



# Collective control of nest climate parameters in bumblebee colonies

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We examined two aspects of the social control of nest climate in bumblebee colonies: which parameters of nest climate bumblebees actively down-regulate by fanning and the dynamics of the colony response as colony size increased. Colonies of *Bombus terrestris* were exposed to an increase in carbon dioxide, temperature or relative humidity. We performed 70 temperature trials (six colonies), 58 CO<sub>2</sub> trials (four colonies) and four humidity trials (two colonies). An increase in CO<sub>2</sub> concentration and temperature elicited a fanning response whereas an increase in relative humidity did not. This is the first report of fanning in bumblebee colonies to control respiratory gases. The number of fanning bees increased with stimulus intensity. The colony response to a CO<sub>2</sub> concentration of 3.2% was comparable to the colony response to a temperature of 30°C. A marked fanning response occurred at 1.6% CO<sub>2</sub>, a concentration never exceeded in a large field nest during a pilot measurement of 10 days. We investigated the colony response over a wide range of colony sizes (between 10 and 119 workers). The proportion of the total workforce invested by colonies in nest ventilation did not change significantly; thus, the number of fanning workers increased with colony size. Furthermore, as colony size increased, the dynamics of the colony response changed: colonies responded faster to perturbations of their environment when they were large (60 or more individuals) than when they were small.

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The majority of social insects possess elaborate regulatory capabilities that enable them to control climatic conditions within their nests (Seeley & Heinrich 1981). These capabilities provide a certain degree of independence from the environment and thus promote growth and survival of the colony. Control over nest microclimate is achieved through a combination of nest design and worker activities. While nest site choice and nest architecture present long-term adjustments, short-term control of nest climate involves behavioural and physiological responses of individual colony members resulting in cooperative activities. These activities aim at returning conditions inside the nest to the state prior to perturbation, a phenomenon known as social homeostasis (Emerson 1956).

Bumblebees live in colonies that are founded by a single queen and grow to a worker population of several hundred within one summer. Owing to their enormous incubating capacities, colonies are able to maintain high nest temperatures even under cool ambient conditions (Heinrich 1979). As colony size increases and during times of high ambient temperatures, colonies may sometimes face the problem of their brood nest overheating. Like other winged hymenopterans, bumblebees ventilate their nest by wing fanning to reduce nest temperature (Vogt 1986a). Using the thermoregulatory measures of incubating and wing fanning, bumblebee colonies are able to maintain stable temperature levels inside their nests.

The ability to maintain stable temperature conditions changes with colony size; small colonies undergo larger fluctuations in brood temperature than large ones (Seeley & Heinrich 1981). An increase in nest climate homeostasis with increasing colony size has also been reported for honeybees, *Apis mellifera* (Seeley 1974) and hornets, *Vespula* spp. (Gibo et al. 1974).

Besides temperature, respiratory gases are presumably important parameters of nest climate. The majority of

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bumblebee species nest in underground cavities originally excavated by small mammals. The gas exchange properties of such cavities may not always fit the colony needs. Many tasks such as incubating require high metabolic activity (Heinrich 1979) and insufficient gas exchange is likely to result in a decrease in O<sub>2</sub> levels and an increase in CO<sub>2</sub> levels. Thus, especially when population size is large, bumblebee colonies presumably face the problem of insufficient exchange of respiratory gases. However, nothing is known about the concentration of respiratory gases in bumblebee nests and whether they are actively controlled by colony members. Similarly, it is unknown whether bumblebees actively control a third parameter of nest climate, relative humidity.

We examined two aspects of the social control of nest climate in bumblebees, *Bombus terrestris*. First, we tested which parameters of their nest climate bumblebee colonies actively control by wing fanning, by exposing colonies to increasing levels of temperature, CO<sub>2</sub> and relative humidity. Since no data on the concentration of respiratory gases in bumblebee nests are available in the literature, we also measured nest climate in an unmanipulated field nest of *B. terrestris*. Second, we investigated why under natural conditions large colonies undergo smaller fluctuations in nest temperature than small colonies; to do this, we analysed a colony's response when small (<60 workers) and when large (≥60 workers).

