Rapidly changing environment modulates the thermoregulatory fanning response in honeybee groups

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Social insect societies maintain homeostasis through decentralized collective effort. In quickly changing environments, homeostasis can be difficult, as information may promptly become outdated. How do decentralized social insect groups respond to rapid environmental changes? Honeybee (*Apis mellifera* L.) workers use thermoregulatory fanning behaviour as part of their repertoire to maintain nest temperatures below 36 °C, as larvae can develop malformations and die if temperatures surpass this threshold. Here, we determine whether honeybees alter their fanning behaviour when experiencing different rates of thermal change. We found that honeybee fanners were significantly more likely to fan when experiencing rapidly increasing temperatures, but this response was only seen in larger groups of bees. Additionally, fanners responded at significantly lower temperatures when temperatures were increased quickly, but again, only when they were in larger groups. Our results show a statistically significant interaction between fanning response and group size. These findings illustrate the importance of exploring both response thresholds and probability of response of animals in social groups experiencing changing environments, as both factors affect homeostatic responses. Understanding how self-organized animal societies maintain homeostasis provides insight into decentralized organization across many biological systems.

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All animals use homeostatic mechanisms to perform optimally in a changing environment. Many aspects of homeostasis are not controlled centrally (Vodovotz, An, & Androulakis, 2013), which leads to questions about how it is effectively maintained. For example, the mammalian immune system mostly operates peripherally, with individual cells responding according to local information (Parkin & Cohen, 2001). Several parallels exist between the immune system and homeostatic mechanisms, such as thermoregulation, in social insect societies (Eberl, 2010; Jacob, Steil, & Bergmann, 2006). Many social insect species utilize decentralized homeostasis to maintain the climate and structure of their nests (Wilson, 1971). The extent to which a system can maintain appropriate conditions depends on how rapidly or slowly the external environment changes. For example, the rate of temperature change of an environment actually alters the critical thermal limits of insects (Ribeiro, Camacho, & Navas, 2012; Terblanche, Deere, Clusella-Trullas, Janion, & Chown, 2007). These induced physiological changes in individuals can scale nonlinearly to shape group-

level responses to changing environments (Bonabeau, Theraulaz, & Deneubourg, 1996; Mangel, 1995; Pacala, Gordon, & Godfray, 1996). However, very little empirical work has been done to explore how nonlinear effects can alter critical homeostatic responses of groups.

Social insect societies give us opportunities to explore the emergence of homeostatic behaviour at levels ranging from individuals to the entire colony. By responding to perturbations, individual workers can trigger many animals in the group to perform the same homeostatic behaviour. This then affects the environment of the colony by returning conditions to a set point. For example, ants initiate foraging depending on the rate at which they encounter other successful foragers (Gordon, 2010). Termites follow this model when they repair mound breaches in colony defence (Emerson, 1956). Honeybees collectively thermoregulate in cold (Heinrich & Esch, 1994) or hot ambient temperatures (Egley & Breed, 2013; Jones & Oldroyd, 2007). These individual reactions to local changes lead to decentralized homeostatic group responses.

However, rapidly changing environments pose a particular challenge to self-organized groups. If conditions change too quickly, information may become outdated by the time a response is mounted, rendering the response ineffective. Furthermore, the roles of workers within divisions of labour in social insects are often triggered by response thresholds, which are internal response

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points at which a task-specific behaviour is performed (Robinson, 1992). Quickly changing environments may overshoot these thresholds before an individual can respond effectively. Rapidly changing temperatures have even been shown to change critical thermal maxima and minima (Ribeiro et al., 2012; Terblanche et al., 2007). Social insect societies theoretically can utilize their relatively large size to collect as much information as possible to buffer against these effects (Bonabeau, Theraulaz, & Deneubourg, 1998). Empirically, ants make increasingly effective foraging decisions when more individuals gather information (Gordon, 2010) and honeybees forage in patches more efficiently with larger hive populations (Donaldson-Matasci, DeGrandi-Hoffman, & Dornhaus, 2013). Honeybees can better choose thermal optima within a larger group of workers (Szopek, Schmickl, Thenius, Radspieler, & Crailsheim, 2013), while larger colonies can regulate carbon dioxide within a much narrower range than small colonies (Seeley, 1974). Larger bumblebee colonies respond to increasing temperatures more quickly than smaller ones (Weidenmuller, Kleineidam, & Tautz, 2002). More populous groups may thus have a regulatory advantage. As decentralized responses emerge from the interaction of many individuals with slightly different information, do larger groups mount more effective responses in a rapidly changing environment?

