

FOLLOW THE LEADER:
THE SOCIAL INFLUENCE OF AN INDIVIDUAL WITHIN THE
THERMOREGULATORY FANNING BEHAVIOR IN
HONEYBEES (*APIS MELLIFERA L.*)

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**Follow the Leader:
The social influence of an individual within the thermoregulatory
fanning behavior in honeybees (*Apis mellifera* L.)**

Abstract

The survival of an animal society depends on individual interactions and how they influence the coordination of a group to respond to environmental changes. Coordinated responses to environmental changes are determined by the interactions between individuals within a particular group. Individuals that are especially influential can affect the behavioral response of other group members. Here, I tested a novel concept I call “Follow the Leader”, in which an individual influences other group members within the thermoregulatory fanning behavior in the western honeybee (*Apis mellifera* L.). In response to increasing temperatures, individual honeybee workers rapidly fan their wings to circulate air through out the hive. Individuals often influence the behavior of other individuals which results in a coordinated group thermoregulatory response for proper colonial homeostasis. My results suggest that individuals have the capability to become a leader within a group by influencing other individuals to follow their fanning response to increasing temperatures. An influential individual, or “leader”, may ultimately affect the ability for a society to efficiently respond to environmental fluctuations.

Keywords: division of labor, thermoregulation, fanning behavior, homeostasis, environmental perturbations, task allocation, leader, response threshold

Background

Social animals are ubiquitous on this planet. One of the reasons why animals who live in groups are so successful is because of their ability to divide labor. Animals can divide labor between just a few individuals, like two birds performing parental care (Clutton-Brock 1991), to societies of millions of individuals who specialize in specific jobs. This division creates efficiency, and the social group can thrive. Social insects are some of the most ecologically successful groups on the planet (Hölldobler & Wilson 1990). These societies are made of thousands of individuals, many of which perform specific tasks. For example, eusocial insects such as ants, bees, and wasps, individuals specialize in nursing, guarding, and foraging tasks. While these complex societies are well studied, the exact mechanisms as to how specific jobs are initiated and performed are still largely unknown.

One hypothesis for the organization of task groups is individual task allocation, which is a process that adjusts the numbers of workers engaged in each task appropriately to the current situation (Gordon 2002). Task allocation relies on the individual and group responses to high demand tasks within a changing colony environment (Huang & Robinson 1992; Pacala et al. 1996). The optimal response to a stimulus is achieved by the adjustment of the ratio of individuals within each task group (Oster & Wilson 1978; Calabi & Rosengaus 1988; Johnson 2010). For example, the increased number of brood increases the number of nurses needed to care for the brood (Schmickl & Crailsheim 2004; Johnson 2010). Additionally, the exchange of fluid via trophallaxis between nurses and foragers informs foragers about the current need of resources for the brood (Camazine 1993; Schmickl & Crailsheim 2004). This system efficiently organizes responses to internal and external perturbations (Mangel 1995; Bonabeau et al. 1996 & 1998; Levin 1998).

The extent by which the colony is able to appropriately respond to an environmental perturbation depends on the dynamics of information and self-organization of the colony (Bonabeau et al. 1998; Stabentheiner et al. 2010). This is largely attributed on individuals' ability to collect and share information and then react to it, however models that attempt to incorporate these components assume that information is transmitted from group-to-group or group-to-individual (Wilson & Hölldobler 1988). By assuming each individual is the same, these models fail to help us understand the process of exchanging information between a variety of individuals within large groups of workers (Camazine et al. 2001; Kitano 2002; Schmickl & Crailsheim 2004). Yet, many of these models allow us to understand the organization to divide labor among individuals for a colonial homeostatic response (Bonabeau et al. 1998; Vodovotz et al. 2013).

Division of Labor

The widespread ecological success of social organisms is believed to be due to division labor (Wilson 1971; Oster & Wilson 1978; Bonabeau et al. 1998). Division of labor in social organisms, such as honeybees, refers to adaptive biases in task performance of individuals within a group (Johnson 2008). Social insects divide labor among workers based on pre-determined traits of individuals, such as sex and age (Wilson 1971; Oster & Wilson 1978; Lubin & Bilde 2007). Division of labor partitions specific tasks among these behavioral groups and results in an organized system of labor within a society (Wilson 1971; Oster & Wilson 1978; Chittka & Muller 2009; Pruitt & Riechert 2011; Schneider et al. 2013).

Description of division of labor within honeybees is important in order to understand how honeybees integrate large numbers of individuals to perform tasks. Specifically, honeybees exhibit obligate reproductive division of labor of which the female queen is the reproductive individual and the female workers are sterile (Haydak 1970; Crespi & Yanega 1995). Within

these pre-determined behavioral groups, worker honeybees also have variable behavioral traits that are flexible on an individual level (Oster & Wilson 1978; Seeley 1982; Robinson 2002; Johnson 2010; Johnson & Frost 2012). Genetic diversity among workers is generated by multiple mating events by the colony's queen (Jones et al. 2004). The plasticity of morphological and physiological traits of individuals within division of labor enables a colony to grow, develop, and reproduce despite changing environmental conditions (Huang & Robinson 1992, 1996).

Honeybee workers also exhibit temporal division of labor, in which tasks are divided among groups of female workers over the course of their lives (Seeley 1982). These temporal transitions are linked to physiological changes which predispose an individual to perform the next task (Robinson 1987; Withers et al. 1993). As they age, workers change their behavior to perform different tasks (Winston 1987; Seeley & Kolmes 1991; Johnson 2008, 2010). The nurse task group is characterized by newly emergent young bees, which care for the brood between 0-10 days. The worker task group is characterized by middle-aged bees, which conduct nest maintenance and food processing tasks for about 10-20 days. Finally, bees switch to foraging after 20 days. Foragers collect resources for the hive and remain in this task group until they die (Winston 1987; Johnson 2003, 2005) [Illustrated within Diagram 1]. Temporal division of labor creates a highly distributed task allocation among bees of specific age and behavior that leads to efficient colonial organization (Beshers & Fewell 2001).

Individual behavioral variation creates flexibility within the organization of division of labor that likely contributes to the robustness of colonial homeostasis (Bonabeau et al. 1998; Levin 1998; Jones et al. 2004; Stabentheiner et al. 2010). Many studies propose that the flexibility of individual behavioral traits are independent of their pre-determined morphology as genetic variation results in phenotypic plasticity (Kolmes 1986; Calabi & Rosengaus 1988;

Gordon 1989; Calderone & Page 1991; Bourke et al. 1995; Beshers & Traniello 1996; Ben-Shahar et al. 2002). Colonial homeostatic responses of a honeybee colony may be the product of the individual variation in performance of tasks and the social organization of these tasks (Calderone & Page 1991). The social network allows monitoring and adjustment of the division of labor accordingly in order to collectively respond to an environmental stressor (Huang & Robinson 1996; Sih et al. 2009).



Diagram 1: Illustration of temporal division of labor in female worker honeybees. Yellow circles indicate focus point of task group members of nurses, fanners, and foragers (left to right). Days indicate age of bees. [Author of photographs: Chelsea Cook (Left Photo), Rachael Kaspar (Middle & Right Photo)].

Response Thresholds

The direct involvement of any bee in a homeostatic response is likely related to the bee's sensitivity to task stimulus (Kronenberg & Heller 1982; Graham et al. 2006). One model for describing individual sensitivity is the response threshold (Robinson 1992). An individual's likelihood to respond to a task specific stimulus depends on their response threshold and intensity of stimulus (Robinson 1992; Beshers & Fewell 2001). Stimuli are factors associated within internal or external environmental conditions, such as increased food resources or

increasing temperatures (Robinson 1992). Individuals are triggered to respond to their task-specific behavior when their internal response threshold is met (Robinson 1992; Breed et al. 2002; Cook & Breed 2013). Response thresholds create a framework for understanding worker responses to changing demands for labor associated with environmental stress (Robinson 1992; Fewell & Bertram 1999; Breed et al. 2002). As environmental conditions fluctuate, colonies can adjust the numbers of workers engaged in each task.