## METHODS

### Field Colony

We opened a large subterranean field nest of *B. terrestris* on 30 June 1999. The colony inhabited an abandoned mouse nest, 20 cm beneath the surface with a 40-cm tunnel leading to the entrance hole (diameter 3 cm). We carefully opened the nest cavity from one side, leaving the tunnel undamaged. The colony consisted of more than 100 individuals, and already contained some males. The nest canopy had several holes, into one of which we inserted a temperature probe (Testo 175, Testo, Lenzkirch, Germany). We also inserted one end of a probing tube (diameter 0.4 cm), covered by fine wire mesh, into the nest to take air samples. The other end of the probing tube was closely sealed. A second temperature probe was installed in the soil next to the nest cavity. We placed a Plexiglas sheet vertically in front of the nest and refilled the hole with soil. A third temperature sensor was placed 20 cm above ground level in the shade. Starting on 1 July, nest climate data of this colony were taken for 10 days. Temperature data of all three sensors were logged every 30 min. To reduce artificial ventilation of the nest, we measured CO<sub>2</sub> concentration no more than every 3 h (three to five times per day) using the pump and sensor described below. Air was drawn from the nest for 3 min at a flow rate of 1.5 litres/min. The maximum CO<sub>2</sub> concentration measured was recorded and the tube was then immediately closed again. We measured CO<sub>2</sub> again in September after the nest was abandoned.

### Laboratory Colonies

For the laboratory experiments, queens obtained from a commercial breeder were allowed to establish colonies in Plexiglas-covered nestboxes (14 × 14 cm and 10 cm high). The nestboxes were divided into an upper compartment (8 cm high) containing the nest and a lower compartment (2 cm high), which we could open and close from one side for manipulations. The two compartments were separated by wire mesh. The nestboxes had three screened ventilation holes (diameter 1.5 cm) and connected via a 60-cm Plexiglas tunnel (diameter 2 cm) to a foraging chamber (30 × 40 cm and 30 cm high) where sugar solution was provided ad libitum. Pollen was fed directly into the nest. Colonies were kept at a room temperature of 22°C. All bumblebees were individually marked with numbered plastic tags.

Before an experiment started, we closed the entrance to the foraging chamber with wire mesh, thus confining all bumblebees to the nestbox and entrance tunnel during data collection. We performed manipulations daily between 1200 and 1500 hours. Temperature, relative humidity or CO<sub>2</sub> concentration was experimentally increased while the other parameters remained constant. An experiment lasted 75 min, divided into 15 observation periods of 5 min each. Manipulations started after 15 min (three observation periods) and lasted 45 min (nine observation periods). Thus, manipulations ended 60 min after the start of the experiment. Climatic conditions then gradually returned to starting conditions. We noted temperature, humidity and CO<sub>2</sub> values at the beginning of each observation period and recorded the number of individuals showing fanning behaviour during an observation period. Fanning behaviour was defined as steady fanning with extended wings while standing still for at least 10 s.

We increased temperature by regulating a commercially available infrared lamp (150 W) positioned 70 cm above the nest. Radiation was increased slowly during the experiment following a fixed temperature regime, regardless of fanning activity of the colony. Since we manipulated nest climate in colonies repeatedly, we did not expose colonies to temperatures above 30°C, to avoid damage to the brood. We manipulated relative humidity by placing a dish of dried silica gel in the lower compartment of the nestbox 3 h before the experiment started. This caused relative humidity to drop to levels of 40–50%. At the start of the manipulation the silica gel was exchanged for a dish of water. This induced a steady increase in relative humidity up to 90%. We increased CO<sub>2</sub> by successively closing the three ventilation holes. The first was closed at the start of the manipulation and the second and third 10 and 20 min later, respectively, causing a gradual increase in CO<sub>2</sub> concentration. To show that the fanning response of the colony was caused exclusively by the self-induced increase in CO<sub>2</sub> concentration, we compared it with the response to an artificial (injected) increase of CO<sub>2</sub>.

We measured temperature and humidity with a temperature and humidity probe (HMP 36B, Vaisala, Helsinki, Finland) inserted into the upper compartment of the nestbox, 4 cm above the wire mesh. We measured

the CO<sub>2</sub> concentration by infrared absorption with a gas sensor type GS 20 ED/CO<sub>2</sub> (Sensor Devices, Dortmund, Germany). Air from the nestbox was drawn into the gas sensor by an open loop circulation, driven by a 12-V membrane pump (Thomas Industries Inc., Sheboygan, USA) at a flow rate of 1.5 litres/min. Two plastic tube openings in the nestbox, covered by fine wire mesh, allowed exchange of air in the circulating air current.