Honeybee colonies potentially face dramatically changing temperatures throughout a day, which can be particularly difficult to buffer against. Despite this, honeybees are highly effective at keeping hive temperatures within a very narrow range of 33–35 °C (Jones & Oldroyd, 2007; Tautz, Maier, Groh, Rossler, & Brockmann, 2003), never letting temperatures surpass 36 °C, as larvae can die (Groh, Tautz, & Rössler, 2004; Himmer, 1932; Winston, 1991). There are several thermoregulatory behaviours in which honeybees engage, such as cooling by heat shielding (Bonoan, Goldman, Wong, & Starks, 2014; Siegel, Hui, Johnson, & Starks, 2005; Starks & Gilley, 1999), which involves bees pressing their bodies against comb, then dispersing to remove heat, spreading water for evaporative cooling (Kühnholz & Seeley, 1997), warming by shivering (Heinrich & Esch, 1994; Siegel et al., 2005) and shivering inside brood cells (Kleinhenz, Bujok, Fuchs, & Tautz, 2003; for a review of insect thermoregulation, see Jones & Oldroyd, 2007). In thermoregulatory fanning behaviour, a honeybee moves its wings rapidly to circulate air within the nest or at the nest entrance. This fanning response occurs in response to increases in temperature (Egley & Breed, 2013) and is more likely to occur in groups of workers, with the fanning response being initiated collectively (Cook & Breed, 2013). This makes fanning an ideal behaviour for studies of individual and group responses to rapidly changing environments.

In this study we tested whether honeybee groups alter their fanning response depending upon differentially changing thermal environments. First, we hypothesized that the rate at which honeybees are heated would affect the probability of initiating fanning behaviour. We predicted that honeybees would be more likely to fan the more rapidly temperatures were increased. Second, we hypothesized that rate of temperature increase would affect the thermal response threshold, or the temperature at which honeybees begin to fan. We predicted that bees that are heated at a faster rate would exhibit thresholds for fanning at lower temperatures. Third, we explored how ambient temperature at time of collection influenced probability and thermal response threshold of fanning. We predicted that honeybees would be more likely to fan when they are collected from warmer temperatures, compared to cooler temperatures. Overall, given the efficiency of groups, we predicted that all of these responses would be more prominent in larger groups. Taken together, we hope to elucidate how a changing environment influences homeostasis in complex societies.

METHODS

Twelve *Apis mellifera* colonies on University of Colorado's East Campus were used for these experiments. Colonies were maintained in 10-frame wooden Langstroth hives with plastic or wood frames. Bees were supplemented with 1 M sucrose and pollen patties (Mann Lake, Hackensack, MN, U.S.A.) as needed. All experiments were conducted during June–September 2014.

Collection of Fanner Honeybees

Fanners are easily identified from their unique posture and orientation at the entrance (Cook & Breed, 2013). Other fanners occur throughout the colony of the hive, but we only sampled entrance fanners as they were easily identified and collected. We selected bees that were observed fanning for at least 10 s (Weidenmuller, 2004). These identification protocols ensured we were not collecting 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). This fanning occurs to spread a pheromone that is used to orient other bees (Free, 1987) and has not been shown to be involved in thermoregulation. These criteria were also used to identify fanning during the behavioural assay. We also avoided fanners that had pollen on their corbicula, as Cook and Breed (2013) found that pollen foragers are significantly less likely to fan in heating assays. Only nestmates were used within one experimental cage (cages described below). Upon collection, bees were immediately brought into the laboratory so that no longer than 10 min elapsed from the time of collection to when transportation to the laboratory was complete.