An individual's response threshold may depend on the morphological composition of the society, as genetic variation and colony demographics interrelate with the response thresholds of individual workers (Breed et al. 1990; Page et al. 1995; Huang & Robinson 1996; Arathi & Spivak 2001). However, these response threshold models do not include individual response variations and group-level adjustments to shifting climates (Mangel 1995; Pacala et al. 1996; Weidenmüller 2004; Johnson 2010). Accompanying the pattern of temporal task allocation in honeybee colonies, individuals can also accelerate, delay, and even reverse their behavioral development in response to changes within their colony's internal and external environment (Huang & Robinson 1996; Pacala et al. 1996; Gordon 2002; Robinson 2002; Johnson 2010). Johnson (2010) suggested a push-pull model for temporal division of labor in which members of one task group push members of another task group to respond to an environmental perturbation. Termites follow this model by increasing the number of individuals repairing mound breaches as a part of colony defense (Emerson 1956). Ants increase the number of foragers as they encounter other successful foragers (Gordon 2010). Sponge-dwelling shrimp increase the number of male guards towards conspecifics when there is an increase in aggressive snaps (Duffy et al. 2002). Honeybee foragers increase the number of individuals when there are more larvae to feed, as foragers need to collect more food (Huang & Robinson 1996). More honeybees fan when they

experience hotter temperatures (Egley & Breed 2013). The changes within the age-dependent developmental sequence are a result of environmental feedback, which can lead to a decline or increase in the number of workers in a task group (Calderone & Page 1991; Johnson 2010; Sih & Watters 2005; Pruitt & Reichert 2011).

Groups are better than single bees at cueing in on environmental change, but the exact mechanism governing interactions to initiate thermoregulation within a group is unknown (Pacala et al. 1996; Cook & Breed 2013; Cook et al. 2016). Ribbands (1953) and Free (1965, 1967) postulated that workers interacted to receive communication and react appropriately to regulate hive conditions. This hypothesis proposed that workers vary in their likelihood of responding to task-related stimuli (Robinson 1992; Huang & Robinson 1992). Thus, response threshold changes with the proportion of bees allocated to that specific task. It is unlikely that individual workers can monitor the needs of the whole colony and adjust behaviors accordingly (Huang & Robinson 1996), but more likely that workers socially allocate information from one another to respond to an environmental perturbation. Each individual pursues a single task at any one time but is highly adept at changing tasks in response to environment factors and interactions with other individuals (Pacala et al. 1996). Proper environmental homeostasis has a direct affect on behavioral plasticity and performance in individual adult honeybees of which make up the colony.

Thermoregulation

Many social organisms, like honeybees, maintain stable and precise environmental conditions within their colony, suggesting that there could be significant fitness costs if conditions are not maintained (Tautz et al. 2003; Groh et al. 2004; Jones et al. 2005). Honeybees ensure proper development and survival of their offspring by regulating the temperature of their

hive (Tautz et al. 2003; Jones et al. 2005). Honeybees regulate their hive temperature in multiple ways, including fanning to ventilate excessive heat (Cook & Breed 2013; Egley & Breed 2013), heat shielding (Starks & Gilley 1999; Starks et al. 2005), and foraging for water (Kühnholz & Seeley 1997).

Hive temperature is more precisely regulated around the brood more than anywhere else within the hive, suggesting an association of brood development and thermoregulation (Kronenberg & Heller 1982). If a honeybee colony does not properly regulate at approximately $34.5 \pm 1.5^\circ\text{C}$, larvae may develop abnormally and perish (Himmer 1932; Kronenberg & Heller 1982). Studies have also found that proper brood-temperature control influences pupal brain development (Groh et al. 2004). Adult bees reared at a relative temperature of 36°C during pupal development have a greater memory and learning capability than bees reared at inconsistent temperatures $< 36^\circ\text{C}$, leading to greater behavioral performance through out their lifetime (Tautz et al. 2003; Jones et al. 2005).

Thermoregulatory responses are tuned to environmental fluctuations in temperature (Robinson 1992; Egley & Breed 2013). Honeybees collectively respond to environmental stimuli, such as temperature, CO_2 , and humidity, in order to maintain homeostasis within the hive (Seeley 1974; Human et al. 2006). For example, a colony can increase the number of water receivers when water needs increase by having bees engaged in other tasks switch to the task of water reception (Kühnholz & Seeley 1998). A colony adaptively controls the collection of water by its foragers, increasing the number of foragers when high temperatures necessitate evaporative cooling inside the hive and decreasing it when the danger of overheating passes (Kühnholz & Seeley 1998). In heat shielding, Starks & Gilly (1999) found that brood received a greater number of heat shielders than honeycomb and was thus better protected from

overheating. Egley & Breed (2013) found that task switching from guards to fanners increased when there was an increase of ambient temperature.

Thermoregulatory Fanning Behavior

Fanning behavior has been described through out the order of Hymenoptera, including bumble bees (*Bombus impatiens* and *terrestris*), the Cape bumble bee (*Apis mellifera capensis*), a Brazilian stingless bee (*Scaptotrigona postica*), and of course, the honeybee (*Apis mellifera* L.) (Seeley 1974; Kronenberg & Heller 1982; Heinrich & Esch 1994; Engels et al. 1995; Weidenmüller et al. 2002; Yang et al. 2010 ; Duong & Dornhaus 2012; Westhus et al. 2013; Cook & Breed 2013). Fanning behavior can be used to spread pheromones via their Nasanov gland to signal to other bees for foraging or defensive purposes (Free 1987; Yang et al. 2010). Within the context of thermoregulation in honeybees, fanning behavior circulates hot air out and cool air into the hive (Kronenberg & Heller 1982; Cook & Breed 2013; Egley & Breed 2013). Specifically, thermoregulatory fanning behavior is characterized by a group of individual worker bees fanning their wings to ventilate the colony (Kronenberg & Heller 1982; Heinrich & Esch 1994; Egley & Breed 2013; Cook & Breed 2013). Since thousands of honeybees all function within a single colony unit, it is necessary for large groups of workers to regulate the hive temperature (Stabentheiner et al. 2010).

Workers socially interact in order to adjust the number of individuals to achieve proper homeostasis (Himmer 1932; Kronenberg & Heller 1982; Simone-Finstrom 2014). For example, the number of fanning honeybee workers is positively correlated with ambient temperature and negatively correlated with humidity (Egley & Breed 2013). In addition, Egley & Breed (2013) found that task switching from guards to fanners increased when there was an increase of ambient temperature. Cook & Breed (2013) found that all task groups (nurses, fanners, guards,

foragers) could fan but that each task group differed in likelihood to fan as well as their thermal response threshold. Seeley (1974) found that a higher probability of larger numbers of bees responded to higher levels of CO₂. Weidenmüller (2002) found that bumblebees (*Bombus terrestris*) increased fanning responses with increased temperature and CO₂, but not humidity. This suggests that the interactions within a group response is essential maintain a consistent temperature within the hive (Simone-Finstrom 2014).

In order to maintain a colony's extremely complex system, honeybees must cue in on internal social interactions to initiate thermoregulation in synergy with external conditions (Huang & Robinson 1992; Egley & Breed 2013; Cook & Breed 2013). Honeybees have a greater probability of fanning in groups than individually, suggesting that there is some sort of interaction between nestmates that enables individuals to better cue in on environmental stress (Pacala et al. 1996; Cook & Breed 2013). Egley & Breed (2013) found that an increased thermal stimulus from the environment resulted in increased fanning response of workers. Seeley (1974) found that larger colonies could regulate carbon dioxide within a much narrower range than small colonies. In addition, the number of fanning workers is positively correlated with ambient temperature and negatively correlated with humidity (Egley & Breed 2013), which shows that fanning behavior may possibly be specific to temperature heat stress. Weidenmüller et al. (2002) found that fanning response probability increased with size of colony and intensity of stimulus. Colonies responded faster to environmental perturbations of their environment when they were large (60 or more) than small (Weidenmüller et al. 2002). Weidenmüller et al.'s (2002) work on the bumblebee (*Bombus terrestris*) concluded that bees were more likely to fan in groups, as had Cook and Breed's (2013) work on the honeybee. These results suggest that an increased social interaction leads to a more readily response to environmental perturbation. Fanning response

threshold is very likely to be influenced by the interaction between environment stimuli and information exchanged by nestmates.

Although the influence of individual experience on thermal thresholds for fanning behavior has been studied little in honeybees, it has been extensively tested in bumblebees (*Bombus terrestris* and *Bombus impatiens*). Weidenmüller et al. (2004) and Westhus et al. (2013) found that response thresholds are regulated by previous experience within bumblebees (*Bombus terrestris*). Weidenmüller et al. (2004) showed that if a bumblebee previously fanned, the bee decreased their thermal response threshold and increased their likelihood to fan. Westhus et al. (2013) found similar suggestions of Weidenmüller et al. (2004), but additionally found that bumblebee (*Bombus terrestris*) who repeatedly fanned with increasing temperatures displayed a decrease in thermal response threshold, also supporting the individual self-reinforcement model for thermal response thresholds. However, Westhus et al. (2013) also found that if a bumblebee experienced increasing temperature but did not perform fanning behavior, their thermal response threshold remained unchanged. Contradicting to Weidenmüller et al. (2004), Duong et al. (2012) found that bumblebee (*Bombus impatiens*) workers displayed no change in thermal response threshold if the bees had previously fanned, suggesting that *Bombus impatiens* do not use a self-reinforcement model for thermal threshold. Thus, it is still unclear if individual thermal response threshold is due to the prior performance of a task rather than prior experience of stimulus (Duong et al. 2012). Yet, these studies suggest that the individual's experience with environmental stimuli and social interactions could affect the social initiation of thermoregulatory fanning behavior and influence the thermal stability of the hive.

