

The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self reinforcement in fanning response

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Interindividual variability in response to environmental stimuli is believed to have a major impact on collective behaviors in social insects. The present study presents a detailed investigation of the variability in individual fanning behavior underlying the collective control of nest climate in bumblebee (*Bombus terrestris*) colonies. Four colonies were repeatedly exposed to increasing temperature and CO₂ levels. The response threshold of each worker (defined as the mean stimulus intensity at which a worker responded by fanning) was determined. Temperature response thresholds of 118 workers and CO₂ response thresholds of 88 workers were analyzed. Workers differed in their response thresholds. Some consistently responded to low stimulus intensities, others consistently responded to high stimulus intensities. No consistent correlation between temperature and CO₂ thresholds was found within individuals. Response thresholds of fanning bees decreased over successive trials, providing empirical support for the idea of specialization through individual threshold reinforcement. In addition to variability in individual response thresholds, workers of a colony differed in two other parameters of responsiveness: response probability (the probability of responding to a stimulus once it exceeded an individual's response threshold) and response duration (the persistency with which fanning was performed once an individual responded). The results of the present study suggest that response threshold, response probability and response duration are important independent parameters of individual responsiveness in the collective control of nest climate in bumblebee colonies. *Key words*: division of labor, nest climate, reinforcement, response thresholds, self-organization. [*Behav Ecol* 15:120–128 (2004)]

An insect society faces the same challenges to survival that confront a single organism—foraging, defense, and protection against climatic extremes in an unpredictable environment. A colony's collective solutions to these challenges have prompted a view of a society as a functional unit, capable of adaptive decision making and coordinated behavior. In contrast to a multicellular organism, the colony lacks mechanisms such as a nervous system that physically integrate its subunits. Thus, the question arises: which analogous mechanisms coordinate the activities of the colony's members?

One of the main features of colony organization is division of labor, whereby each member of the colony specializes (permanently or temporarily) in a subset of all tasks required for successful group functioning. An important aspect of division of labor is its plasticity: workers switch between tasks in response to external changes and internal perturbations. Division of labor has been studied in great detail for nearly a century, the main focus being on its description and functional significance (Oster and Wilson, 1978; Seeley, 1982; Wheeler, 1928). Within the past two decades, the focus has shifted from the ultimate causes to the proximate mechanisms underlying this important feature of colony organization (for review, see Beshers et al., 1999; Robinson, 1992). Various models have been presented to account for division of labor in social insects. They are based on behavioral rules that

can account for specialization and flexibility and attempt to link patterns of task performance at the individual and the colony level. All models are based on the idea that tasks are performed in response to specific stimuli. Some models assume that workers of a colony are initially the same but encounter different stimuli environments, leading to differences in behavior and resulting in division of labor (for review, see Tofts and Franks, 1992). Most models, however, are based on the idea that it is interindividual variability in the response of workers to their environment that gives rise to division of labor. The models demonstrate that relatively small interindividual variability in response thresholds may cause large interindividual differences in task performance and division of labor results as emergent property of the system (Fewell and Page, 1999; Page and Mitchell, 1991, 1998). Variability between workers can arise from numerous sources, for example, genetic, neural, hormonal, experience, and interactions with the environment or other workers (for review of models, see Beshers and Fewell, 2001).

The idea that division of labor is based on caste-specific differences in sensitivity to task-associated stimuli first appeared in the 1970s in Wilson's (1976) work on ants. Soon, others followed and provided data on hormonally (Robinson, 1987a,b; Robinson et al., 1989) or genetically influenced response thresholds in honey bees (Calderone and Page, 1988, 1991; Frumhoff and Baker, 1988; Robinson and Page, 1988). The role of response thresholds in division of labor has also been discussed in wasps (Jeanne et al., 1988) and ants (Calabi and Rosengaus, 1988; Detrain and Pasteels, 1991, 1992). Several investigators demonstrated behavioral differences between groups of workers from different patrilines or

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worker castes (Detrain and Pasteels, 1991, 1992; Wilson, 1984, 1985). In honey bees, dance thresholds have been shown to differ between individuals (Seeley, 1994), and a correlation has been found between the threshold concentration of sucrose solution for extending the proboscis in honey bees and forager preferences for water, nectar, or pollen (Page et al., 1998; Pankiw and Page, 1999, 2000).

However, studies that quantify stimulus intensities and the corresponding responses of all colony members involved in a collective response are lacking (Beshers and Fewell, 2001; Beshers et al., 1999). Such studies are necessary to measure the distribution of response thresholds within a colony, which has been shown in the models to have great impact on the colony response. Repeated measurement of individual responses within the colony context to known stimulus intensities are further needed to understand whether and how experience influences individual response thresholds. Such experiments require controlling or at least being able to measure the intensity of the stimulus workers are responsive to. This is extremely difficult for most tasks.