Set-up of Experimental Groups

We had two treatment variables: group size and rate of heating. As we collected fanning bees, we randomly placed them in one of three group sizes (1, 3 or 10 bees/group) into individual mesh cages (cylindrical: height: 20 cm, radius: 6 cm). We chose 10 as the largest group size because it is the largest group with which we could distinguish and analyse individual behaviour. While small with respect to the typical size of honeybee colonies, interactions within groups of 10 bees mimic those found in larger groups (Cook & Breed, 2013) and is typical of the group size of fanners at the hive on a summer day (C. N. Cook, personal observation). However, we have seen a large range of fanning bees at the hive, from the rare single bee to over 50 bees. For each collection event, hives were randomly selected but collection was distributed uniformly across hives. When sampling, we recorded outside temperature, whether the hive was in the sun or the shade, the time of collection and the date. We then transported the bees into the laboratory.

Temperature Regimes, Experimental Apparatus and Behavioural Assay

Once in the laboratory, we placed caged bees into 1-gallon (3.785-litre) glass jars (Specialty Container, Inc., Owensboro, KY, U.S.A.). Cages were propped on wooden stilts so the cages did not touch the sides or bottom of the jar. Jars sat on top of a single heating apparatus (Corning or Simplex Proctor hot plate). We inserted temperature probes (Cole Parmer High Accuracy (±0.3 °C) Digital Temperature Probe) into the jar and gently secured the lid. We allowed bees to acclimate in each jar for 25 min before the heating regime began. This acclimation time is based on the time required for the bees to become less behaviourally agitated, as observed in preliminary tests, and based on the protocol from Cook

and Breed (2013). After 25 min, we recorded the initial air temperature of the chamber (which was on average $25.24 \pm 0.110\,°C$) and the trial start time. Temperatures were taken at approximately the centre of the chamber where bees were restricted in the cage.

Our second treatment variable, heating rate, was randomly assigned before the trial began. We treated bees with one of three temperature-ramping regimes: $0.5\,°C/min$, $1\,°C/min$ and $2\,°C/min$. Rate was controlled by the heat settings on the hotplate; we placed hotplates on higher settings earlier for faster rates. We chose rates of change that we acknowledge were extreme but still fitted within the upper limits of what bees might experience in natural environments. When exploring critical thermal temperatures in beetles, Allen, Clusella-Trullas, and Chown (2012) used temperature rates from $0.05\,°C/min$ to $0.5\,°C/min$. Ribeiro et al. (2012) used rates between $0.17\,°C/min$ and $2\,°C/min$ to assess maximum critical temperatures in leaf cutter ants, *Atta sexdens rubropiosa*. The assigned target rate that we aimed for was often close, but not exact. The actual mean $\pm$ SD and range for each rate was as follows: $0.5\,°C/min$ rate (0.533 ± 0.109, range $0.37–0.749\,°C/min$); $1\,°C/min$ rate (1.039 ± 0.222, range $0.75–1.49\,°C/min$); $2\,°C/min$ rate (2.080 ± 0.436, range $1.5–3.35\,°C/min$). Rate was calculated as: (end temperature ($°C$) – start temperature ($°C$)/total trial time (min)).

We have repeatedly observed that, in a group, bees initiate fanning virtually simultaneously; their responses are not staggered as temperature increases. Because bees within a group start fanning simultaneously, in the present study, we measured the probability and response threshold at the first initiation of group fanning (Cook & Breed, 2013). Therefore, we measured fanning as a group-level response. For single bees, we ran 15 trials at $0.5\,°C/min$, 16 trials at $1\,°C/min$ and 20 trials at $2\,°C/min$. For groups of three, we ran 13 trials at $0.5\,°C/min$, 15 trials at $1\,°C/min$ and 20 trials at $2\,°C/min$. For groups of 10, we ran 16 trials at $0.5\,°C/min$, 14 trials at $1\,°C/min$ and 19 trials at $2\,°C/min$. We ran between one and four trials simultaneously, constantly observing and listening to bees in each trial, as the heating apparatuses were 5 cm apart. We initially recorded data into notebooks, then transferred the data into Excel spreadsheets. We did not measure CO_2, as our container was not sealed. Additionally, based on Seeley (1974), honeybees fan to regulate CO_2 when concentrations exceed 1%. Based on Harrison and Fewell (2002), we calculated that honeybees in our apparatus for the duration of the acclimation period and trial until fanning (between 28 and 45 min) would reach 0.13% in a sealed apparatus.