Exploratory Studies

At the beginning of my involvement with honeybee research, I worked with Dr. Chelsea Cook on her PhD project. Our prior work was the source of ideas for my thesis, therefore it is necessary to present and discuss our previous research in order to fully understand my experiments. We hypothesized that social fanning behaviors in honeybees were affected by group size and rate of increasing temperature (Cook et al. 2016). In order to test this hypothesis, we heated three different group sizes--one, three, and ten bees per cage--each treated with three different rates of temperature increase, 0.5°C/per minute, 1.0°C/per minute, and 2.0°C/per minute.

We found that best predictors of probability were i) the interaction between group size and rate of temperature increase, (ii) the interaction between group size and outside temperature, and (iii) group size. Honeybees fanned at significantly lower temperatures when they were in groups of 10 compared to when they were alone (Figure 1). Bees also fanned at significantly lower temperatures when they are being heated at faster rates, compared to slower ones (Figure 2). No significant relationship was found between group size and lethal threshold, indicating that thermal lethal threshold of rate of heat is on a purely individual basis.

These results indicated that larger group sizes of honeybees are more likely to fan when there is a faster temperature increase than smaller groups (Figure 1 & Figure 2). Overall, our prior results suggest that fanning response threshold is likely influenced by interaction between change of environment stimuli and information from nest mates. Following this research, I questioned if groups could also be more responsive as a consequence of an influential individual.

Probability of Fanning Changes Across Both Group Size and Rate of Ramping

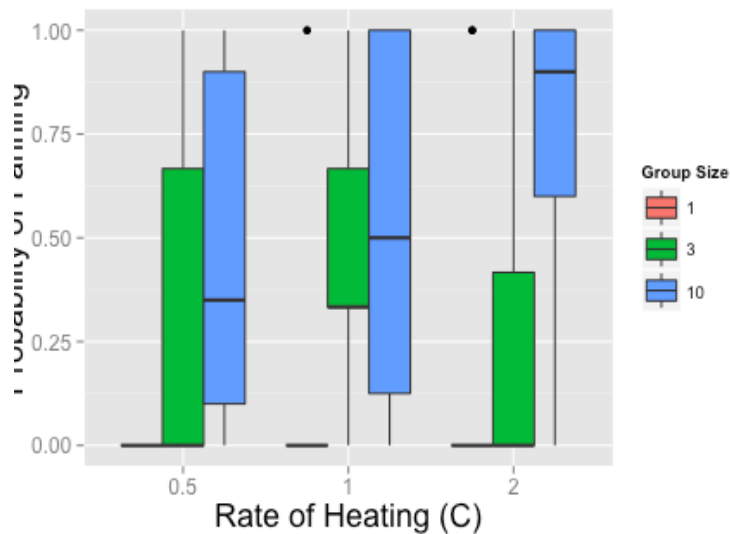


Figure 1: Horizontal bars are medians, boxes are 25 – 75th percentile, bars are 1.5 * IQR, points are Tukey outliers (N= 74, $\chi^2=11.554$, P = 0.003). Created using R Package ggplot2. [Source: Cook et al. 2016]

Thermal Response Threshold Across Group Size and Heating Regime

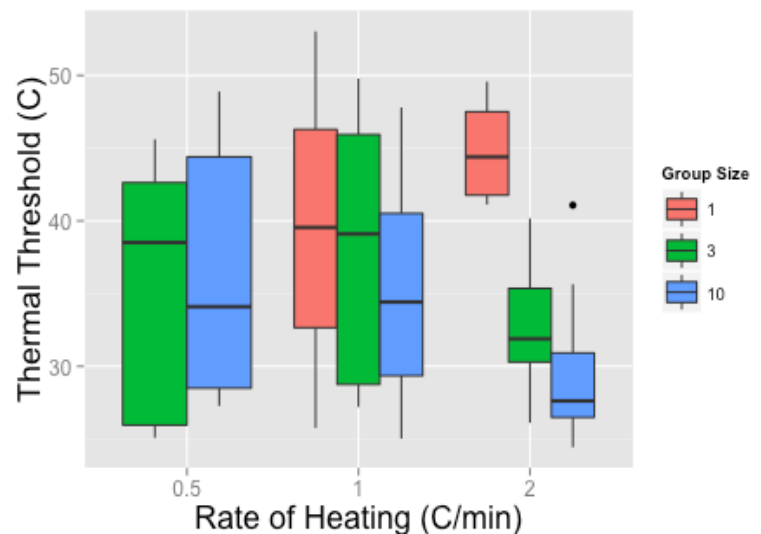


Figure 2: Zero solitary bees fanned when they were heated at 0.5°C/minute, which is why there is no single bee boxplot at that rate. Horizontal bars are medians, boxes are 25 – 75th percentile, lines are 1.5 * IQR, points are Tukey outliers (N=148, $\chi^2=7.566$, P = 0.023). Created using R Package ggplot2. [Source: Cook et al. 2016]

The Follow the Leader Concept

The social processes of the coordination of various worker bees to organize into succinct fanning groups create a compelling system for study. Here, I illustrate a novel concept called “Follow the Leader” to further understand individual variation within group coordination. An event demonstrates the “Follow the Leader” concept if the behavior of an individual influences the behavior of other individuals as well as the group response. Parallel to Weidenmüller observations (2004), I previously observed that other individuals influenced the fanning behavior of an individual bee. Yet, no study has tested the influence of an individual within the group coordinated response in the thermoregulatory fanning behavior of honeybees. Thus, I questioned

the possibility of the presence of a leader who influences other individuals within the collective group fanning response.

Although there is individual variation within honeybee colonies, it is unlikely that honeybees exhibit keystone individuals or hierarchy of dominance. First, there is little concern for a dominant status within mating or resource opportunities as there is an interplay of decisions between the queen and sterile female workers to adjust reproduction of male drones in accordance to environmental conditions (Hrassnigg & Crailsheim 2005; Boes 2010). Second, worker honeybees collaboratively allocate resources for the hives through both indirect and direct social interactions, such as direct mandibular contact or indirectly using the environment as a medium of communication (Bonabeau et al. 1998; Huang & Robinson 1996; Schmickl & Crailsheim 2004; Sih et al. 2009). Furthermore, these social interactions occur thousands of times a day among colony members through out the hive to maintain homeostasis (Wilson & Hölldobler 1988; Schmickl & Crailsheim 2004; Sih et al. 2009). Such an enormous amount of individual interactions likely diminishes the emergence of a single keystone or dominant individual. The emergence of an individual who varies largely compared to other group members may be independent of task specialization or temporal division of labor, but this is still unknown (Calderone & Page 1991).

Within honeybee colonies, individuals are unlikely to be characterized as a keystone or dominant individual. However, they may influence other group members to collectively perform a task (Power et al. 1996; Modlmeier et al. 2014). An influential individual can influence the behavior of another individual that in turn changes the behavior of other group members (Modlmeier et al. 2014). With the concept of “Follow the Leader”, an individual who influences other group members is classified as a “leader”. A leader may not necessarily be more efficient

in responding to increasing temperatures, but may be so influential that they change the behavioral output of others to follow their own behavior. The collective performance of fanning groups may be determined by the presence and behavior of a single influential individual.

Introduction

The success of many types of societies, such as snapping shrimp, ants, and humans, is characterized by the division of tasks among individuals (Wilson 1971; Duffy et al. 2002; Chittka & Muller 2009; Schneider et al. 2013;). Within groups, each individual varies in how they respond to environmental stimuli (Emerson 1956; Pacala et al. 1996; Weidenmüller 2004; Jeanson & Weidenmüller 2014). This variation allows an individual to respond to labor fluctuations in a flexible and adaptive manner (Theraulaz et al. 1998; Stabentheiner et al. 2010). For example, Pruitt & Keiser (2014) found that extremely bold individuals within the social spider society of *Stegodyphus dumicola* increased the foraging aggressiveness of the entire colony (Pruitt & Keiser 2014). This suggests that individual variation and their interactions can ultimately affect the homeostatic group response (Bonabeau et al. 1998; Levin 1998; Stabentheiner et al. 2010; Modlmeier et al. 2014; Pruitt & Pinter-Wollman 2015). Yet, little experimental work has been conducted to determine individual components and how these components influence the societal success of organisms (Jeanson & Weidenmüller 2014). Some suggest that individual behavioral variation creates flexibility within group dynamics which allows for greater robustness for a colony to respond to environmental perturbations (Jones et al. 2004; Stabentheiner et al. 2010). Others argue that influential group members may reduce a society's robustness to respond to perturbations by imposing their behavior on other individuals to perform a task when in fact they should abandon it (Pacala et al. 1996; Pruitt & Pinter-Wollman 2015).