We tested colonies over a period of several weeks. Four colonies were alternately exposed to both temperature and CO<sub>2</sub> manipulations and two additional colonies only to increasing temperatures. We measured colony response to an increase in relative humidity twice in two colonies and colony response to an increase in temperature/CO<sub>2</sub> 9–16 times per colony, resulting in 132 trials in six colonies (70 temperature, 58 CO<sub>2</sub>, four relative humidity). Worker populations of the colonies ranged from 10 to 119 workers.

## Data Analysis

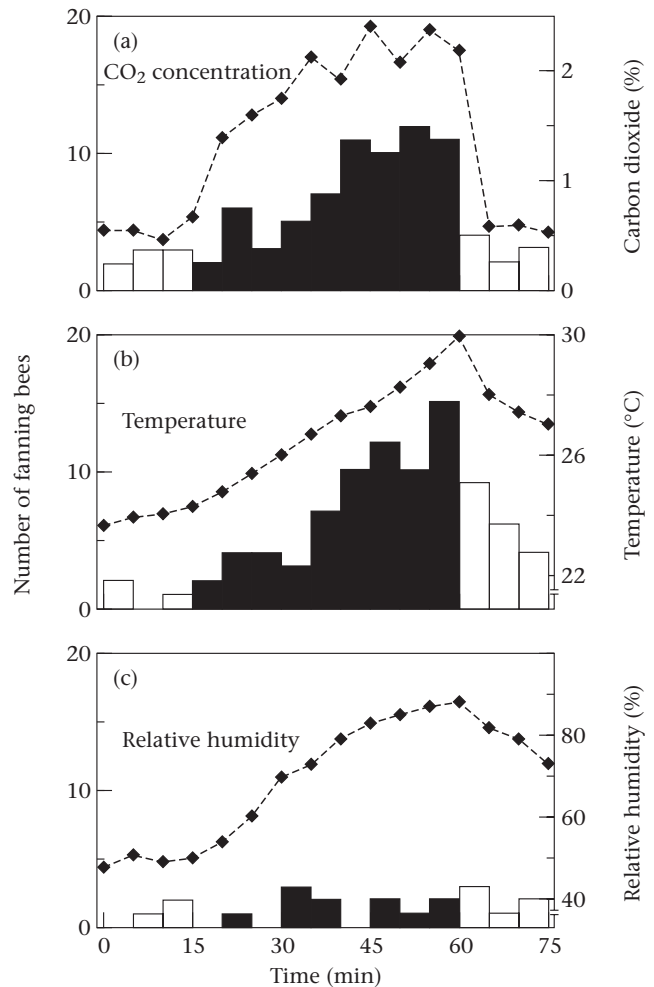
To investigate the influence of colony size on colony response, we classified colonies as small if they contained fewer than 60 individuals and thereafter as large. We used the Wilcoxon test for matched pairs to compare the maximum response to high temperature conditions of colonies when small and when large. The controlled increase in nest temperature allowed us to analyse a second parameter of colony response, the latency in response, across colony size. To determine the time to maximum increase in number of fanning bees in each trial (for temperature only), we used a sigmoidal fit (model:  $y = a + b / (1 + \exp(c - x))$ ) between time ( $x$ ; corresponding to temperature) and proportion of bees showing fanning behaviour ( $y$ ); ( $a, b$ : saturation limits of the sigmoid curve). The turning point ( $c$ ) of the sigmoidal fit was used as a measure for the maximum increase in the number of fanning bees only if the model described more than 75% of the data.

We used the  $t$  test for matched pairs to compare the latencies of the responses of colonies when small and when large. All data were analysed with Statistica 5.5 for Windows (StatSoft, Tulsa, U.S.A.). All tests were two tailed. Unless noted otherwise, descriptive statistics are presented as mean  $\pm$  SD.