Our response variables were the proportion of fanners out of the total number of bees in the group and the temperature at which bees began to fan (hereafter thermal response threshold). After the initial fanning bout, we continued the trial to see whether fanning occurred later in the trial and recorded that, as well, but we treated those data separately (and do not include them in this study). Trials concluded when the last bee reached lethal temperature and died, which we also recorded. Time of trial conclusion was recorded and actual rate of temperature change was calculated.

Statistical Analysis

Our null hypothesis was that honeybees fan independently of each other. Under this null hypothesis, individual honeybees in groups would have the same probability of fanning as solitary honeybees, and the observed number of bees fanning should follow a binomial distribution with parameters P and n, where P is the probability of observing a solitary bee fanning during a trial and n is the group size. To test this null hypothesis we estimated P from observations of solitary honeybees to be 0.135 (95% CI: 0.0313, 0.238; $n = 52$ bees). We then performed a goodness-of-fit test in R (using the function 'goodfit()' provided by the package 'vcd') with

parameters $P = 0.135$ and $n =$ group size (3 or 10) to compare the observed distributions from the groups of 3 and 10 bees to the expectation that the numbers fanning fitted a binomial distribution.

To analyse our data for the two hypotheses postulating effects of group size, heating rate, and their interactions, we used generalized linear mixed models. Specifically, we examined the probability of fanning using a mixed model logistic regression (link = logit) with the 'glmer' function ('lme4' package in R) on a binomial error distribution. Probability of fanning was calculated from a two-column response variable of bees that fanned and bees that did not fan. When a two-column proportion is run through a logit transformation, the logit function calculates a probability.

We analysed thermal response threshold using a generalized linear mixed model using the 'lmer' function (lme4) on a Gaussian error distribution, then used an ANOVA (type II Wald chi-square) to analyse the magnitude of each main effect. For categorical factors, we used a Tukey post hoc test to analyse the effect within the variable.

We approached each of these models with backward selection using Akaike's information criterion, AIC (Symonds & Moussalli, 2011). Our main predictor variables in all of these models included rate of ramping ($0.05\,°C/min$, $1\,°C/min$, $2\,°C/min$), group size (1, 3, 10), outside temperature and presence of sun on hives, as well as the interactions of rate of ramping, group size and outside temperature (see Results, Table 1). We treated hive as a random effect, which allowed us to control for the inherent differences between hives, which we acknowledge likely exist, but are not relevant to the hypotheses. Once we arrived at a model with only significant predictor variables or interactions (see Results, Table 2), we performed a model fit analysis to directly compare predictive value of the models and ensure we relied on the best one. We used R (v.3.0.2, R Foundation for Statistical Computing, Vienna, Austria) and RStudio (v.0.98.1103, RStudio, Boston, MA, U.S.A.) and the package 'lme4' (Bates, Mächler, Bolker, & Walker, 2014).

RESULTS

Do Honeybees Fan Independently of Each Other?

Honeybees in groups did not fan independently of each other. Using the probability of observing fanning from our solitary

Table 1
Comparison of the full model to the simplest, most predictive model (ANOVA: $P = 0.018$) of probability of fanning

Main effects	Interactions	AIC
Full model		
Rate	Rate*group size	635.2
Group size	Outside temp*group size	
Sun	Outside temp*rate	
Outside temp	Outside temp*rate*group size	
Most predictive model		
Group size	Rate*group size	**630.737**
	Outside temp*group size	

AIC: Akaike's information criterion. Bold values indicate a significant response variable effect.