In this article, I analyze the response of individual bumblebee workers in the context of nest climate control. Bumblebee workers are able to manipulate nest climate by actively increasing air circulation through the nest and, in this way, lower temperature and CO₂ levels in their colony (Vogt, 1986a; Weidenmüller et al., 2002). Control of nest climate is an example of a flexible colony level response that is graded and highly adaptive. It is an ideal study system to investigate interindividual variability in responsiveness, because temperature/CO₂ intensity and fanning behavior present simple, measurable, and causally linked stimulus-response pairs. By examining the fanning behavior of workers, important questions concerning individual response and interindividual variability in responsiveness can be addressed. I determine whether workers differ in their response to a stimulus and how response thresholds are distributed among the workers of a colony. Further, I address the question whether response thresholds are fixed or variable with experience and how response thresholds to different stimuli are arranged within an individual.

METHODS

I studied interindividual variability in the fanning response of bumblebee workers. To this end, I analyzed the fanning behavior of all workers from four colonies that were repeatedly exposed to increasing temperature and CO₂ levels.

Colonies

Bumblebee colonies (*Bombus terrestris*) were obtained from a commercial breeder and housed in Plexiglas-covered nest-boxes. The nest-boxes (14 × 14 × 10 cm) were divided into an upper compartment containing the nest and a lower compartment that could be opened and closed from one side for manipulations. The two compartments were separated by a wire mesh. The nest-boxes had three screened ventilation holes (diam 1.5 cm) and connected via a 60-cm Plexiglas tunnel (diam 2 cm) to a foraging chamber (30 × 40 × 30 cm) where sugar solution was provided ad libitum. I fed pollen directly into the nest. Colonies were kept at a room temperature of 22°C under natural day/night cycle. Every second day, all newly emerged workers were marked with numbered plastic tags (Opalithplättchen) so that they were of known age and could be recognized and analyzed individually.

Measurement of nest climate

I measured nest air temperature by using a temperature probe (Vaisala HMP 36B; accuracy = ±0.2°C) inserted into the

upper compartment of the nest-box, 4 cm above the wire mesh. The CO₂ concentration was measured by IR-absorption with a gas sensor type GS 20 ED/CO₂ (Sensor Devices; accuracy = ±0.1%). Air from the nest-box was drawn into the gas sensor by an open loop circulation, driven by a 12-V membrane pump (Thomas Industries) at a flow rate of 1.5 l/min. Two plastic tube openings in the nest-box, covered by fine wire mesh, allowed exchange of air in the circulating air current.

Manipulation of nest climate and data collection

I studied the fanning response of workers from four colonies (colonies S, T, W, and X). Each colony was alternately exposed to an increase in temperature or CO₂. Colonies were exposed to an increase in temperature or CO₂ 9 to 16 times over a period of several weeks, resulting in a total of 108 trials (50 temperature, 58 CO₂). Worker populations of the tested colonies ranged from 10 to 119 workers.

I increased nest air temperature by regulating a commercially available IR lamp (150 W) positioned 70 cm above the nest. Following a fixed, feedback controlled regime, air in the nest-box was gradually heated from 24°C to 30°C. Because colonies were repeatedly exposed to manipulations of their nest climate, I did not expose them to temperatures above 30°C to avoid damage to the brood. I increased CO₂ by successive closing of the three ventilation holes (for further details of experiments, see Weidenmüller et al., 2002).

Experiments were performed daily from 1200–1500 h. Before an experiment started, I closed the entrance to the foraging chamber with a wire mesh, confining all bumblebees to the nest-box and entrance tunnel. An experiment lasted 75 min, divided into 15 observation periods of 5 min each. Each experiment started with 15 min (three observation periods) of observation on the undisturbed colony. Nest climate was then manipulated during 45 min (nine observation periods). Either temperature or CO₂ concentration was experimentally increased while the other parameter remained constant. After 45 min of manipulation, the lamps were turned off or the ventilation holes were opened and the colony was observed for another 15 min (three observation periods) while stimulus intensities slowly returned to normal.

During an experiment the colony was continuously observed. At the beginning of each 5-min observation period, I noted temperature and CO₂ levels. Whenever a worker started fanning, defined as steady fanning with spread wings while standing still for at least 10 s, the momentary stimulus intensity (degrees Celsius or percentage CO₂ at onset of fanning) was recorded. For every observation period, I recorded whether a worker was still fanning, had stopped, or had restarted fanning. Stimulus intensity was noted only at first onset of fanning for every individual.

After experiments ended, colonies were deep-frozen and worker size was measured. Maximal head width and length of the left wing were determined to the nearest micrometer by using a micromanipulation table and a stereomicroscope at 50× magnification (Wild M3Z).

Data analysis

Fanning parameters

Only workers that experienced at least five trials per parameter (temperature or CO₂) were included in the analysis. I analyzed the following parameters of individual fanning behavior: (1) first is response threshold. Based on all trials in which a worker fanned, I calculated her response threshold as the mean stimulus intensity at onset of fanning. Response thresholds were calculated only for workers that

responded in at least three trials. (2) Second is response duration. Based on all trials in which a worker fanned, I calculated her response duration in two ways. First, for every worker I calculated the mean number of observation periods (5-min blocks, see above) she fanned in per trial. Second, I normalized response duration data for remaining time (time after a worker had started fanning until stimulus intensity decreased again) and calculated the percentage of remaining observation periods fanned in (normalized value). Response duration values were calculated only for workers that responded in at least three trials. (3) Third is response probability. Based on all trials a worker experienced, I calculated her response probability as the proportion of trials in which she fanned.

Workers that showed fanning behavior before stimulus intensity increased (during the first 15 min) were not included into the analysis.