How do a variety of individuals coordinate an effective group response? Social interaction and information exchange allow coordinated group responses to environmental change (Ribbands 1953; Free 1967; Wilson & Hölldobler 1988; Bonabeau et al. 1998; Calderone & Page 1991; Sih et al. 2009). Both indirect and direct interactions can result in an increased efficiency to respond to environmental stimuli by certain individuals (Calderone & Page 1991). A highly responsive individual may influence other group members to collectively perform a task (Power et al. 1996; Modlmeier et al. 2014). Variations among an individual's experiences and connections may ultimately affect the sensitivity of group to respond to a task (Bonabeau et al. 1996; Sih et al. 2009; Modlmeier et al. 2014; Pruitt & Keiser 2014). This social organization of individuals creates an efficient collaborative system within a society (Schneider et al. 2013; Winston 1987). However, the full scope of the influence of a single individual within a group response in a honeybee society is still unclear.

Social insect societies, such as honeybees, allow us to explore individuals coordinating a response on the broad scale of colonial homeostasis. Insect societies can coordinate responses by dividing tasks among individuals based on age or sex (Beshers & Fewell 2001). However, an individual's performance of a task varies due to genetics and environment (Calderone & Page 1988, 1991; Bonabeau et al. 1996). Unfortunately, many models of division of labor ignore individual behavioral variation within groups because of the difficulty in assessing stressor effects on individuals. Specifically, many argue that the effects of environmental stressors are difficult to predict from the standpoint of an individual within a large social insect colony (Wilson & Hölldobler 1988; Chittka & Muller 2009; Sokolowski 2010; Jeanson & Weidenmüller 2014). Instead, these models assume that all individuals respond with equal likelihood (Camazine et al. 2001; Kitano 2002; Schmickl & Crailsheim 2004). Thus, these models fail to

include components such as the state of the surrounding climate or the degree of coordination among individuals (Mangel 1995; Pacala et al. 1996; Power et al. 1996; Beshers & Fewell 2001; Johnson 2010). The exclusion of individual interactions within societal models likely reduces our understanding of coordinated responses (Jeanson & Weidenmüller 2014). Individual variation thresholds likely influence the societal response to environmental fluctuations, but it is still largely unclear if certain individuals have the ability to influence the group response (Bonabeau et al. 1998; Levin 1998; Jones et al. 2004; Stabentheiner et al. 2010; Modlmeier et al. 2014; Jeanson & Weidenmüller 2014; Pruitt & Pinter-Wollman 2015).

Honeybee colonies are excellent societies to study how individuals influence group responses to environmental fluctuations. Individual honeybee workers cue in on both internal social interactions and external conditions to initiate thermoregulatory fanning behavior (Huang & Robinson 1992; Cook & Breed 2013; Egley & Breed 2013). Each individual honeybee differs in their likelihood to respond increasing temperatures due to age, genetic variation, morphological characteristics, or environmental experience (Calderone & Page 1991; Robinson 1992; Huang & Robinson 1996; Breed et al. 2002; Johnson 2008). For example, fanners (middle-aged bees) are significantly more likely to fan than any other temporal task group (Cook & Breed 2013). Nurse (young) bees have a lower thermal threshold response than older bees, but not significantly (Cook & Breed 2013). Additionally, groups of workers perform fanning behavior more often than individuals (Weidenmüller et al. 2002; Cook & Breed 2013; Cook et al. 2016). This group response suggests that the interactions between nestmates enable individuals to cue in on environmental stress (Pacala et al. 1996; Cook & Breed 2013; Cook et al. 2016). These worker bees interact to exchange information for proper task coordination in order to maintain colony homeostasis (Schmickl & Crailsheim 2004). Ultimately, the interactions among

individuals and the number of individuals within a group can strongly influence the behavioral response of an individual (Calderone & Page 1991).

Research Questions & Hypotheses

In order to empirically test the “Follow the Leader” concept, I manipulated the social environment of the nurse and fanner task group to test the influence of a single fanner within a group of nurses. My hypotheses were: 1) Presence of a fanner influences the nurse’s individual fanning response threshold, 2) presence of a fanner influences the fanning response threshold of multiple bees, 3) fanners influences the temperature of the first to fan, and 4) fanners are more influential on other group members when they fan first. Overall, exploration of my hypotheses fills the gap of our current knowledge on how individuals influence a group 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 1M sucrose or pollen patties (Mann Lake) as needed. All experiments were conducted from June-September 2015 for a total of 90 trials. Data was recorded within 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.

Experimental Design

In order to test an individual’s influence on the response of fanning behavior, I applied Weidenmüller (2004) “Influence of Experience” experiment. Rather than looking for a change of an individual’s response threshold over time, I was interested in how an individual’s response

threshold was influenced by another individual. I 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 comprised of just fanners, and a group comprised of just nurses. There was a treatment group (hereafter mixed group) comprised of a single fanner and four nurses.

Hypothesis 1) Presence of a fanner influences the nurse’s individual fanning response threshold

I assessed the influence of a single fanner by analyzing each bees’ individual thermal response threshold. I classified the individual thermal response threshold by the temperature at which each individual bee performed fanning behavior.

Hypothesis 2) Presence of a fanner influences the fanning response threshold of multiple bees

I classified the group thermal response threshold by the temperature at which more than one bee fanned together as a group. However, as suggested by Jeanson & Weidenmüller (2014), the probability of an individual to respond to a stimulus is also an important component to understand response thresholds. Therefore, I also analyzed the likelihood to fan as an individual and as a group. I measured the individual probability as the number of bees to fan throughout the entire trial and measured the group probability as the number of bees to fan together as a group.

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

Additionally, I was interested in the individual who was the first to fan within each trial. I analyzed both the individual who was the first to fan within each trial and whether they were the first to fan within a group response. I classified the individual who was the first to fan within a group response as the ‘initiator’. To determine if group dynamics influenced the initiator, I also analyzed the initiators thermal response threshold.

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

Lastly, in order to determine the likelihood of bees to fan following an initiator, I analyzed the probability of individuals to fan after a fanner or nurse initiator. Within just the 30 trials of the mixed group, I analyzed the number of individuals to fan after i) fanner initiator and ii) nurse initiator.

Group Size

Groups of five bees were collected from the same hive and inserted into a mesh cage (cylindrical: 20cm x 6cm) in order to allow bees to communicate by touching one another and to allow continuous airflow (Diagram 2). Although a group of five bees is relatively small compared to honeybee colonies, Cook & Breed (2013) illustrated that smaller groups of bees mimic those found in larger groups. I have personally observed a rare single bee fanning resulting in a group of over 50 bees fanning. However, this study is not interested the outcome of different sized groups of bees fanning rather the influence between task group members within a single group size. In addition, proper analysis of individual behavior required critical recognition of individual paints on bees. Thus, this study used group size of 5 bees as a control. For each sampling event, hives were randomly selected but collection was distributed uniformly across hives.

Collection of Fanner and Nurse Bees

As described in Cook & Breed (2013), fanners are easily identified from their unique posture and orientation at the entrance. I selected bees that were observed fanning for at least 10s. These identification protocols ensure that I 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). Because Cook & Breed 2013 described that pollen foragers were significantly less likely to fan in heating assays, I avoided porch fanners that had

pollen on their corbicula. I selected nurses that were walking on top of brood and inserting their heads into brood comb, as these behaviors are indicative of the nurse task group (Seeley & Kolmes 1991). In order to avoid risk of added aggression or disturbance bias by opening the hive to collect nurses, I selected porch fanners before I selected nurses. Nestmates were only used within groups of five bees in a single mesh cage. There were two controls: only five fanners and only five nurses. There was one treatment: four nurses with one fanner. Bees were collected and brought into the lab so that no longer than 15 minutes elapsed for collection and transportation. During collection, each bee was marked with a unique color of paint (Sharpie Water-based Paint Marker) in order to observe both individual and group responses (Diagram 2). When sampling, I recorded outside humidity and temperature, date and time of collection, sun or shade over the hive, and hive number.