Table 2
Significant effects predicting the probability of fanning in the best model

	Intercept	Slope	Z	P
Main effect				
Group size	−0.543	0.242	−2.575	**0.010**
Interactions				
Rate*group size	0.085	0.016	3.049	**0.0023**
Outside temp*group size	0.007	0.0014	2.764	**0.0057**

Significant outcomes ($P < 0.05$) are shown in bold.

honeybee experiments (0.135; 95% CI: 0.0313, 0.238), applied to a binomial distribution, we found that the distribution of honeybees fanning in groups did not fit a predicted binomial distribution (groups of 3: Pearson: $\chi_3^2 = 506.817$, $P = 1.589e^{-109}$; likelihood ratio: $\chi_3^2 = 57.81$, $P = 1.726e^{-12}$. Groups of 10: Pearson: $\chi_{10}^2 = 10\,651.23$, $P = 0.00e^{+00}$; likelihood ratio: $\chi_{10}^2 = 295.23$, $P = 1.585e^{-57}$; Fig. 1). The differences in fanning behaviour between groups were not due to individual probabilities or thresholds, but due to the influence of other bees in each group.

Factors Affecting the Probability of Fanning

Following the model selection procedure outlined above, the best model (Table 1) included the following predictors (Table 2): (1) the interaction between group size and rate of temperature increase ($Z = 5.331$, $N = 148$, $P < 0.0001$), (2) the interaction between group size and outside temperature ($Z = 5.050$, $P < 0.0001$) and (3) group size ($Z = -4.159$, $P < 0.0001$). The significant interactions are particularly interesting. The significant interaction between group size and rate of temperature increase shows that honeybees were significantly more likely to fan when being heated at a faster rate, but only when they were in the largest group of 10 bees (Fig. 2). We observed fanning in 17 out of 19 trials with groups of 10 bees heated at 2 °C/min, in nine out of 20 trials with groups of three bees at 2 °C/min and in only four out of 20 trials with solitary bees heated at 2 °C/min. For groups of 10, fanning occurred in 13 out of 16 trials at 0.5 °C/min, in 11 out of 14 trials at 1 °C/min and in 17 out of 19 trials at 2 °C/min. Results for the significant interaction between ambient temperature and group size are given below (see the Effect of Ambient Temperature on Fanning Probability and Thermal Threshold).

Factors Affecting the Thermal Response Threshold

The best model for thermal response threshold included rate of temperature increase and group size as significant predictor variables. Honeybees fanned at significantly lower temperatures when they were in groups of 10 than when they were alone ($Z = -3.357$, $N = 74$, $P = 0.0021$). They also fanned at significantly lower temperatures when they were heated at rates faster than 0.5 °C/min ($Z = -2.306$, $N = 148$, $P = 0.023$; Fig. 3). Mean $\pm$ SE fanning temperature of bees in groups of 10 was 36.3 $\pm$ 2.08 °C ($N = 16$) when heated at 0.5 °C/min, 35.3 $\pm$ 2.06 °C ($N = 14$) when heated at 1 °C/min and 29.14 $\pm$ 1.00 °C ($N = 19$) when heated at 2 °C/min. No solitary bees fanned when heated at 0.5 °C/min. The main effects were significant, whereas the interactions were not. This shows that for thermal response threshold, bees were likely cueing in on group size and heating rates independently. There was no significant difference among other group sizes or rates.