Influence of experience

To test whether individual response thresholds were fixed or changed over time, I looked for a change in temperature response threshold over time. I analyzed only temperature trials because the course of the temperature increase followed a regular feedback controlled pattern and was highly consistent across trials, whereas CO₂ concentrations could sometimes drop during measurements as a result of massive fanning. I analyzed fanning thresholds of workers from colonies X and W, because individual responses were documented without interruption only in these two colonies. Only thresholds of workers that responded in at least six trials were analyzed. For every trial in which a worker fanned, I calculated the difference between her response threshold in this trial and her mean response threshold across all trials. I ordered the calculated values successively (skipping non-responded trials), pooled data of workers from a colony, and analyzed the mean deviation in first, second, etc. responded trial. I analyzed individual response duration and normalized response duration data in the same way, again calculating for every worker the deviation from mean response duration for every responded trial.

Size

To test whether size influenced any of the analyzed parameters, I plotted each measure of individual fanning performance (response threshold, response probability, and response duration) against size.

Statistical analysis

I tested for differences between colonies with a one-way ANOVA if data were shown not to differ from normality (Shapiro-Wilks' *W* test); otherwise I used the Kruskal-Wallis test.

Correlations between two parameters were tested by using a nonparametric test for association (Spearman's rank correlation coefficient). Correlations were performed separately for each colony. Unless noted otherwise, descriptive statistics are presented as mean \pm SD. To ensure an overall type I error rate of 0.05 or less, I used an α level of $p < .01$ as rejection criterion (multiple test correction).

RESULTS

Differences in fanning behavior among the workers of a colony

Colonies responded to an increase in stimulus intensity with an increasing number of fanning workers (Figure 1A). I

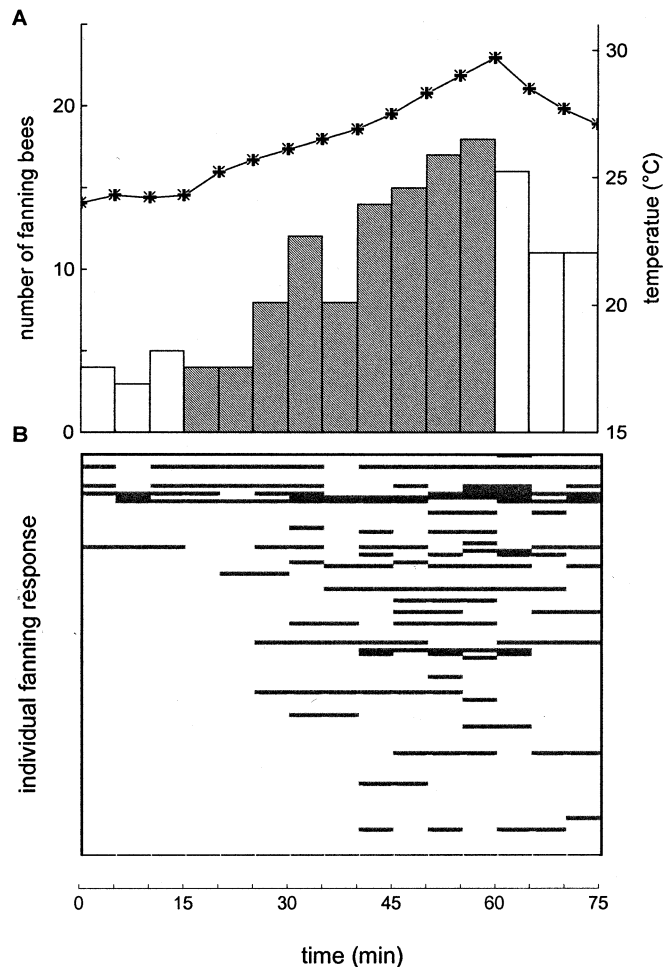


Figure 1
Example of the fanning response of one colony to an increase in temperature. (a) Colony level response: number of fanning workers per 5-min observation period; line denotes temperature increase; gray bars denote times when heating lamp was on. (b) Individual fanning responses; black lines denote fanning activity.

analyzed the responses of individual workers that constitute this collective response, shown in an example in Figure 1B. A total of 303 workers from four colonies experienced an increase in temperature at least five times; 326 workers experienced an increase in CO₂ at least five times. I included only these workers in further analysis. Workers differed in their responsiveness. Around 40% of the tested workers never showed fanning behavior. Some workers responded in three or more trials of each parameter (general fanners, 18%), others responded in three or more trials of one parameter and in less than three trials of the other (specific fanners, 8%), and a small percentage responded exclusively to one of the two parameters (exclusive fanners, 3%) (Table 1).