Behavioral Assays

Once transported into the laboratory, groups were acclimated for 20 minutes within a 2-liter glass jars with fitted lids (Specialty Container Inc.). 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 (Thermo Scientific Cimaric Digital Hot Plate) (Diagram 2). Each group was treated with a 1.0°C/per minute temperature increase. Cook & Breed (2013) established this acclimation period and heating assay, however preliminary tests solidified this required protocol based on time required for the bees to reach a level of behavioral stability. Because of my success with this methodology in my prior research with honeybees, I decided to continue this regime. Each mesh cage was held by wooden structures within the jar to ensure the cage was not in contact with the glass jar. I recorded the initial air temperature of the chamber and the trial start time. Although ambient temperatures differed across trials, because they 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 center of the chamber where bees were restricted in the cage. Trials were concluded when the last bee reached lethal temperature. Time of trial conclusion was recorded and rate of temperature was calculated. I conducted 30 trials per group for a total of 90 trials. Within each trial, I recorded several response variables. Individual response variables consisted of i) individual thermal response threshold), ii) initiator), and iii) the temperature of each individual's death. Group response variables included i) the temperature at which the group fanned together (hereafter group thermal response threshold) and ii) proportion of bees that fanned together as a group. I acknowledge hive differences likely exist, but these differences are not relevant to my hypotheses.

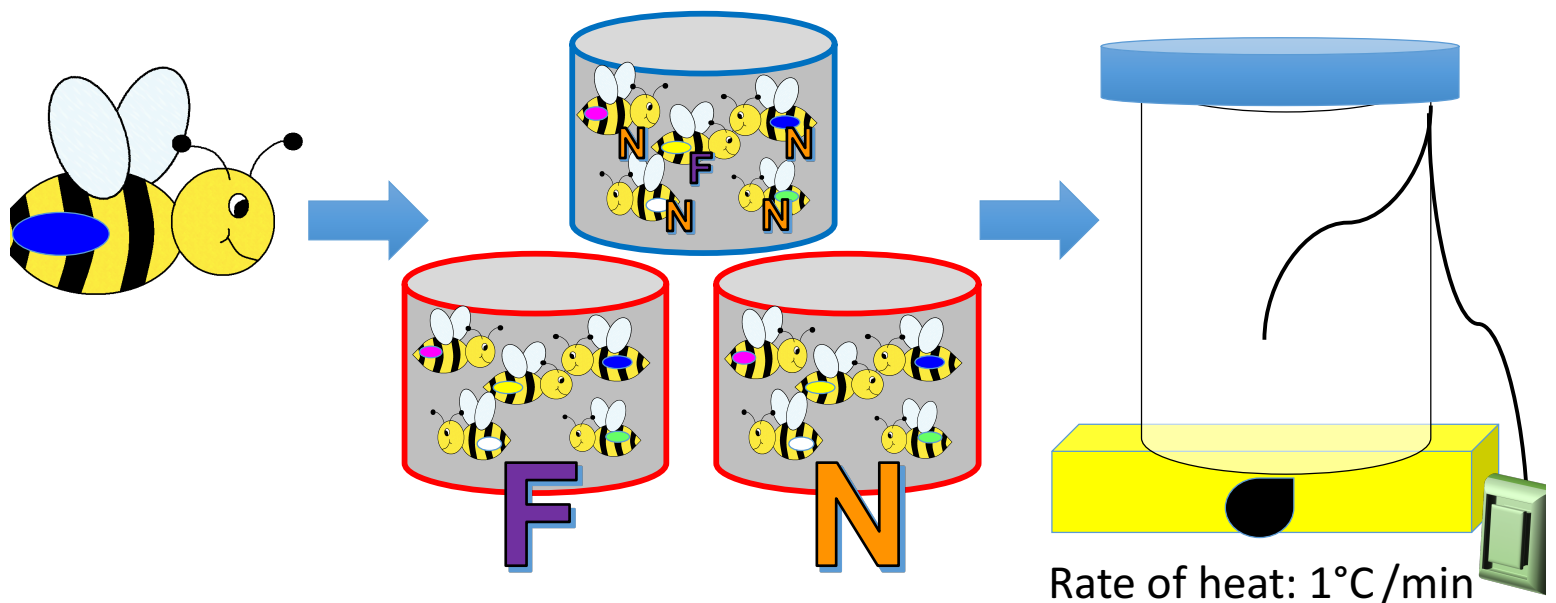


Diagram 2: Simplified illustration of collection and heating assays of bees. Color on bees (pink, yellow, blue, white, green) illustrate individual paint color marking. Letters indicate task group: purple F = fanner, orange N = nurse. Blue cage illustrates treatment with four nurses and one fanner. Red cages illustrate control groups with only five fanners and only five nurses. All groups were heated at a rate of 1°C/min.

Statistical Analysis

Hypothesis 1 & 2) Presence of a fanner influences the nurse's individual fanning response threshold and the fanning response threshold of multiple bees

To analyze both individual and group thermal response threshold for each trial group, I used a general linear model to conduct an analysis of variance (ANOVA) using R function `aov()`. When the ANOVA test showed significant difference between means, I conducted multiple comparisons using all pair-wise means to determine exactly how they differ through Tukey post-hoc test using R function `TukeyHSD`.

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

In order to determine who was the initiator of the group fanning response, it was necessary to analyze each initiator thermal response threshold between all trial groups. I conducted an ANOVA test using R function `aov()` among the temperature of fanning for the i) initiators within control fanners, ii) if initiators within the mixed group was a fanner, iii) if initiators within the mixed group was a nurse, and iv) the initiators within the control nurses. When the test determined significance, I conducted Welch Two-Sampled t-test 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, I performed a logistic regression with a binomial error distribution (link=logit). I did this by using a two column response variable (# fanners, # non fanners), and using a general linear model using `glm()`. We did a logistic regression because the response variable is a proportion, and is therefore not normally distributed. The methodology of analyses for probability of fanning was also used for Hypothesis 1 & 2. Then, I conducted a post-

hoc Tukey test to determine the significance of the number of bees to fan as a group following an initiator using R function TukeyHSD.

Results

1) Presence of a fanner influences the individual fanning response threshold

Nurses had a significantly lower thermal response compared to fanners or the mixed group (ANOVA: $F = 16.39$, $P = < 0.0001$, $N = 90$; Figure 3). There was no significant difference between the thermal response threshold of the control fanners and the mixed group (Tukey: $P = 0.6620$; Figure 3). There was no significant difference between the probability of a fanner or a nurse to perform fanning behavior (GLM: $Z = 0.479$, $P = > 0.5$).

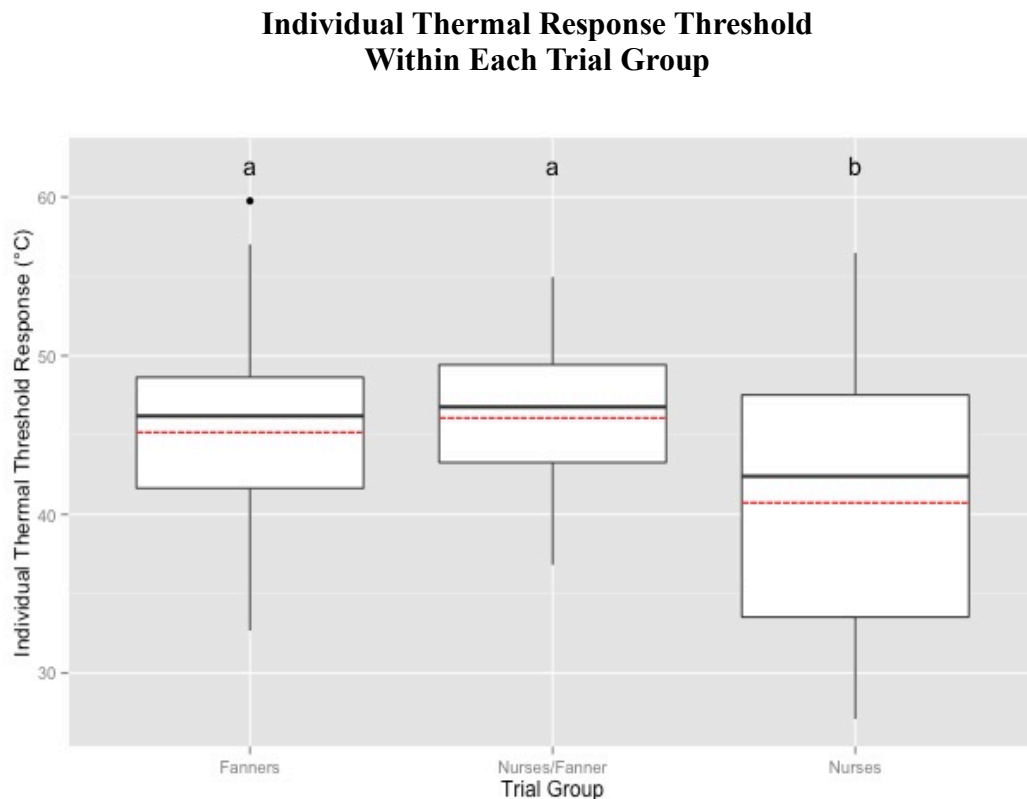


Figure 3: Bars left to right: control fanners, mixed group, control nurses. The letter b denotes statistical difference in significance. Black horizontal bars are medians and red horizontal bars are means. Points are outliers. Boxes are 25 – 75th percentile, bars are 1.5 * IQR, points are Tukey outliers (N=90). Created using R Package ggplot2.