Effect of Ambient Temperature on Fanning Probability and Thermal Threshold

The interaction between group size and ambient temperature in predicting the probability of fanning was also significant. Honeybees were significantly more likely to fan when they were collected in higher ambient temperature conditions, but again, this was only seen for bees that where then placed in groups of 10 (10 bees: $Z = 4.437$, $N = 49$, $P < 0.0001$; 3 bees: $Z = 0.476$, $N = 48$, $P = 0.634$; 1 bee: $Z = 0.750$, $N = 51$, $P = 0.453$; Fig. 4). We made sure that this was not an artefact of collection, as warmer days allowed us to collect more bees; group sizes were evenly distributed across all ambient collection temperatures. Finally, there was no significant
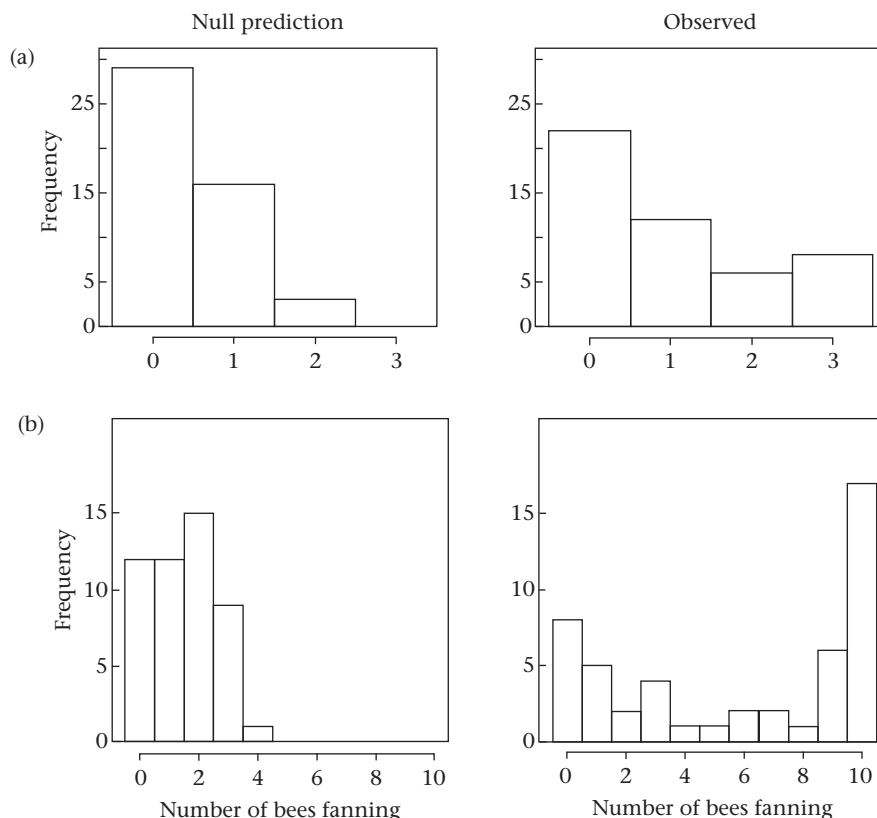

Figure 1. Expected and observed distributions of the fanning response in groups of (a) three honeybees and (b) 10 honeybees. The expected distribution is a binomial distribution based on honeybees behaving as though their responses were independent of each other.
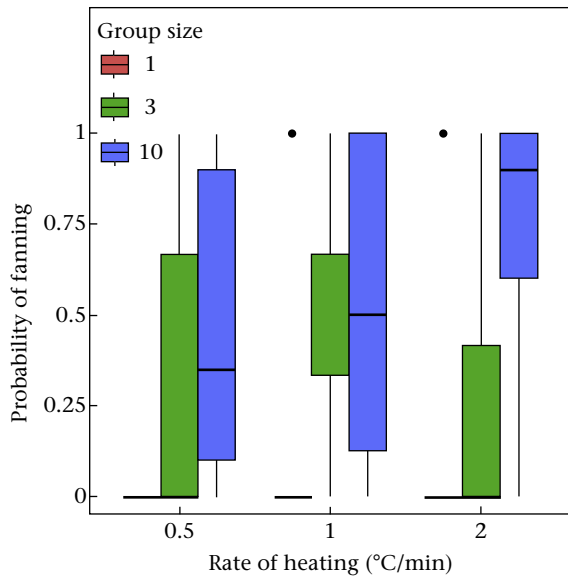
Figure 2. Probability of fanning across groups and heating regimes. Horizontal bars are medians, boxes are 25th–75th percentiles, bars are 1.5 × IQR, points are Tukey outliers (*N* = 148). Created using R package 'ggplot2'.
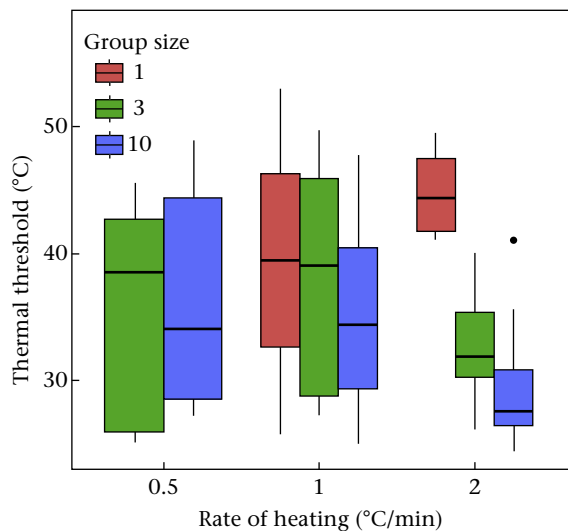
**Figure 3.** Thermal response threshold across group sizes and heating regimes. Note: no solitary bees fanned when heated at 0.5 °C/min. Horizontal bars are medians, boxes are 25th–75th percentiles, lines are 1.5 × IQR, points are Tukey outliers (*N* = 74). Created using R package 'ggplot2'.