Response thresholds

I analyzed temperature response thresholds of 118 workers and CO₂ response thresholds of 88 workers. As an example, Figure 2 shows the individual response thresholds to temperature and CO₂ of workers from one of the four tested colonies. Workers differed in their response thresholds, defined as the mean stimulus intensity across responded trials at onset of fanning. Some workers started fanning when stimulus intensity was still comparatively low; others

Table 1
Number of trials workers experienced, number of trials workers responded in with fanning, and categorized fanners in the four tested colonies

	Colony S		Colony T		Colony X		Colony W	
	Temp	CO ₂	Temp	CO ₂	Temp	CO ₂	Temp	CO ₂
No. of workers experiencing five or more trials	84	84	62	85	85	85	72	72
Maximum no. trials experienced	16	11	9	11	12	13	13	14
No. of trials fanned in (median)	6.0	5.0	4.0	4.0	5.0	4.0	4.5	4.0
Workers fanning three or more trials (%)	39.8	20.2	17.7	18.8	38.1	32.9	54.1	36.1
General fanners (%)	14.5	14.3	9.7	7.1	20.5	23.5	33.3	33.3
Specific fanners (%)	15.7	4.7	6.4	8.2	10.5	8.2	13.9	1.4
Exclusive fanners (%)	9.6	1.2	1.6	3.5	7.1	1.2	6.9	1.4

General fanners indicate workers that responded three or more temperature and CO₂ trials; specific fanners, workers that responded in three or more trials of either parameter and in less than three trials of the other; and exclusive fanners, workers that responded exclusively to one parameter.

consistently started fanning at high stimulus intensities. Inter-individual differences were apparent for both temperature and CO₂ thresholds. Within the general fanners, that is, those workers that repeatedly responded to both parameters, a low temperature threshold did not necessarily imply a low CO₂ threshold or vice versa. A correlation between temperature threshold and CO₂ threshold was found in only one out of the four colonies (colony T: $r_s = .88$, $n = 6$; $p < .01$; colony S: $r_s = .59$, $n = 12$; colony W: $r_s = .22$, $n = 24$; colony X: $r_s = .09$, $n = 20$; all: $p = ns$; Spearman's rank correlation). Note that the colonies that did not show the correlation had a larger sample size. Because of the sample sizes and especially because of the small correlation coefficients, the statistical power of the tests applied is low for most colonies (colony T: 0.81; colony S: 0.53; colony W: 0.18; colony X: 0.06).

Figure 3 shows the distributions of thresholds within colonies. The distribution did not differ from normality ($p > .2$, Shapiro-Wilks' W test). The mean response threshold for temperature within colonies ranged from 27.7°C–28.7°C. The mean response threshold for CO₂ within colonies ranged from 1.6–2.5%.

Colonies differed in their response thresholds (ANOVA: $F_{temp} = 20.3$, $df = 3$, $p < .001$; $F_{CO_2} = 29.4$, $df = 3$, $p < .001$).

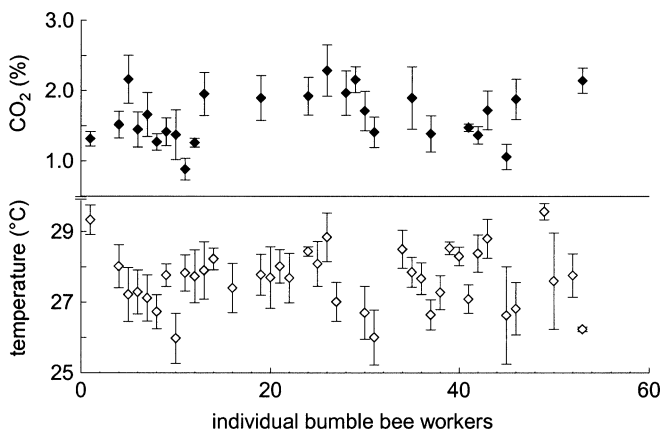


Figure 2
 Example of individual response thresholds (mean \pm SE) for CO₂ and temperature of workers from one of the tested colonies (colony W). On the x-axis, workers are plotted in order of their emergence.

The mean response threshold for temperature was significantly higher in colonies S and T than in colonies X and W, respectively ($p < .001$ for all pairs, LSD test). No difference was found between colonies S and T and between colonies X and W ($p > .3$ for both pairs, LSD test). The mean response threshold for CO₂ differed significantly among all colonies

