee workers: Impact of experience and rate of temperature change. *Animal Behaviour*, *85*, 27–34.
- Wilson, E. O. (1971). *The insect societies*. Cambridge, MA: Belknap.
- Wilson, E. O., & Hölldobler, B. (1988). Dense hierarchies and mass communication as the basis of organization in ant colonies. *Trends in Ecology & Evolution*, *3*(3), 65–68.
- Winston, M. L. (1987). *The biology of the honey bee*. Cambridge, MA: Harvard University Press.
- Withers, G. S., Fahrbach, S. E., & Robinson, G. E. (1993). Selective neuroanatomical plasticity and division of labour in the honeybee. *Nature*, *364*, 238–240.