2) Presence of a fanner influences the fanning response threshold of multiple bees

The group thermal response threshold of nurses was significantly lower than the fanners and mixed group (ANOVA: $F = 5.242$, $P = 0.0089$, $N = 90$; Figure 4). Additionally, there was no significant difference between the thermal response threshold between the fanners or the mixed group (Tukey: $P = 0.934$).

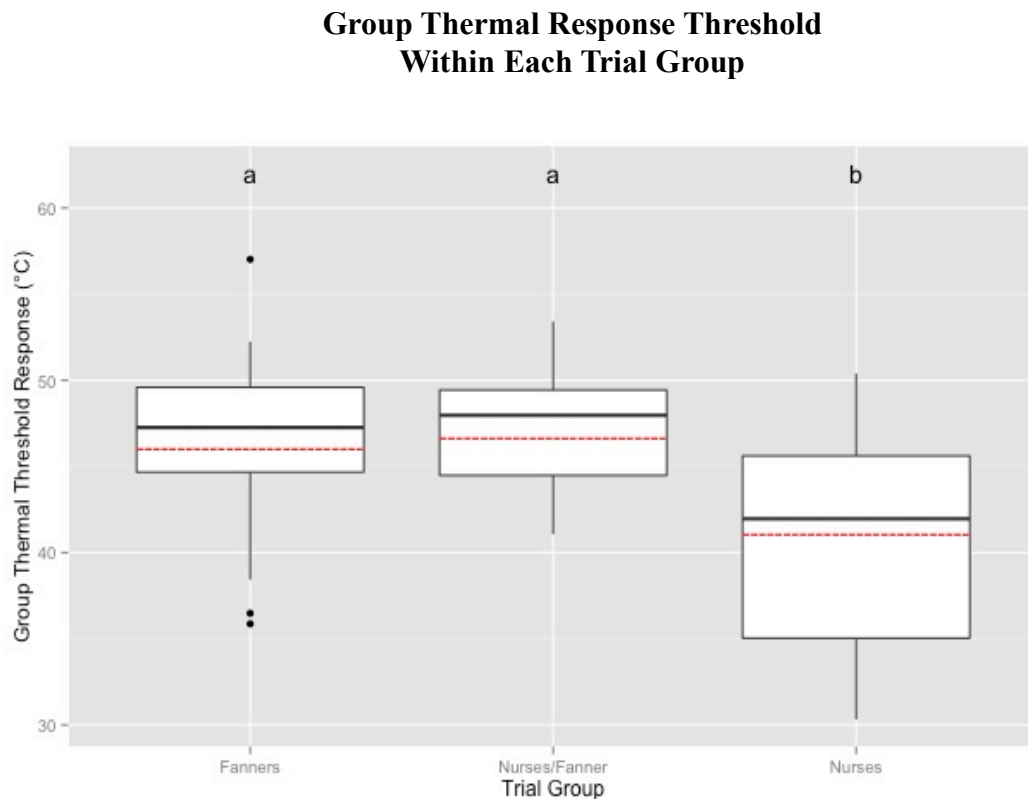


Figure 4: Bars left to right: control fanners, mixed group, control nurses. The letter b denotes statistical difference in significance. Black horizontal bars are medians and red horizontal bars are means. Points are outliers. Boxes are 25 – 75th percentile, bars are 1.5 * IQR, points are Tukey outliers (N=90). Created using R Package ggplot2.

3) Fanners influence the temperature of the first to fan

The initiator thermal response threshold within the control nurses was significantly lower than both the fanners and the sub-analyzed mixed group (ANOVA: $F = 3.036$, $P = 0.034$, $N = 90$; Figure 5). The thermal response threshold of the initiator within the control nurses was significantly lower than the nurse initiator within the mixed group (T-Test: $T = 2.299$, $DF = 39.40$, $P = 0.027$). The thermal response threshold of the fanner initiator within the mixed group was significantly higher than the control nurses (T-Test: $T = 2.440$, $DF = 24.71$, $P = 0.022$), but was not significantly lower than the initiator of the control fanners (T-Test: $T = 0.580$, $DF = 15.40$, $P = 0.569$).

Temperature of First to Fan Within Each Trial Group

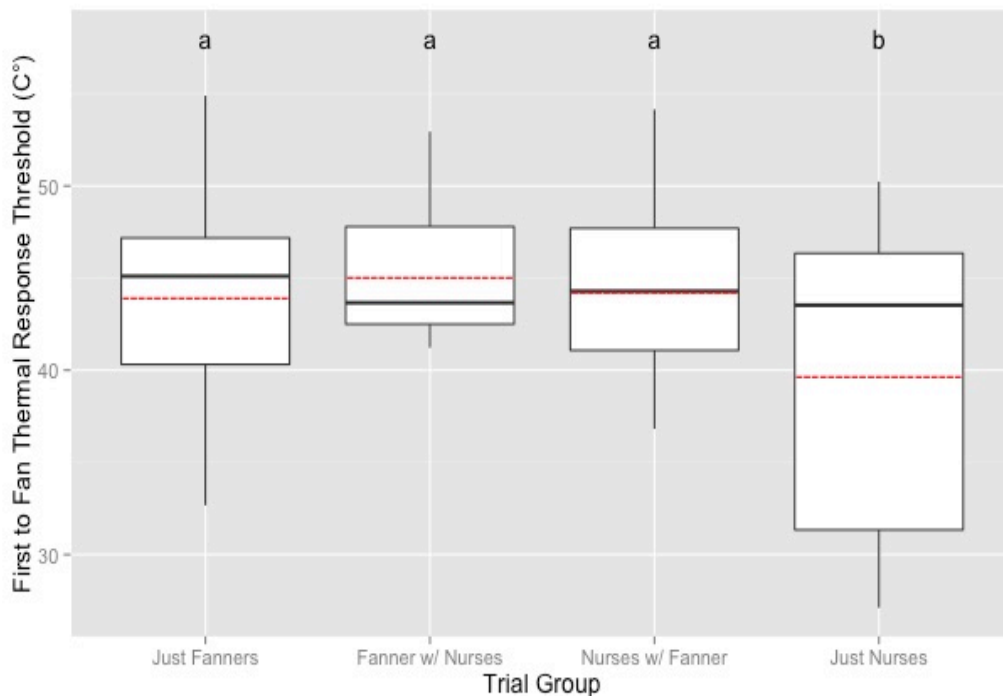


Figure 5: Bars left to right: control fanners, fanner initiators within mixed group, nurse initiators within mixed group, control nurses. The letter b denotes statistical difference in significance. Black horizontal bars are medians and red horizontal bars are means. Boxes are 25 – 75th percentile, bars are 1.5 * IQR, (N=90). Created using R Package ggplot2.

4) Fanners are more influential when they fan first

When fanners were the initiators within the mixed group, bees were significantly more likely to fan as a group (GLM: $Z = 2.219$, $P = 0.026$). The number of individuals fanning significantly increased after the fanner was the first to fan (Tukey: $P = < 0.001$).