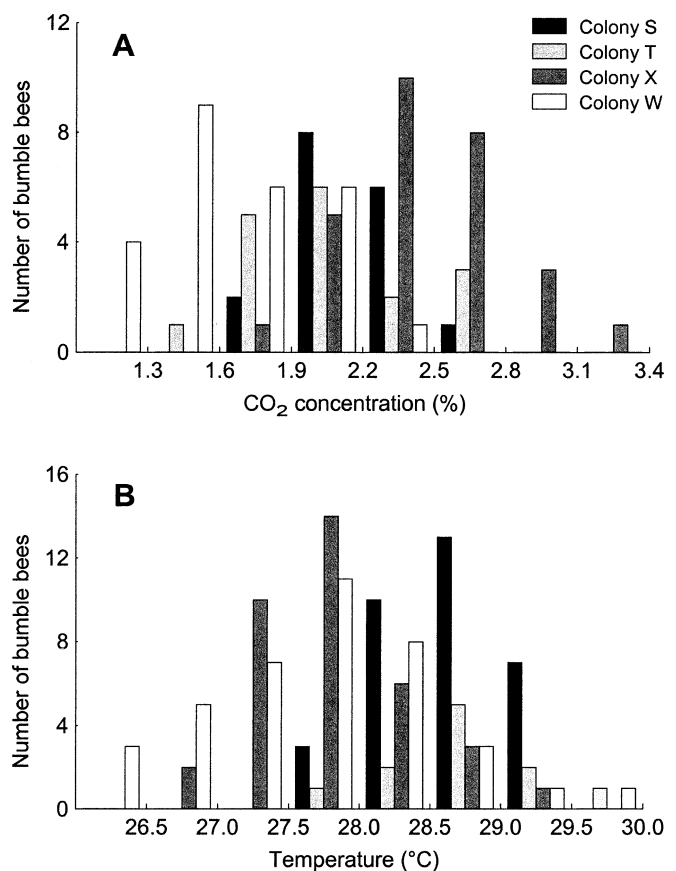


Figure 3
 Distribution of individual response thresholds in four colonies. (a) CO₂ response thresholds; (b) temperature response thresholds. Data are presented in bins of 0.3% CO₂ and 0.5°C.

Table 2
Response probability and fanning activity of workers in the four tested colonies

	Colony S		Colony T		Colony X		Colony W	
	Temp	CO ₂	Temp	CO ₂	Temp	CO ₂	Temp	CO ₂
Response probability								
% (median)	45.5	50	44.4	36.4	50.0	41.0	50.0	34.5
25–75% quartile	33.3–62.5	36.4–63.6	33.3–55.5	27.3–50.0	36.4–62.5	30.8–57.8	36.4–62.5	30.0–42.9
Fanning activity (mean ± SD)	2.0 ± 0.5	3.5 ± 0.2	2.0 ± 0.2	2.2 ± 0.2	2.6 ± 0.2	3.2 ± 0.2	2.3 ± 0.1	2.6 ± 0.1
Normalized fanning activity								
% (median)	61.7	70.1	73.2	50	67.0	60.3	61.5	51.9
25–75% quartile	52.1–67.5	66.1–77.2	64.0–80.1	43.8–67.8	56.8–71.6	51.4–70.8	54.5–74.7	44.8–59.7

Response probability was calculated as the proportion of experienced trials a worker fanned in. Fanning activity was calculated in two ways: (1) mean number of observation periods a worker fanned in per trial (fanning activity), and (2) the percentage of remaining observation periods a worker fanned in after she had started fanning (normalized fanning activity).

($p < .01$ for all pairs, LSD test) except between colony S and T ($p = .33$, LSD test). Thus, besides interindividual variance in response thresholds my data show intercolonial variance. Because of the differences in thresholds, data were not pooled and correlations (see below) were performed separately for each colony.

Response probability

Differences in individual responsiveness were not fully described by response thresholds. Workers varied not only in the mean stimulus level that elicited a fanning response but also in the probability with which they responded to the stimulus across experienced trials. I therefore analyzed a second parameter describing individual responsiveness: response probability. Response probability of all workers varied from 0–100%.

Within colonies, the distribution of response probabilities was biased toward low probabilities in five out of eight cases (Shapiro-Wilks' W test). The median ranged from 0–33% for temperature and from 0–19% for CO₂. Response probabilities of workers that fanned in at least three trials and, thus, could be assigned response thresholds, varied from 19–100%. The median response probability of these fanners ranged from 45–50% for temperature and was usually lower for CO₂, ranging from 34–50% (Table 2).

Colonies did not differ significantly in response probability of their fanners during temperature trials ($H_{temp} = 1.16$, $df = 3$, $p = .76$; $H_{CO_2} = 6.51$, $df = 3$; $p = .09$; Kruskal-Wallis test).

Response duration

Workers of a colony differed not only in *when* and *how often* they responded to an increase in temperature or CO₂, they also differed in *how* they responded. Because observations were plotted on a 5-min grid (see Methods), my data give only a coarse representation of individual fanning duration. However, interindividual differences are evident. Some workers fanned on average in five observation blocks (equaling 25 min), whereas others fanned in only one or two observation blocks (5–10 min).

Workers with low thresholds started fanning earlier and thus had more time left until stimulus intensity decreased again compared with workers with high thresholds. To exclude the influence of variable response thresholds on response duration data, normalized response duration data were analyzed. Normalized response duration data, that is, the proportion of remaining manipulation time a worker fanned

once she had started, revealed interindividual differences. Some workers stopped soon after they had started fanning or fanned intermittently, whereas others continuously fanned until stimulus intensity decreased. The median normalized response duration of fanners ranged from 50–73% (Table 2).

The distribution of response duration within colonies was not significantly different from normality (Shapiro-Wilks' W test) except in colony T for CO₂. Colonies did not differ in the fanning duration (normalized) of their workers under increased temperature levels ($H_{temp} = 6.20$, $df = 3$, $p = .10$; Kruskal-Wallis test). Colonies differed in fanning duration of their workers under increased CO₂ concentrations ($H_{CO_2} = 18.42$, $df = 3$, $p < .001$; Kruskal-Wallis test).

Independent parameters

The colony response to an increase in temperature or CO₂ is not merely the result of random individual responses but is based on interindividual differences in at least three parameters of fanning behavior: response threshold, response probability, and response duration. I further analyzed these parameters in order to find out whether they are independent or linked.

Except in one colony, no correlation between individual response threshold and response probability was found. This was true for temperature and for CO₂. Only in colony X did workers with low temperature thresholds have a higher probability of responding than workers with high thresholds ($r_s = -.43$, $p < .01$; Spearman's rank correlation).