## RESULTS

### Field Colony

The field nest had a mean CO<sub>2</sub> concentration of  $1.27 \pm 0.1\%$  (range 0.91–1.51%). The CO<sub>2</sub> concentrations showed slight daily fluctuations with higher concentrations at night ( $1.33 \pm 0.1\%$ ) than during the day ( $1.19 \pm 0.1\%$ ). The abandoned nest cavity measured 0.28% CO<sub>2</sub>. Ambient air temperature showed daily fluctuations ranging between 13.2 and 34.4°C ( $20.3 \pm 4.0^\circ\text{C}$ ), whereas brood temperature underwent minor fluctuations, ranging between 31.3 and 33.4°C ( $32.3 \pm 0.4^\circ\text{C}$ ). The soil surrounding the nest was cooler and averaged  $20.1 \pm 0.8^\circ\text{C}$  (range 18.9–22.2°C).

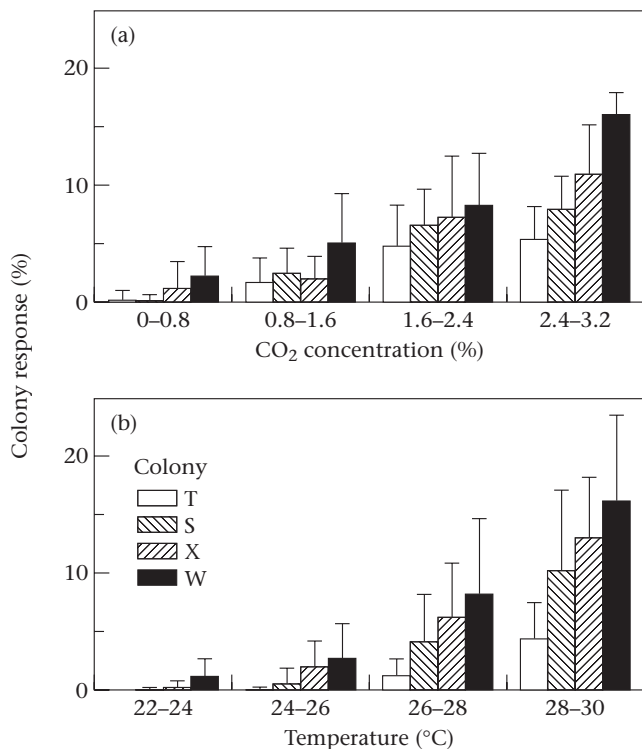


**Figure 1.** Example of the fanning response of a *Bombus terrestris* colony exposed to an increase in (a) CO<sub>2</sub>, (b) temperature and (c) relative humidity. Curves: stimulus intensities; □: number of fanners before and after manipulation; ■: number of fanners during manipulation of nest climate. The colony consisted of 78 worker bees.

### Laboratory Colonies

Figure 1 shows examples of the fanning response of a laboratory colony exposed to an increase in CO<sub>2</sub> concentration, temperature and relative humidity. As CO<sub>2</sub> concentration rose (Fig. 1a) there was a gradual increase in the number of fanning bees. Fanning decreased as soon as the stimulus intensity declined. Colonies showed the same graded fanning response when exposed to an increase in nest temperature (Fig. 1b) but not to an increase in relative humidity (Fig. 1c). We performed three more trials with increasing relative humidity but never observed a fanning response. We therefore continued to study only the colony response to an increase in CO<sub>2</sub> and temperature.

Colony size increased over the course of the experiments. When first tested, colonies had between 10 and 33 individuals. During the final experiments (ca. 4 weeks later) the colony size ranged between 91 and 119 workers. Starting conditions (conditions before manipulation,

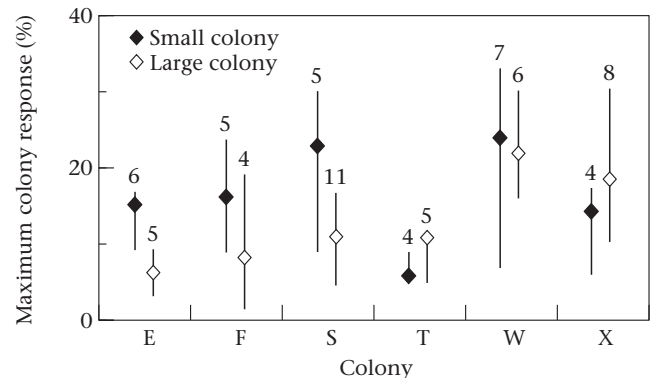


**Figure 2.** Colony response (in percentage of workers fanning) of four colonies to different (a)  $\text{CO}_2$  concentrations and (b) temperatures. Pooled data from 58  $\text{CO}_2$  and 50 temperature trials are shown, presented in bins of 0.8%  $\text{CO}_2$  and 2°C. Means  $\pm$  SDs are shown.

