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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 In quickly changing environments, homeostasis can be difficult, as information may promptly become outdated.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

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