There was a correlation between the response threshold of a worker and the duration of her fanning when exposed to an increase in temperature, with the exception of colony S (colony T: $r_s = -.82$; colony X: $r_s = -.77$; colony W: $r_s = -.56$, $p < .001$ for all colonies). As mentioned above, this is not surprising because those workers that had lower thresholds started fanning earlier and had more time left until stimulus intensity decreased again. Workers with low thresholds tended to spend more time fanning than did workers with high thresholds. For CO₂, no correlation between response threshold and response duration was found. When response thresholds were plotted against normalized response duration, no correlation was found for either parameter.

A correlation between response probability and response duration when temperature increased was found in one of the four colonies (colony W: $r_s = .44$; $p < .01$). In this colony, workers with higher response probability tended to spend more time fanning under increased temperatures than did workers with low response probability. For CO₂, this

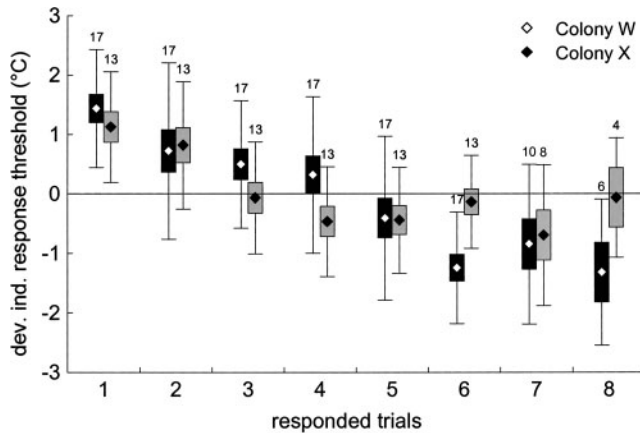


Figure 4

Reinforcement of individual response thresholds during the first six to eight temperature trials a worker fanned in (colony W: $r_s = -.58$; colony X: $r_s = -.44$; both $p < .001$). For every trial a worker fanned in, the difference between stimulus intensity first responded at in this trial and mean individual response threshold across responded trials was calculated. The individual response values were ordered successively (skipping nonresponded trials). Diamonds denote means, boxes denote standard error, whiskers denote standard deviation.

correlation was also found in one of the four colonies (colony S: $r_s = .52$, $p < .05$; colony X: $r_s = .46$; $p < .01$). When probability was plotted against normalized response duration, no correlation between the two parameters was found.

Influence of experience

An important question concerning response thresholds is whether they are fixed or change with experience. Figure 4 shows the deviation from individual mean temperature response threshold over the first six to eight trials in which each worker fanned. Temperature thresholds decreased from trial to trial in both colonies analyzed (colony W: $r_s = -.58$; colony X: $r_s = -.44$; both: $p < .001$).

The duration of fanning increased from trial to trial (colony W: $r_s = .46$; colony X: $r_s = .30$; both: $p < .001$). This increase seems to be caused by the decrease in temperature thresholds. Normalized fanning duration in temperature trials did not change; workers spent a constant proportion of their time fanning.

Size

Workers varied in size from 2.9–4.8-mm head width (3.7 ± 0.3) and 6.7–13.3-mm wing length (10.1 ± 1.0). Workers that fanned three or more times did not differ in size from those that never fanned or fanned less than three times ($p > .01$ for all colonies, t test). Within the fanners, body size influenced none of the parameters of individual fanning behavior (response threshold, response probability, response duration, and normalized response duration) ($p > .01$ for all colonies).

DISCUSSION

The aim of the present study was to analyze a collective behavior, the control of nest climate in bumblebee colonies, at the level of the individual colony members, focusing on the question of whether workers of a colony show consistent responses to parameters of nest climate and how they vary in their response. The results of my study demonstrate that bumblebees vary in at least three parameters of their fanning

response: response threshold, response probability, and response duration. Thus, to accurately describe individual behavior, we need to consider not only individual thresholds but also individual responsiveness, which is measured by the three aforementioned parameters. We can now address the question of how these three parameters of individual behavior and the differences between individuals give rise to the collective response seen at the colony level.

Interindividual variability in fanning response

Workers that repeatedly responded to a manipulation of nest climate differed in their response thresholds, that is, the mean stimulus intensity that elicited fanning behavior. Some consistently responded at low stimulus intensities; others consistently started fanning when stimulus intensities were already quite high. Moreover, some fanned only when temperature increased; others fanned only during CO₂ manipulations.

A small proportion of a colony's workers had relatively low response thresholds. At low stimulus intensities, only these low-threshold bees will respond. Under natural conditions, their fanning will often suffice to reduce stimulus intensities, thus leaving the majority of the work force to other tasks. If, however, stimulus intensity increases further and presents a danger to the colony, the number of workers whose response threshold is exceeded increases dramatically and the colony responds with massive fanning. The distribution of individual response thresholds underlies the graded colony response to increasing stimulus intensities (Weidenmüller et al., 2002) and allows the close matching of supply of fanning workers to the need for fanners. In principle, a graded colony response also could emerge from individuals with variable response thresholds (within a certain stimulus range) from trial to trial. The advantages of relatively low variation in individual responses and consistent interindividual threshold differences will be discussed below.