during the first three observation periods) remained constant within each colony throughout all experiments. Temperatures at the beginning of the experiments ranged between 22 and 24°C. Since the experimentally induced temperature increase was controlled, it was steady across all experiments and between colonies, independent of colony size. The maximum temperature was reached 45 min after the heating lamps were switched on. Concentrations of  $\text{CO}_2$  at the beginning of the experiments ranged between 0.3 and 0.8%. Maximum concentrations were reached 30–45 min after we closed the first ventilation hole. Only worker bees fanned in response to high temperature and  $\text{CO}_2$  levels, except in one colony where the queen sometimes fanned. Drones were never observed fanning.

All colonies in all trials showed the graded colony response to increasing  $\text{CO}_2$  concentrations or temperature levels (Fig. 2). A marked increase in the number of fanning workers was usually observed at  $\text{CO}_2$  concentrations of more than 1.6% or temperatures above 26°C. Colonies responded to temperatures of around 30°C with the same intensity as to  $\text{CO}_2$  levels of about 3.2%. Differences in intensity of response between the four colonies tested under both temperature and  $\text{CO}_2$  increase were consistent over the whole range of stimulus intensities (except for colony X at a  $\text{CO}_2$  concentration of 0.8–0.6%  $\text{CO}_2$ ).

We analysed two parameters of the colony response at different colony sizes: the maximum response and the



**Figure 3.** Maximum fanning response (maximum percentage of workers observed fanning per observation period during one trial) of six colonies under temperature stress. For each colony, paired medians ( $\diamond$ ,  $\blacklozenge$ ) and ranges (vertical lines) are shown for when colonies were small (<60 workers) and when they were large ( $\geq 60$  workers). Numbers indicate sample sizes.

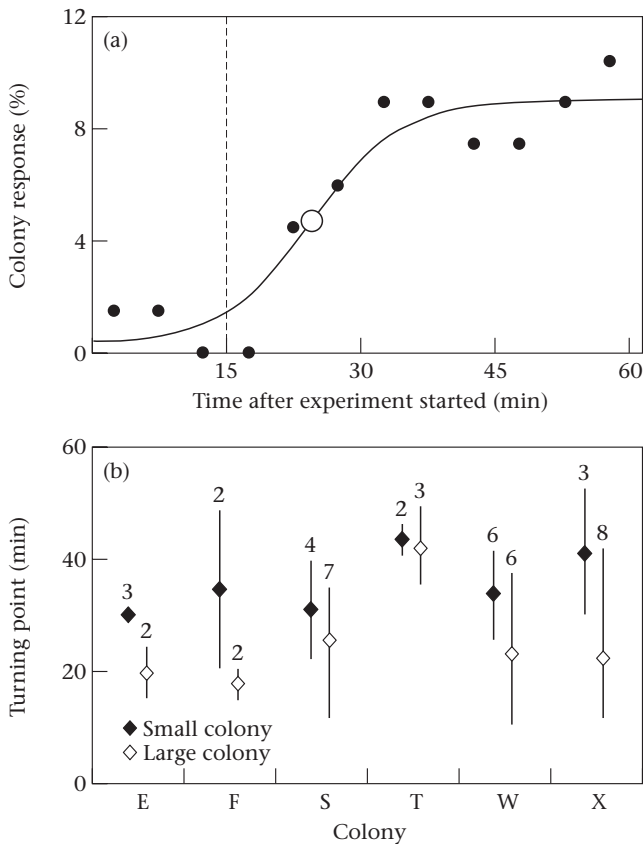
dynamics of the response to temperature stress. Only temperature trials were analysed because the temperature increase followed a strict temperature regime whereas  $\text{CO}_2$  concentrations could sometimes drop during measurements as a result of massive fanning.

The maximum response (maximum percentage of workers fanning per observation period during one trial) to temperature stress was highly variable, with between 2 and 33% of workers fanning. We found no consistent change in the proportion of the available workforce maximally invested in nest ventilation (Fig. 3). The proportion of fanning workers did not vary with colony size (Wilcoxon test for matched pairs:  $T=5.00$ ,  $N=6$ ,  $P=0.25$ ). A colony responded to temperature stress with more fanning workers when large than when small.