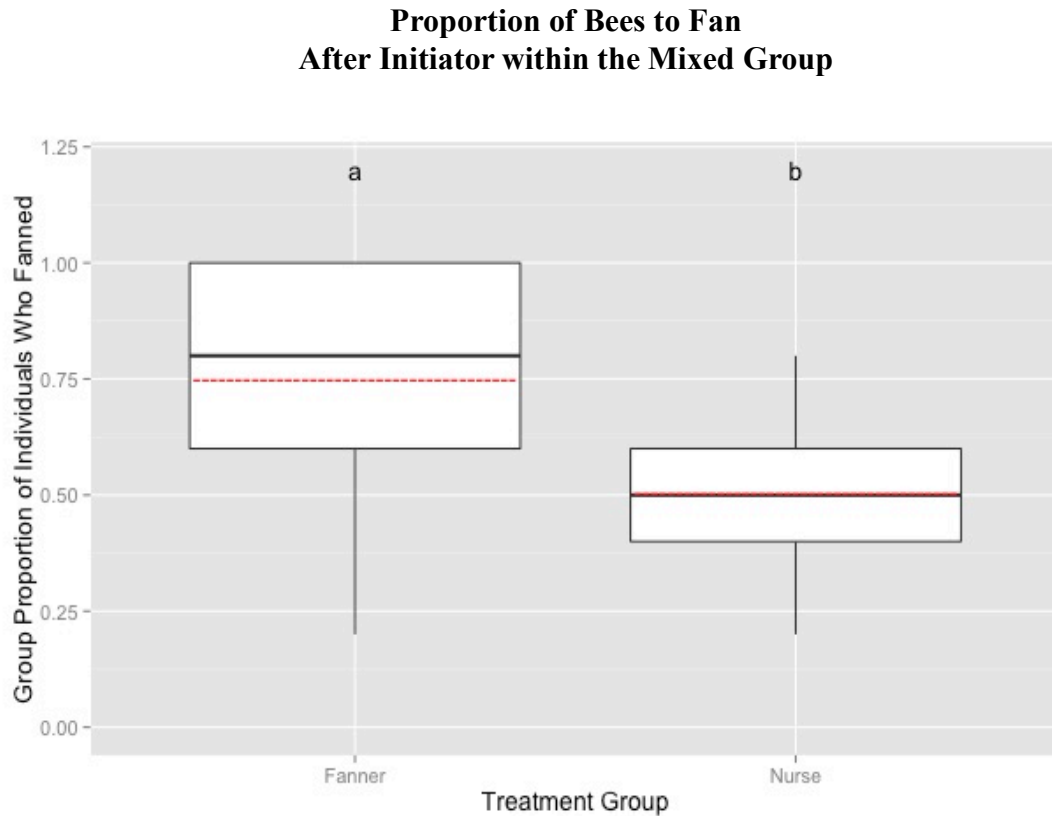


Figure 6: Bars left to right: Bees to fan after fanner initiator, bees the fan after nurse initiator. The letter b denotes statistical difference in significance. Black horizontal bars are medians and red horizontal bars are means. Boxes are 25 – 75th percentile, bars are 1.5 * IQR, (N=30). Created using R Package ggplot2.

Discussion

This study indicates that an influential individual can lead other individuals to perform different group outcomes, supporting my “Follow the Leader” concept. Specifically, individual interactions influence group response thresholds within honeybee colonies. Individuals within the nurse task group fan at a lower temperature than individuals within the fanner task group. Furthermore, nurses fan as a group at a lower temperature than fanners. But, when a single fanner is present among nurses, fanners influenced both nurses’ individual and group behavior by increasing their thermal response threshold. When fanners were the first to fan within the mixed group, the likelihood for nurses to fan significantly increased. This indicates fanners exhibit the role of a leader by influencing other individuals and group behavioral response thresholds, but are most influential when they are the initiators.

The response threshold hypothesis carries over within initiation of thermoregulation via social influence. There is strong evidence for division of labor to be socially regulated based on response thresholds (Ribbands 1953; Free 1965 & 1967; Huang & Robinson 1992, 1996; Cook & Breed 2013). An individual’s behavior can shape a group response to changing environments (Mangel 1995; Bonabeau et al. 1996; Pacala et al. 1996). Sometimes, individuals have a significant effect on group dynamics due to the diverse number and types of internal and external interactions (Sih & Watters 2005; Modlmeier et al. 2014; Pruitt & Keiser 2014). Within the “Follow the Leader” concept in honeybees, it is likely that a variety of interactions may promote an environment for the emergence of an influential leader (Calderone & Page 1991; Huang & Robinson 1996; Bonabeau et al. 1998; Sih & Watters 2005). This leader influences the behavior of other members which in turn affects the group fanning response and may ultimately affect the robustness of colonial homeostasis.

In other cases, a dominant or keystone individual can arise as a consequence of many interactions among other group members (Power et al. 1996; Modlmeier et al. 2014). A dominant individual may emerge within a group to reinforce their role, such as asserting aggression for reproduction and resources (Clarke & Faulkes 1997). Keystone individuals may emerge within a community and exhibit a highly influential role for long periods of time (Bernstein 1966). Keystone individuals differ from dominant individuals in that their presence on other group members proceeds long enough to for their indirect effects to become evident on the community level (Paine 1969; Power et al. 1996). However, leaders within my study are unlikely to be characterized as a keystone or dominant individual. Within honeybees, there is little concern among individuals to assert dominance because female workers collaboratively work among one another to regulate homeostasis and interact with the queen to adjust the outcome of reproduction (Hrassnigg & Crailsheim 2005; Boes 2010; Bonabeau et al. 1998; Huang & Robinson 1996; Schmickl & Crailsheim 2004; Sih et al. 2009). In addition, workers socially interact with one another thousands of times a day which likely suppresses the emergence of a keystone individual (Wilson & Hölldobler 1988; Schmickl & Crailsheim 2004; Sih et al. 2009). Here, it may be more likely that the emergence of an influential leader is due a variety of components such as the task and age differences within temporal task groups, the prior experience of the performance of fanning behavior or stimulus to increasing temperatures, indirect social interactions, and individual behavioral or genetic variation (Calderone & Page 1991; Huang & Robinson 1996; Weidenmüller 2004; Westhus et al. 2013).

By testing my “Follow the Leader” concept, I have also identified differences in fanning thermal response thresholds between the younger nurse and middle-aged fanner task group. Nurses fan at a lower temperature individually and within a group, but only when the group

consists of just nurses. Due to the difference in ages as a consequence of temporal division of labor, it could be quite possible that nurses have a lower thermal response threshold than fanners (Johnson 2008). Nurses may be especially sensitive to increasing temperatures because the role of a nurse is to primarily care for the brood, of which are extremely sensitive to temperature fluctuations (Seeley & Kolmes 1991; Johnson 2008, 2010). If nurses are less likely to fan than fanners, fanning may not be the primary goal of the nurses; rather the priorities are cleaning and feeding the brood (Oster & Wilson 1978; Cook & Breed 2013). But, if the temperature of the hive is not being properly regulated, nurses may respond to warming temperatures at a lower threshold to ensure the survival of the brood (Kronenberg & Heller 1982).

Unlike bumblebees (Westhus et al. 2013), honeybee fanners may have previously experienced the performance of fanning behavior and are more accustomed to higher temperature increases as a result of their age. Therefore, fanners may have a higher thermal response threshold. 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 the group consists of a single fanner. Furthermore, nurses are more heavily influenced to fan if the initiator is a fanner. One single fanner influences nurses by increasing their thermal response threshold as well as their likelihood to fan. Although nurses may be more energetically inclined to conduct other brood care tasks, they are influenced by a fanner to perform fanning when temperatures are dangerously high. This makes sense in the context of social insect societies, where the survival of individuals depends on survival of the group.

An individual's prior performance of a task can result in a more efficient and specialized response to environmental stimuli (Calderone & Page 1991; Pacala et al. 1996). Prior studies

have suggested that fanning behavior may not be a specialized task (Free 1987; Yang et al. 2010; Cook & Breed 2013). Cook & Breed (2013) found that all task groups fanned but found that porch fanners have the greatest likelihood to fan. Egley & Breed (2013) found that worker bees can switch from other tasks to fanning as needed. Additionally, Egley & Breed (2013) found that the majority of fanners on the porch of the hive are uniform in age, which suggests temporal task specialization. However, both Egley & Breed (2013) and Cook & Breed (2013) focused on bees fanning at colony entrances, rather than bees fanning inside the hive or on brood frames. Inside bumblebee (*Bombus impatiens*) nests, Jandt et al. (2009) found no evidence of fanning specialization among task groups. This suggests that the performance of fanning behavior may not be specialized across task groups, but it is likely that the probability and thresholds varies between each individual.

The influence of prior experience of fanning behavior on individual thermal response thresholds within temporal task groups may suggest an adaptable task allocation component to thermoregulation (Calderone & Page 1991). Here, middle-aged fanners may be more ‘experienced’ and may influence younger ‘inexperienced’ nurses. Within honeybees, temporal task groups may be related to the temperature at which an individual responds and the likelihood of performing fanning behavior. My results are similar to the findings of temporal task groups of Bonabeau (1996) in the ant, *Pheidole pallidula*, that minors (youngest ants) had lower response thresholds for performing tasks than majors (older ants). If the degree of task specialization and temporal task allocation within individual phenotypes can be adapted independently of one another (Calderone & Page 1991), then it is possible that nurses modify their individual thermal threshold to comply to the higher thermal threshold of the fanner. This suggests that the temporal

caste is not only to be defined by the labor profile, but also by the change in response to labor as a function of age (Oster & Wilson 1978).