A recent article on fanning in bumblebee colonies (O'Donnell and Foster, 2001) also reports variability in fanning behavior among workers of a colony. Although the investigators did not differentiate between temperature and CO₂ fanners and scanned unmanipulated and free flying colonies only every 10 min, they showed that workers fanned at different temperatures.

In my study, the mean of the threshold distribution within colonies ranged from 27.7°C–28.7°C air temperature and 1.6–2.5% CO₂ concentration. To avoid temperatures above 30°C, which would impair brood development (Heinrich, 1979; Himmer, 1927; Vogt, 1986b), the colony needs to respond strongly even at temperatures below 30°C. This is achieved by a large number of workers with response thresholds around 28°C.

The distribution of thresholds for all tasks that need to be performed in a colony (colony threshold distribution *sensu* Beshers et al., 1999) should affect patterns of behavioral specialization, that is, which tasks are likely to be found in a worker's repertoire. My experiments allowed the measurement of two thresholds within an individual: temperature and CO₂ response thresholds. Linked thresholds for temperature and CO₂ should result in general fanning specialists; that is, a certain subset of workers should respond with fanning to low stimulus intensities irrespective of whether the colony was experiencing heat stress or insufficient oxygen supply. However, I found no consistent correlation between the thresholds for the two parameters temperature and CO₂. Workers appear to be "stimulus specialists" rather than "task specialists." Independent thresholds for temperature and CO₂ may be of biological significance when the colony faces

trade-offs in regulating the two parameters. Furthermore, stimulus specialists may be of advantage when different nest climate parameters pose different requirements, such as adopting certain fanning positions in the nest, and when the efficiency in task performance increases with experience.

Interindividual variability in response threshold alone is not sufficient to accurately describe the variability in worker responsiveness. My study has also revealed variability in worker response probability. Nearly half of the workers never responded to a manipulation of nest climate. These workers either had thresholds higher than the tested stimulus maxima or were completely unresponsive. However, even within the group of fanners, some workers fanned nearly every time they were exposed to a stimulus intensity exceeding their individual response threshold, whereas others fanned only rarely. This was the case even though all workers were confined to the nest during manipulations and were therefore exposed to the increase in stimulus intensity.

Response threshold and response probability were two independent parameters of individual responsiveness. Note that this is an important difference to response threshold models (for review, see Beshers and Fewell, 2001), in which response probability and response threshold are linked per definition: an individual's response probability is a function of its response threshold and the stimulus intensity. Describing the fanning behavior of individual bumblebee workers as accurately as possible for the stimulus intensities applied in my experiments, I found no dependency between the two parameters.

What is the significance of interindividual variability in response probability for the colony? A response probability below 100% distributes the task of nest climate control more broadly among the workers of a colony: the group of fanners will be composed of different individuals every time the colony experiences climatic stress conditions. Thus, decreasing the probability of response decreases the importance of a single individual for the fulfillment of a certain task. Furthermore, and maybe more importantly, if workers learn certain tasks and increase their efficiency by doing so, as is commonly assumed (Oster and Wilson, 1978), intermediate response probabilities "train" more workers, this way increasing the overall efficiency and reliability of the colony response. Thus, variable response probabilities enhance flexibility in that a reserve of workers becomes trained to efficiently perform different tasks.

Workers differed in a third parameter, namely, in how persistently they responded to a given stimulus intensity. Although some workers fanned until stimulus intensity decreased, others showed only very short or intermittent fanning behavior. Workers of all colonies on average fanned during 60% of the time they were exposed to a stimulus exceeding their threshold. Interrupted fanning may serve the flexibility of the colony; workers that frequently resample the stimulus they are responding to or other task-related stimuli remain responsive to changes and available for other urgent tasks.

Specialization and the influence of experience

Different terms have been used in the literature to describe interindividual variability in task performance. The term "specialist" usually describes workers that perform a subset of tasks more frequently than their nest mates (Oster and Wilson, 1978). "Elitism" describes the existence of individuals who are exceptionally active or entrepreneurial within age-size cohorts and "do almost all the work" (Plowright and Plowright, 1988: 420), or show an unusually high frequency of task performance, either as a specialist or a generalist

(Jeanne, 1999; Oster and Wilson, 1978). Both terms have been used as descriptors, without reference to any underlying mechanism or social process (Robson and Traniello, 1999). Considering the parameters introduced in this study, under natural conditions (i.e., conditions in which fanning will have the effect of decreasing stimulus intensity; note that this effect was counterbalanced in my experiments) the fanning specialists of a colony should be those workers with low response thresholds and high response probabilities, whereas elite workers should be workers that additionally show exceptionally high response durations.

Specialization is believed to be a key element of colony organization that increases the overall colony efficiency and thus ultimately the ecological success of social insects (Oster and Wilson, 1978). Different mechanisms have been discussed that may sharpen the differentiation between specialists and the remaining work force. In an extension of the response threshold model for division of labor, Theraulaz et al. (1998) included learning in form of self-reinforcement: performing a task induces a decrease in the corresponding threshold, not performing the task induces an increase; this combined reinforcement process leads to the emergence of specialized workers. However, so far no data documented self-reinforcement of thresholds through experience.