effect of outside temperature on thermal response threshold (GLM: *T* = −0.637, *N* = 73, *P* = 0.526).

DISCUSSION

Rapidly changing environments can be especially challenging for maintaining homeostasis. Despite this, honeybees maintain a tightly controlled thermal environment inside the hive. Here, we show that honeybees behave differently when temperatures increase more rapidly, but that the differences depend upon social context (i.e. group size). When experiencing a temperature increase of 2 °C/min, honeybees were significantly more likely to begin to fan than honeybees that were being heated slowly. We saw this result only in our larger groups, which consisted of 10 bees. The rate
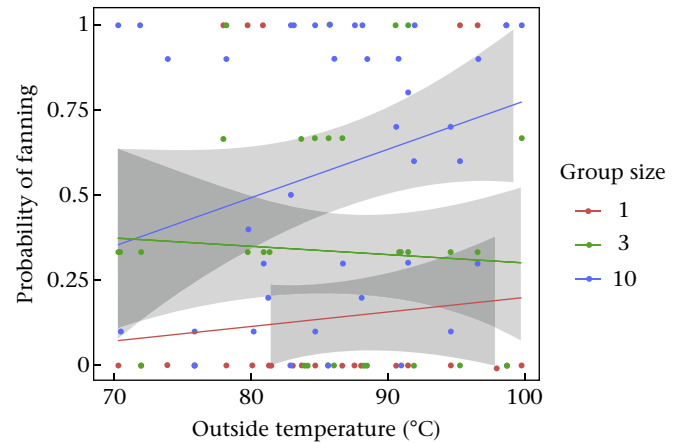
Figure 4. Relation between outside temperature and group size on the probability of fanning. Shaded areas around lines denote 95% confidence intervals (*N* = 74). Created using R package 'ggplot2'.

of temperature increase had no effect on the probability of fanning for a bee by herself or for bees in groups of three. We verified that honeybees do not fan independently; when in groups, honeybees fanned more than predicted from the behaviour of single bees and fanning in groups did not fit a binomial distribution. While we knew that honeybees are more likely to fan and begin to fan at lower temperatures in groups of 10 (Cook & Breed, 2013), our results show that they are also cueing in on how quickly temperatures are changing. Theoretically, larger groups should be able to respond to rapidly changing environments more effectively, as they collect and synthesize more information more quickly (Bonabeau et al., 1998; Pacala et al., 1996; Seeley, 1974). When honeybees experience quickly increasing temperatures, they are more likely to respond, but only in larger groups.

Our results show that honeybees begin to fan at significantly lower temperatures when temperatures are increased at faster rates, but again, only when bees are in larger groups. For the collective fanning response to be effective, a certain number of bees must initiate fanning at high ambient temperatures. But participation is not enough: the temperature at which the bees begin to fan and the bees' response threshold also influence whether the fanning response is effective. Starting to fan at too high of a temperature will not be as effective as starting at lower temperatures. Bees that are in smaller groups or by themselves are not as likely to respond, even when being heated quickly. This is seen in bumblebees (*Bombus terrestris*) as well: Weidenmuller et al. (2002) found that larger bumblebee colonies respond faster to increasing temperatures. In the present study, we found a significant effect of decreased thermal threshold even with a group size of only 10 bees. Response thresholds are often considered to be a static characteristic; an individual simply reaches that threshold and responds (Beshers & Fewell, 2001; Jones, Myerscough, Graham, & Oldroyd, 2004). In bumblebees, response thresholds are modulated by both rate and previous experience (Westhus, Kleineidam, Roces, & Weidenmüller, 2013). Our results show that when groups of 10 bees are heated at fast rates, they are both more likely to begin fanning and more likely to fan at lower temperatures, essentially anticipating rapidly increasing temperatures.