The second parameter of colony response we analysed as a function of colony size was the delay in the colony's response to an increase in temperature. The 75% criterion for the sigmoidal fit (Fig. 4a and see Methods) was met in 4–12 trials per colony. Figure 4b shows the turning points of these sigmoidal fits, used as a measure for the maximum increase in number of fanning bees. As colony size increased, the response delay decreased. When colonies had fewer than 60 individuals the maximum increase in response occurred on average  $36.0 \pm 5.4$  min after manipulations started. Later in colony development when colonies contained 60 or more individuals, the maximum increase occurred after  $25.4 \pm 8.7$  min. Thus, colonies increased their fanning population earlier when large ( $t$  test for matched pairs:  $t_4=4.04$ ,  $P<0.01$ ).

## DISCUSSION

While the thermoregulatory abilities of bumblebee colonies are well documented, it is now clear that colonies also control the concentration of carbon dioxide. We have shown that the colony response to both temperature and  $\text{CO}_2$  increase is graded and changes as colonies grow. We found no consistent change in the proportion of the total workforce invested in nest ventilation but



**Figure 4.** Response delay in relation to colony size. (a) The turning point of a sigmoidal fit ( $\circ$ ) was determined for each temperature trial (dashed line: start of heating). (b) Turning points are shown as a measure of the delay in response when colonies were small (<60 workers) and large ( $\geq 60$  workers). For each colony, paired means ( $\diamond$ ,  $\blacklozenge$ ) and ranges (vertical lines) are shown. Numbers indicate sample sizes.

colonies responded faster to perturbations of their colony environment when they were large than when they were small.

### Responses to Manipulation of Nest Climate

Wing fanning promotes evaporation and convection. Thus, it influences temperature,  $\text{CO}_2$  concentration and relative humidity. However, fanning was used only to lower nest temperature and to meet the colony's needs for gas exchange; high relative humidity levels did not elicit fanning.

Colonies responded to high  $\text{CO}_2$  levels and high temperatures in a similar way: as soon as stimulus intensity increased, individual bees started fanning their wings. The number of fanning bees increased with stimulus intensity. The finding of an active down-regulation of high  $\text{CO}_2$  concentrations in bumblebee colonies is in close agreement with findings on honeybees (Seeley 1974). Like high temperatures which disrupt metamorphosis and lower eclosion rate (Himmer 1927; Heinrich 1979; Vogt 1986b), high levels of  $\text{CO}_2$  may be detrimental to the colony. They have been reported to change acidity

of the haemolymph and hormone titres (Röseler & Röseler 1984; Nicolas & Sillans 1989). Furthermore, and maybe more importantly, since  $\text{CO}_2$  production and oxygen depletion are directly linked, the  $\text{CO}_2$  concentration in subterranean dwellings is a reliable indicator of oxygen availability. Insects are unable to measure oxygen concentrations; in honeybees, oxygen depletion alone evokes no fanning response (Seeley 1974). However, as has been shown for ants (Kleineidam & Tautz 1996; Kleineidam et al. 2000), social insects are able to measure absolute  $\text{CO}_2$  concentrations with specialized antennal sensilla (Lacher 1964; Dumpert 1972; Ågren & Hallberg 1996). A rapid fanning response to increasing  $\text{CO}_2$  concentrations thus ensures sufficient oxygen supplies for the colony. When exposed to high  $\text{CO}_2$  concentrations, bumblebee workers eject larvae from their colony. When poor gas exchange properties cannot be compensated for by nest ventilation, colonies thus reduce the metabolic mass in their nest cavity to decrease  $\text{CO}_2$  levels and increase oxygen availability (Kukuk et al. 1997).

In our experiments, the intensity of the fanning response to  $\text{CO}_2$  concentrations of about 3.2% corresponded to the intensity of the colony response to a temperature stress of about  $30^\circ\text{C}$  (Fig. 2). Bumblebee colonies respond more strongly when temperatures increase further: Vogt 1986a() reported up to 60% of a colony's workers fanning when ambient temperatures rose above  $35^\circ\text{C}$ , a temperature condition that is known to have lethal effects on the brood (Himmer 1927). Thus, the colony response suggests that concentrations of 3%  $\text{CO}_2$  present a moderate stress level to the colony.

