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Thresholds of Response in Nest Thermoregulation by Worker Bumble Bees, *Bombus bifarius nearcticus* (Hymenoptera: Apidae)

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Abstract

Regulation of nest temperature is important to the fitness of eusocial insect colonies. To maintain appropriate conditions for the developing brood, workers must exhibit thermoregulatory responses to ambient temperature. Because nest-mate workers differ in task performance, thermoregulatory behavior provides an opportunity to test threshold of response models for the regulation of division of labor. We found that worker bumble bees (*Bombus bifarius nearcticus*) responded to changes in ambient temperature by altering their rates of performing two tasks – wing fanning and brood cell incubation. At the colony level, the rate of incubating decreased, and the rate of fanning increased, with increasing temperature. Changes in the number of workers performing these tasks were more important to the colony response than changes in workers' task performance rates. At the individual level, workers' lifetime rates of incubation and fanning were positively correlated, and most individuals did not specialize exclusively on either of these temperature-sensitive tasks. However, workers differed in the maximum temperature at which they incubated and in the minimum temperature at which they fanned. More individuals fanned at high and incubated at low temperatures. Most of the workers that began incubating at higher temperatures continued performing this task at lower temperatures, when additional nest-mates became active. The converse was true for fanning behavior. These data are consistent with a threshold of response model for thermoregulatory behavior of *B. bifarius* workers.

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Introduction

Insect societies represent an important grade of biological organization, wherein the behavior of functional units (colonies) derives from the integration of autonomous individuals (workers) (Seeley 1997). In many insect societies, members of the worker force are idiosyncratic in performing tasks. Nest-mate workers are not equally likely to respond to a given set of stimulus conditions. However, if worker behavior is adaptive to the colony, the workers should adjust their behavior such that colony-wide work rates can track changes in demand for different tasks (Oster & Wilson 1978). Adaptive models of task performance generally predict that more workers will be active at a task when colony needs are greater (Oster & Wilson 1978).

A reliable increase in the number of workers that respond to extreme conditions can be achieved in two ways. First, workers can differ in their threshold of response to a stimulus (Robinson & Page 1989; Detrain & Pasteels 1991; Moritz & Fuchs 1998). The threshold model posits that workers differ in the minimum level of stimulus to which they will respond by performing a task. Workers with low thresholds will become active at low stimulus levels, and continue to respond when the demand for performance increases. Low threshold workers will remain active as nest-mates with higher thresholds begin to perform the task. If this model is correct, then some proportion of workers will be found to respond to a wide range of stimulus levels, while others will respond only to high stimulus levels. This type of task regulation automatically leads to an increase in the number of active workers as colony need increases. Furthermore, positive feedback following repeated task performance could enhance the efficiency or reliability of the low-threshold workers (Plowright & Plowright 1988; Theraulaz et al. 1998).

Secondly, as an alternative to threshold models, we propose that workers could differ in their preferentia of performance. Under this model, individual workers would respond to a narrow set of colony conditions – for example, some workers would perform a task only in response to the highest possible level of colony need, another set of workers would respond to the next lowest level of need, and so on. More workers would exhibit preferentia that matched conditions of high colony need, but each individual would be active under a narrow set of conditions. A possible selective advantage to this type of task regulation is that workers experience less wear or energy expenditure from continuous performance of costly or risky tasks. Task regulation by performance preferentia would also guarantee that a set of workers would be available to perform other tasks at all stimulus intensities.

The goal of our study was to assess how thermoregulatory behavior is regulated in bumble bee (*Bombus bifarius nearcticus*) workers. Nest temperature regulation by bumble bees provides an excellent opportunity to test threshold and preferentia models for the regulation of worker task performance. Variation in a single, easily quantified environmental variable – ambient temperature – elicits alternative, complementary behavioral acts that function to warm or cool the nest

(Heinrich 1979; O'Donnell et al. 2000). As in many winged social insects, bumble bee workers fan the nest when temperatures rise, which serves to cool the nest (reviewed by Wilson 1971). Bumble bee workers respond to falling temperatures by incubating, a behavioral act which involves the worker coiling her body around brood cells and transferring heat produced by muscular contractions to the nest (Heinrich 1979).