The results of this study suggest that in the control of nest climate, reinforcement may play an important role in specialization. Response thresholds of those workers that repeatedly fanned across trials decreased over time. Under natural conditions, low-threshold bees will fan more often than will high-threshold bees, because they will often reduce stimulus intensities and thus exclude higher-threshold bees from the task of fanning. Therefore, the low-threshold bees are most likely to experience a decrease in their response threshold, resulting in an increase in variance of thresholds at the colony level. Reinforced thresholds may also explain the finding of an earlier study that experienced colonies respond faster to an increase in temperature than do inexperienced colonies (Weidenmüller et al., 2002). It remains unclear whether reinforcement of thresholds occurs only during the first times a task is fulfilled and whether those individuals that perform a task only rarely experience negative reinforcement, as proposed in the reinforcement model (Theraulaz et al., 1998). Also, the proximate mechanisms behind threshold reinforcement remain to be investigated.

In addition to changes in response threshold with experience, a second mechanism sharpening the differentiation between specialists and the remaining work force in a colony may be an increase in efficiency with experience, for example, because individuals learn to perform a task (Dukas and Visscher, 1994). Learning and increase in task efficiency have often been considered as the main reason for the efficiency of division of labor (Jeanne, 1986; Oster and Wilson, 1978; Seeley 1982). My data suggest that control of nest climate will prove a good system to study the increase in task efficiency with experience. The two parameters, temperature and CO₂, may require different fanning responses: fanning on the brood may locally increase evaporative cooling, whereas fanning in the entrance tunnel may increase general air exchange (Southwick and Moritz, 1987). The efficiency of an individual worker may increase with experience because her probability of adopting "correct" positions increases (Weidenmüller, 2001). However, this remains to be investigated in more detail.

Under natural conditions, the combined effect of decreasing thresholds and increasing efficiency of a small subgroup of workers can result in strong specialization. Examples of "task fixation" or "habituation" described in ants and bees may be based on similar mechanisms of

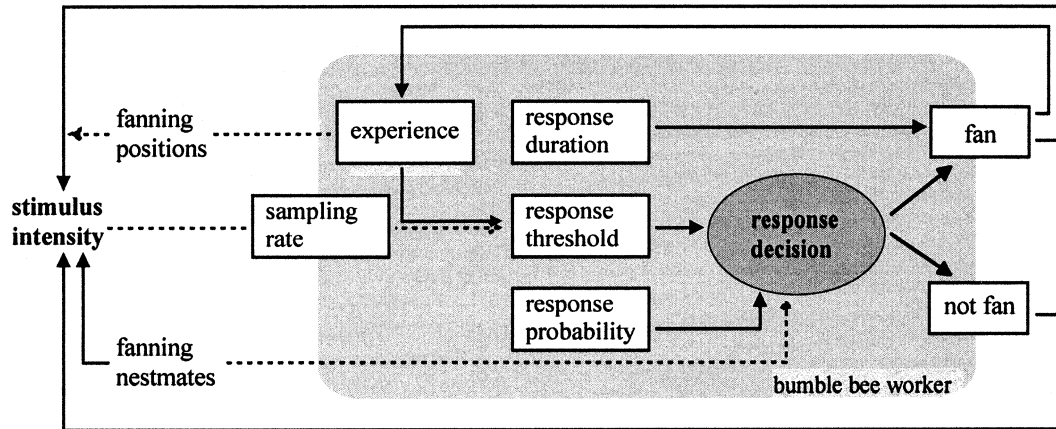


Figure 5
Schematic diagram of the factors influencing individual fanning behavior. Solid lines denote factors analyzed in this article; dotted lines, hypothetical or unpublished factors.

reinforcement. Ants become increasingly entrained on certain tasks they practice and perform such tasks in preference to others (Sendowa-Franks and Franks, 1993). In bumblebees and honey bees, the probability of reversion, for example, from foraging to nursing, is a decreasing function of time spent performing a task (Free, 1955; Seeley, 1982).

Figure 5 summarizes the findings presented in this article and outlines several open questions that remain to be investigated. Organization of insect colonies generally includes multiple pathways of negative feedback for the control of key variables of a colony's physiology (Seeley, 1995). One important factor in control of nest climate is the individual information sampling rate. We need to know whether workers measure air temperature, measure brood temperature, or even receive some kind of stimulus directly from the brood, and whether fanning behavior is interrupted in order to resample stimulus intensity. Furthermore, it remains to be shown whether workers tend to be more effective with experience by adopting more efficient fanning positions in the nest. Finally, it remains to be investigated if and how workers receive feedback on the efficiency of their nest mates, for example, via air currents. A pilot experiment in which those workers that fanned repeatedly were removed from the colony shortly before a manipulation of nest climate suggests that the decision to fan is influenced by the behavioral outputs of other workers: the response probability of the remaining workers increased (Weidenmüller, personal observation).

To truly understand a behavioral system as complex as flexible division of labor, one needs to know how the "real" subunits of the system behave, and one needs to discover the many pathways of feedback and information flow between them. Careful observations of both colony and individual behavior are a promising approach to unravel the mechanisms behind various colony features. These observations can then lead to the formulation of new models that test whether the sets of behavioral rules and processes identified through empirical analyses do indeed produce the actual performance of an intact group.

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