We found no information on  $\text{CO}_2$  concentrations in natural nests of bumblebees in the literature. Our measurement of  $\text{CO}_2$  concentration in a field nest showed that this did not exceed 1.5% even though the colony was large and the cavity had a long, narrow entrance tunnel. Presumably, under natural conditions down-regulation of  $\text{CO}_2$  through fanning is effective and even a few fanning individuals can create a sufficient ventilation effect.

The field colony maintained its brood at a stable temperature of  $32^\circ\text{C}$ . At first glance this seems to contradict the finding that workers in the laboratory started fanning at lower temperatures. However, in our laboratory experiments we measured air temperature rather than brood temperature, which is known to be about  $2^\circ\text{C}$  higher (Vogt 1986b). Furthermore, the fact that the colonies experienced a rapid increase in temperature may have contributed to an early colony response.

An increase in relative humidity did not elicit a fanning response. Obviously, high humidity levels do not compromise colony development and colonies therefore do not invest valuable workforce into down-regulating them. Whether relative humidity is up-regulated by colonies living in an arid habitat to avoid desiccation of the brood remains to be examined. Honeybees have been reported to down-regulate high humidity (Winston 1987). To secure winter survival, honeybees need to collect large quantities of nectar and transfer it into storable honey by evaporating water. This concentration process is promoted by low relative humidity in the nest

and strong nest ventilation by fanning (Reinhardt 1939). Fanning to concentrate nectar keeps CO<sub>2</sub> concentrations below 1% during summer (Simpson 1961; Seeley 1974). During winter, in swarms and in small colonies, CO<sub>2</sub> concentrations of 2–6% have been measured (Simpson 1961; Nagy & Stallone 1976) and fanning in winter seems to occur in order to control respiratory gases (Simpson 1961).

### Influence of Colony Size

Under natural conditions the requirements of a bumblebee colony in controlling the climatic conditions inside the nest will change with colony size. Small colonies face the challenge of heating their brood nest, while large colonies are likely to experience both overheating and insufficient nest ventilation caused by crowding. However, depending on the location of their nests, high temperatures caused by external heat may be experienced by both small and large colonies. Thus, the temperature increase up to 30°C experienced by our laboratory colonies may well represent a natural stress situation.

Social homeostasis, the control of the physical environment of a colony through cooperative activities, is a phenomenon found in most species of social insects. In many cases, the degree of stability achieved increases with colony size. Honeybee colonies containing 35 000 bees undergo smaller CO<sub>2</sub> fluctuations than colonies containing 10 000 bees (Seeley 1974). In species with annual colonies, the highest precision in regulating brood temperature is usually reached in the middle of the colony cycle when colonies have large contingents of workers (Seeley & Heinrich 1981). The mechanisms underlying this increase in stability are not well understood.

Colonies can increase the stability of a regulated parameter by adjusting the intensity of the response and decreasing the delay in their response. In our study, the proportion of the total workforce allocated to nest ventilation did not change with colony size; a colony responded to a stimulus intensity with more fanners when large than when small. In addition, when large, colonies responded to increasing temperatures faster. Previous studies have explained strong fluctuations of brood temperature in small colonies by the fact that small colonies have fewer provisions and thus 'run low on fuel' more often than large colonies, or that small colonies need to invest more heavily in foraging or brood care and can thus spare fewer individuals (Seeley & Heinrich 1981). These parameters may influence the control of nest climate under natural conditions. However, since our colonies had sufficient nectar supplies and all workers were confined to the nest, small colonies could have easily allocated more than 30% of their workforce to fanning. Apparently only a certain percentage of the colony workforce is susceptible to the task-related stimulus intensity at one time.

Our results raise questions about the rules governing the behaviour of the individual and the degree of flexibility in individual behaviour. Nest climate is controlled by a colony-level response, which is the sum of individual

worker responses. Understanding the functioning of the whole requires an understanding of how, why, when and to what the individuals respond. In this context, questions concerning individual response thresholds (Detrain et al. 1999), feedback loops and amplifying phenomena (Turner 2000), and the role of learning in task efficiency, remain to be investigated. In our experiments, larger colonies were also more experienced colonies. Certain fanning positions in the nest may be more effective than others (Southwick & Moritz 1987) and learning of effective positions by single individuals may influence the overall efficiency of the colony response. Thus, the next step in understanding the collective response to nest climate perturbations will involve an investigation of the rules governing individual behaviour and the mechanisms that integrate individual behaviours into a collective response.

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