The simple architecture and small size of bumble bee nests aids in the study of nest thermoregulation. *Bombus* nests typically comprise a single open chamber (Heinrich 1979). All workers on the nest are therefore exposed to similar information about their colony's need for thermoregulation. The responses of individuals to colony conditions at any given time can be compared directly, which is often not true for larger insect societies with more complex nests.

We quantified colony-level and individual workers' responses to variation in temperature. First, we correlated colony-wide rates of brood incubation and fanning with temperature to confirm that performance rates increased with stimulus intensity. We then examined the individual variation in performance of these tasks over a range of temperatures to test the predictions of the preferential and threshold models for the control of task performance. If workers exhibited different preferential performance, we expected that individuals would be active over a narrow range of temperatures, and that different, exclusive sets of workers would be active at different temperature levels. Alternatively, differences in response thresholds would be supported if those individuals that became active at less extreme temperatures remained active under more extreme conditions.

Methods

Observation Colonies

We collected newly emerged *B. bifarius nearcticus* queens from Iron Horse State Park, Washington, USA in Apr. 1998. Queens were placed in cotton-supplied, insulated nest boxes in the laboratory and supplemented with pollen and sugar water (Plowright & Jay 1966; Foster 1992). After the first brood of workers emerged in late May, we transferred the colonies into glass-topped observation hives. Two colonies (henceforth A and B) that had established worker populations of at least 30 adults by late June were detached from their feeder boxes and moved to an observation shelter on the University of Washington campus in Seattle, WA (47°37' N, 122°21' W). We placed the observation hives in insulated containers (Styrofoam coolers) approximately 1 m above ground in a screened enclosure. Above-ground nesting sites are frequently chosen by *B. bifarius* in nature (Foster 1992). We ran clear plastic (Tygon) tubes from the nests through the screen walls of the enclosure, allowing the bees free outdoor access for foraging. Colonies were not supplemented with food after opening. Forager arrivals and departures, and the activities of bees within the nests, were clearly visible through the tube and the glass lid of the observation boxes (O'Donnell et al. 2000).

Marking Workers and Determining Worker Longevity

Beginning in mid-June we marked workers emerging in the observation colonies for individual recognition. We marked the bees using a code combining position and color of dots of enamel paint on the thoracic dorsum. Workers were marked every 1 to 3 days, such that their date of adult emergence was known to within 2 d (callow adults less than 24-h-old can be distinguished from older adults). We marked 110 workers in colony A and 86 workers in colony B. Workers were assumed to have died on the last day that they were observed during foraging or scan data collection (below). *Bombus bifarius* gynes (future queens) are much larger than workers, and males have a distinct coloration pattern. Both sexes of reproductives are readily distinguished from workers in this species. The presence of gynes and males was noted during observations, but they were not marked or counted as they emerged.

Behavioral Observations and Variables

Behavioral data were collected by two observers. One observer collected all data from each colony, thereby avoiding observer effects on within-colony behavioral measures. We observed colony A between 20 July and 11 Aug. 1998, and colony B between 20 July and 6 Aug. 1998. Observation periods were continuous and lasted 40–60 min. Colony A was observed five times per week, once in the morning (between 09:45 and 11:50 h) and once in the afternoon (between 13:00 and 16:35 h) on each day. With few exceptions, colony B was observed on the same day during the same time periods.

At 10-min intervals, each observer scanned the nest interior through the glass covers, and recorded the behavior and identity of all visible marked workers that were performing tasks. We recorded the following nest maintenance tasks (ethogram modified from Gamboa et al. 1987): antennating brood, mandibulating wax, incubating, fanning, guarding the entrance, and pulling cotton insulation material. Observers also recorded all foraging arrivals and departures during observation periods, noting the identity of the foraging worker and time to the nearest second. Because not all bees in the nest were recorded performing tasks, we combined the foraging arrival and departure data with the scan data to determine which bees were on the nest during each scan. Total behavioral sampling effort was as follows: colony A, 28 observation periods, 192 scan samples, 27.5 h observation; colony B, 27 observation periods, 184 scan samples, 27.3 h observation.