Generally, repeated performance of a given task promotes increased task specialization which results in a decreased response threshold (Theraulaz et al. 1998). Many researchers have suggested that this self-reinforcement model is an illustration of social learning among individuals (Seeley 1982; Oster & Wilson 1978; Theraulaz et al. 1998). Aforementioned, Weidenmüller et al. (2004) and Westhus et al. (2013) found that bumblebee (*Bombus terrestris*) increased their likelihood to fan and decreased their thermal response thresholds when individuals repeatedly performed fanning behavior. Within honeybees, there are many examples of associative self-reinforcement learning found in the foraging behavior, but there are no published studies on social learning for thermoregulation (Menzel 1993; Bittermen 1996; Giurfa et al. 1999). Could it be possible that middle-aged ‘experienced’ fanners exhibit a self-reinforcement model? Thermoregulatory experience within a temporal task group may have an influence on social learning between individuals, but my experiments did not directly test social learning within fanning behavior.

The interactions between members within a particular group can influence the behavioral variation of an individual (Calderone & Page 1991; Bonabeau et al. 1998; Sih & Watters 2005; Pruitt & Reichert 2011). For example, when group size increases, individuals may be influenced to perform a task even when they should abandon it (Pacala et al. 1996). Although this study did not test group size, multiple other studies have concluded that the number of individuals to fan within a group increased with temperature (Weidenmüller et al. 2002; Westhus et al. 2013; Egley & Breed 2013; Cook & Breed 2013; Cook et al. 2016). This suggests that groups are better able to distinguish temperature increases than individuals (Cook et al. 2016). Similarly, this study has

found that a leader influenced other individuals' response threshold as well as the group response threshold to environmental stimuli. Rather a larger group size, a strong leader within a group socially influenced other group members to collectively respond to environmental stimuli (Pacala et al. 1996; Weidenmüller et al. 2002; Cook & Breed 2013).

It is likely that a variety of interactions may promote an environment for the emergence of influential individuals within a honeybee colony (Huang & Robinson 1996; Bonabeau et al. 1998; Calderone & Page 1991; Sih & Watters 2005). These interactions can result in an increased response efficiency to environmental stimuli in certain individuals (Calderone & Page 1991; Pacala et al. 1996). For example, direct interactions of trophallaxis between nurses and foragers determine if an individual forager will obtain more or less food for the colony (Camazine 1993; Schmickl & Crailsheim 2004). Rather, indirect interactions, such as the mere presence of an individual, influence the behavior of other group members (Drews 1993; Bonabeau et al. 1998; Modlmeier et al. 2014). Within this study, is it possible that there are direct interactions between individuals, however I did not observe any prominent direct interactions before the initiation of fanning. Fanners were likely the most influential leaders when they needed greater assistance with thermoregulation. Their indirect presence changes the threshold of nurses for an efficient temperature control (Bonabeau et al. 1996). Thus, my study suggests that mere composition of an environment can indirectly influence the behavior of an individual which ultimately effects the group response.

Temporal task groups may be exceptionally responsive to environmental conditions due to individual genetic variations, and thus it is important to consider that influence between task group members may be due to these genetic variations (Winston 1987; Huang & Robinson 1992). It may be likely that the task group members sense differences in morphological and

physiological characteristics between the other task group members. In other terms, nurses may sense differences in characteristics of a fanner compared to another nurse. For example, chemical communications between nest mates indicate if there an individual is an intrusive conspecific or a heterospecific (Duffy et al. 2002). Worker honeybees have the ability to distinguish between larvae that are highly related over larvae that are conspecifics as well as distinguish larvae that are destined to become queens (Page & Erickson 1984). It may be likely that inserting a fanner into a group of nurses may affect the cohesion of task group dynamics by changing the proportion of group members.

Individual behavior may vary within a common environment due to genetic variation (Calderone & Page 1991). The important role of genotype variation is that it creates flexibility within the context of general qualitative mechanisms, such as behavioral temporal task groups (Calderone & Page 1988, 1991; Breed et al. 1990; Fewell & Bertram 1999; Kryger et al. 2000; Oldroyd & Fewell 2007). It is important to recognize that different physiological specializations underlie each temporal task group, which creates a highly distributed task allocation among nestmates (Seeley 1982; Bersher & Fewell 2001). Specifically, there could be matrilineal genetic and (or both) cuticular hydrocarbons between younger and middle-aged task group members (Howard 1993; Santomauro et al. 2004; Jones et al. 2004; Simone-Finstrom 2014). Simone-Finstrom (2014) looked at the hive as a whole to see if genetic diversity influenced thermoregulation efficiency, however, found no significant correlation between genetic diversity and thermoregulatory stability in the inner or outer brood comb. This suggests that the degree of genetic diversity expected under normal conditions is not predictive of thermoregulatory stability. Jones et al. (2004) were able to show a difference in temperature regulation ability of genetically diverse versus genetically uniform colonies. But, genetically uniform colonies are

extremely unusual in nature (Simone-Finstrom 2014). Therefore, at natural levels of diversity, it is unknown if there is a difference between individual variation and ability to maintain stable in-hive temperatures (Simone-Finstrom 2014).

Efficiency of stability of thermoregulation may in fact be purely based on interaction among nestmates along with the plasticity of behavioral task groups (Huang & Robinson 1992, 1996; Cook & Breed 2013; Egley & Breed 2013). Such social and behavioral effects likely contribute to the maintenance of behavioral variability on a colonial scale (Huang & Robinson 1996; Calderone & Page 1988, 1991). Variation in individual behavioral responses with respect to both task specialization and temporal task allocation is the basis for evolutionary changes within individual and colony phenotypes (Calderone & Page 1991; Woodward et al. 2011). Year-round thermoregulation affects task allocation demands found within their social lifestyle suggesting that evolutionary behavioral genetic changes within honeybees may be due to unique metabolic demands (Kronenberg & Heller 1982; Woodard et al. 2011).

Taken together, I found that an individual has the ability to influence other individuals' and group dynamics, supporting the "Follow the Leader" concept. My findings suggest that the response threshold of a leader has strong implications on the survival of individuals and likely the hive as a whole. Fanners not only influence the thermal response threshold of other fanners, but also the response threshold of the nurse task group. These results indicate that fanners are indeed leaders. Fanners are more influential leaders when they fan first, but are even leaders when they do not fan first. This study suggests that the social interactions between nurse and fanners influence their task group thermoregulatory response thresholds. Social thermoregulatory fanning behavior in honeybees furthers our understanding of how individual variance influences a synchronous homeostatic response to environmental stressors. The extensive sociality within

the honeybee colonies forms the evolutionary basis for group behavior as well as the survival of individuals within a society (Menzel 1993).

Conclusion

This study has found that an individual influences group behavior within the extraordinarily critical thermoregulation behavior in honeybees, specifically between the nurse and fanner task groups. Bees who are more likely to fan demonstrate the concept of “Follow the Leader”, by becoming influential leaders to bees who are less likely to fan. It is possible that differences in experience between the two task groups determined the influence of an initiator within fanning behavior. Furthermore, this study indicates that individual interactions between bees’ influence group response thresholds within honeybee colonies. It is well understood that task group dynamics make honeybee colonies extremely effective at completing hive tasks, but further research is needed to determine if task group dynamics make the hive more efficient at responding to increasing temperatures. Taken together, the flexible and adaptive system of division of labor plays a very important role in the societal success of honeybees because a colony must develop and produce reproductive individuals despite constant changes in external and internal environmental conditions (Himmer 1932; Kronenberg & Heller 1982; Robinson 2002; Tautz et al. 2003; Groh et al. 2004; Jones et al. 2005). However, I argue that the absence of individual variation components and their influences on group dynamics within many classic insect models, such as division of labor and response thresholds, contributes to the disparities between studies. Inclusion of more precise individual influence within group behavioral responses in social insect models is necessary, such as my “Follow the Leader” concept. But, further research is needed to address the proximate mechanisms of social influence between task group members in thermoregulation. The influence of prior environmental and social experiences

of individuals on other group members within honeybees illustrates the need to understand coordination of individuals to complete a task within social organizations. These conclusions further our understanding of individual and group behavioral factors that maintain homeostasis in other biological self-organized systems.

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