We found that honeybees that were brought into the laboratory were significantly more likely to fan if they were collected in hot ambient temperatures, compared to bees collected in cooler temperatures. This effect was only seen when bees were heated in larger groups, compared to small groups or by themselves. Although ambient temperatures 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, because they were performed in a laboratory setting. Bees that were collected in hotter ambient temperatures experienced a more dramatic temperature change when they were brought into the laboratory than bees collected at cooler temperatures. However, this probably did not influence their increased fanning response, as bees collected in hot ambient temperatures but placed solitarily or heated more slowly did not show an increase in fanning probability or thermal response threshold.

In many social organisms, a group response does not occur until a quorum of individuals are readied by collective information (Rangel & Seeley, 2008; Sumpter & Pratt, 2009). In larger groups, information is shared by more individuals, so more individuals are synthesizing information and potentially readying for a response (Donaldson-Matasci et al., 2013; Page & Mitchell, 1998). For the fanning response, honeybees that are exposed to higher temperatures outside may be more likely to fan based on the thermal information they acquired before being collected. The larger group size of fanners could allow them to reach a critical amount of thermal information more quickly, meaning they were hotter already, hence the increased chance of fanning seen only in larger groups of bees. This also has implications of efficiency at the hive. Donaldson-Matasci et al. (2013) found that larger honeybee colonies are more effective at communicating forage information than smaller colonies. Size can have implications for a colony's ability to effectively regulate their temperature.

Self-organization occurs in many biological systems. While it is critical to explore how self-organization occurs, understanding the rules that organisms use can provide insight into created systems, and vice versa (Seeley, 2002). Social insect societies offer opportunities to test hypotheses about decentralized homeostasis. These groups are diverse, open, self-organized systems whose colonies range in worker specialization and population size. All of these societies function on some level with many individuals collecting information and responding to environmental perturbations. Furthermore, group size is known to increase efficiency of many decentralized tasks in social insects, including foraging (honeybees: Donaldson-Matasci et al., 2013; ants: Pacala et al., 1996; wasps: Jeanne & Bouwma, 2002), thermoregulation (bumblebees: Weidenmuller et al., 2002; honeybees: Cook & Breed, 2013), nest site selection (Sasaki, Granovskiy, Mann, Sumpter, & Pratt, 2013) and overall colony organization (Naug, 2009). These systems can be explored from many different levels of organization, thus providing information about how regulation of group behaviours in societies occurs.

Organization of decentralized biological systems is similar to that of some engineered systems, specifically computational (Kitano, 2002; Vodovotz et al., 2013) and chemical systems (Androulakis, 2014). These systems are often modelled with the assumption that every unit is the same, whereas in reality, units are diverse (Camazine et al., 2001; Kitano, 2002). Furthermore, stochastic events could affect self-organized systems differently (Cohen & Harel, 2007) as well as differentially affect small versus large systems (Jeanne & Bouwma, 2002). While modelling decentralized systems provides a way to generate hypotheses of how they will behave, exploring established self-organized biological systems offers a powerful comparison as they provide insight into stochastic events or emergent properties not predicted by mathematical models (Rubenstein, Cornejo, & Nagpal, 2014; Fewell, 2003). By integrating mechanisms from all of these perspectives, researchers can improve upon hypotheses, predictions and models as well as the methods by which to explore decentralized systems.

Response thresholds and probability of performance are critical organizing components of division of labour in social insects

(Jeanson & Weidenmüller, 2014). These behavioural responses are modulated both by how quickly the environment changes and by the social environment that an individual experiences, so much so that these two contexts show strong interactive effects. Our study emphasizes the necessity of exploring self-organization in the context of changing environments, which inevitably influences the organization of biological systems.

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