To calculate each worker's per-scan rate of behavior, we summed the number of scans during which she performed a task and divided this by the total number of scan samples during which she was present in the nest. We calculated colony-wide rates of task performance in two ways. First, we counted the number of times that we observed a given task during an observation session, then divided this by the number of scans; this yielded the colony per-scan rate of performance. Secondly, we counted the number of different workers that were observed

performing a given task at least once during an observation period, as well as the proportion of workers that were on the nest that performed the task during an observation period.

Temperature Data

Ambient air temperatures were recorded hourly at the University of Washington campus. We used the mean of two (if an observation period started on the hour) or three (if an observation period started at half past the hour) temperature readings as an estimate of ambient temperature for each observation period. The observers were blind to temperature readings whilst they collected the data. To ensure that ambient temperature was a good predictor of temperature in the nest cavity air space, we exposed an active observation colony (nest box similar in design to subject colonies) to temperatures ranging from 18 to 35°C in the laboratory. This temperature range overlapped the ambient temperatures experienced by the free-flying subject colonies. We placed the laboratory colony in a $30 \times 50 \times 30 \text{ cm}^3$ enclosed space, warmed by an adjustable ceramic heating lamp. One thermometer measured the ambient temperature and a second thermometer simultaneously measured the temperature in the air space of the nest cavity. We collected 10 paired readings at eight different temperature settings separated by 2–5°C. We allowed the two temperatures to equilibrate for 15 min after the lamp's settings were changed (no further changes were seen after 15 min in initial readings).

Data Analysis

Correlations among continuous variables are parametric Pearson correlations unless otherwise noted. We used Spearman rank correlations to estimate correlations among continuous variables when the data violated parametric test assumptions (e.g. unequal variances). We used linear regression to quantify relationships among variables when the direction of causality of the relationship could be assumed (e.g. ambient temperature would affect variation in bee behavior). We used multiple regression to test and account for colony differences. Polynomial (quadratic) terms were included in regression models when they explained significantly more variance ($p < 0.05$) than the simple linear model (SAS Institute 1985).

Results

Colony Level Patterns of Nest Thermoregulation

Temperature in the laboratory nest-cavity airspace was nearly identical to ambient temperature, although at 35°C, the nest cavity was warmer than ambient by approximately 2°C. The correlation between ambient and nest cavity

temperature in the laboratory was $r = 0.99$ ($p < 0.001$). Mean ambient temperatures during observation periods ranged from 16.4 to 31.9°C (total range 15.5°C) for colony A, and from 16.4 to 32.5°C (total range 16.1°C) for colony B. The mean temperature variation within observation periods was 1.5°C for both colonies, with minimum within-period variations of 0°C for both colonies and maximum within-period variations of 3.9°C for colony A and 3.3°C for colony B. The number of workers present on the nests during observation periods did not correlate significantly with temperature (colony A, $r = 0.32$, $p > 0.10$; colony B: $r = 0.02$, $p > 0.90$).

Colony per-scan incubation and fanning rates were strongly negatively correlated within observation periods (Spearman correlation; colony A: $r = -0.58$, $p < 0.005$; colony B: $r = -0.59$, $p < 0.005$). Fanning and incubation co-occurred during some observation periods (colony A: 28.5% of observation periods; colony B: 11.1% of observation periods). However, performance of these tasks was nearly exclusive: high rates of fanning were only observed when incubation rates were low or zero, and vice versa (Fig. 1).

Ambient temperature had strong effects on colony rates of fanning and incubation. Colony per-scan rates of incubation decreased linearly with temperature (Fig. 2; colony A: $r^2 = -0.37$, $p < 0.001$; colony B: $r^2 = -0.46$, $p < 0.001$), while colony per-scan rates of fanning increased exponentially with temperature (Fig. 2; colony A: $r^2 = 0.82$, $p < 0.001$; colony B: $r^2 = 0.83$, $p < 0.001$). Colonies did not differ significantly in the relationships of incubation rates with temperature (multiple regression, $F_{2,52} = 0.02$, $p > 0.75$) or of fanning rates with temperature (multiple regression, $F_{2,52} = 3.4$, $p > 0.05$). Furthermore, when they were observed simultaneously, the two colonies' rates of fanning ($r = 0.95$, $p < 0.001$) and of incubation ($r = 0.64$, $p < 0.05$) were correlated.

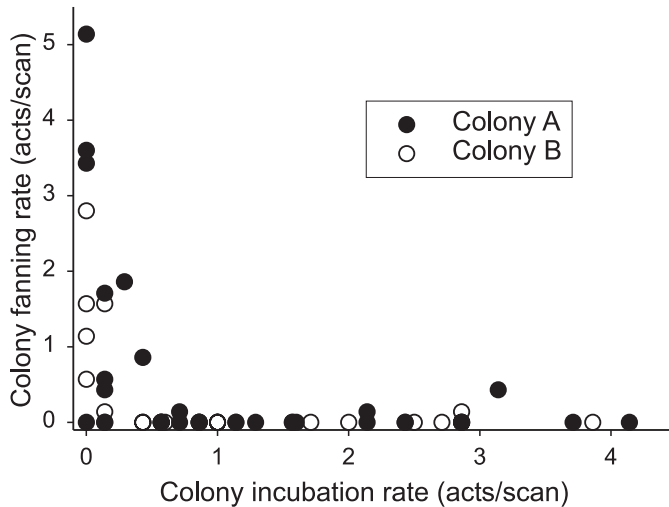


Fig. 1: Relationship between colony-wide worker fanning rates and worker incubation rates for two *Bombus bifarius* colonies. Each data point represents one observation period

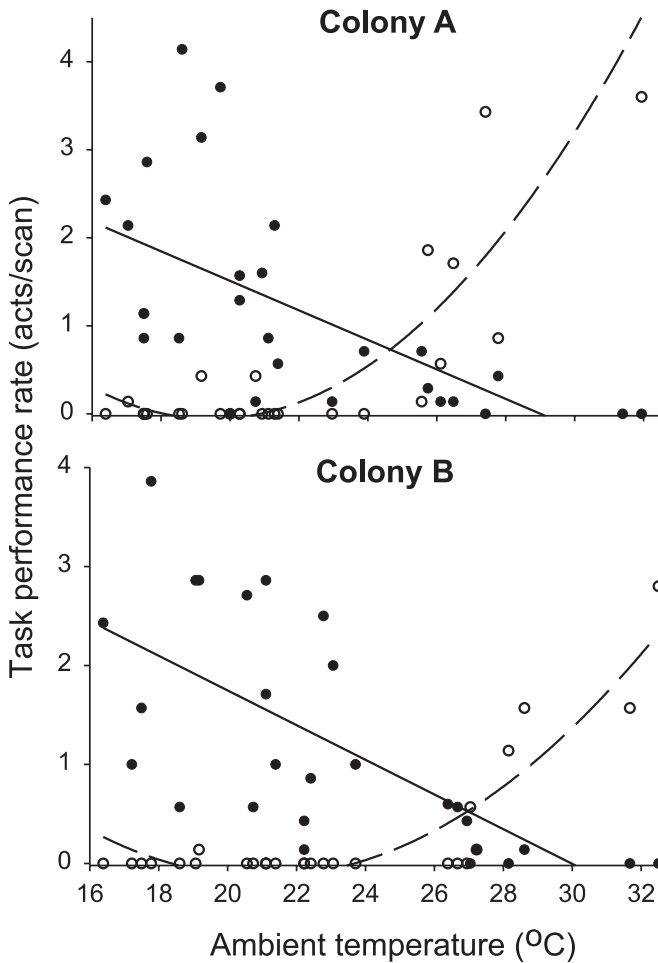


Fig. 2: Relationship between colony-wide incubation and fanning rates and ambient temperature for workers in two *Bombus bifarius* colonies. Each data point represents one observation period. Solid lines show best fit (linear regression) of incubation rate with temperature; dashed curves show best fit (polynomial regression) of fanning rate with temperature

After accounting for colony effects, both the number of workers and the proportion of workers that incubated decreased with temperature (multiple regression; number of workers incubating: $F_{2,52} = 28.4$, $p < 0.0001$, proportion of workers incubating: $F_{2,52} = 45.3$, $p < 0.0001$), and both the number of workers and the proportion of workers that fanned increased with temperature (multiple regression; number of workers fanning: $F_{2,52} = 58.6$, $p < 0.0001$, proportion of workers fanning: $F_{2,52} = 51.6$, $p < 0.0001$).

Table 1: Individual variation in rates of incubating at different temperatures for *B. bifarius* workers. Temperatures are presented in intervals of 2°C except at the highest range; at least two observation periods (14 scans) were conducted in each temperature interval (no observations were made between 24.4 and 26.3°C in colony B). Values in the cells of the table are the individual's per-scan rate of incubating when observed at temperatures in the interval; temperature ranges at which a worker incubated are in bold type. Workers that were not present for three or more temperature intervals were not included in the table. Mean rates of incubation were calculated by including only workers that incubated in each temperature interval. Workers that were not present at a given temperature interval are indicated by 'x'

Worker ID	Ambient temperature range (°C)					
	16.4–18.3	18.4–20.3	20.4–22.3	22.4–26.3	26.4–28.3	28.4–32.5
*Colony A						
lg/y	0	0.26	0.29	0.04	0.10	0
lgw	0.07	0.19	0.29	0	0.10	0
p/r	0.19	0.29	0.21	0.14	0	0
oo	0.43	0.33	0.30	0.17	0	0
or	0.29	0.07	0	0.07	0	0
og	0.24	0.19	0.15	x	0	0
bo	0.14	0.09	0.17	x	0	0
o/y	0	0.06	0.06	0	0	0
po	0.05	0	0.06	0	0	0
o/olg	0.07	0.12	0	0	0	0
p/o	0.02	0.08	0	0	0	0
p/p	0.07	0.09	0	0	0	0
Rg	0.12	0.12	0	0	0	0
Ro	0.14	0.09	0	0	0	0
b/o	0.05	0.14	0	0	0	0
b/y	0	0.02	0	0	0	0
go	x	0.04	0	x	0	0
lg/p	0	0.03	0	0	0	0
o/p	0	0.05	0	0	0	0
o/w	0	0.02	0	0	0	0
oy	0	0.06	0	0	0	0
ob	x	0.23	0	0	0	0
blg	0.14	0	0	0	0	0
lgp	0.07	0	0	0	0	0
pw	0.14	0	0	0	0	0
r/o	0.07	0	0	0	0	0
wlg	0.07	0	0	0	0	0
wp	0.14	0	0	0	0	x
y/o	0.14	x	0	0	0	x
o/lg	0.14	x	0	0	0	x
Mean	0.13	0.12	0.19	0.11	0.10	0
Pr (workers active)	0.75	0.75	0.26	0.15	0.07	0

Table 1: (Continued)

Worker ID	Ambient temperature range (°C)					
	16.4–18.3	18.4–20.3	20.4–22.3	22.4–26.3	26.4–28.3	28.4–32.5
†Colony B						
gb.b	0	0.14	0.07	0.29	0	0.14
bp	0.19	0.57	0.23	0.10	0.06	0
g/p	0.36	0.14	0.19	0.19	0.03	0
lgr	0.29	0.14	0.24	0.09	0.03	0
y/b	0.36	0.48	0.43	0.25	0.06	0
yr	0.21	0.36	0.31	0.28	0	0
w/w	0.07	0.07	0.21	0.03	0	0
pg	0.33	0	0.11	0.10	0	0
gw	0.29	0.29	0	0.07	0	0
yy	0.07	0.43	0	0.21	0	0
lg/r	x	0.14	x	0.07	0	0
lgb	0	0	0	0.07	0	0
gp	0	0	0	0.07	0	0
lgp	0	0	0	0.14	0	0
wp	0.14	0.14	0	0	0	0
lg/p.b	0.14	0.29	0	0	0	0
lg/p	0	0.14	0	0	0	0
g/g	0.57	0	0	0	0	0
Mean	0.25	0.26	0.23	0.14	0.04	0.14
Pr (workers active)	0.71	0.72	0.47	0.77	0.22	0.05

*An additional 15 workers were present at four or more temperature intervals but never incubated.

†An additional four workers were present at four or more temperature intervals but never incubated.

Individual Variation in Thermoregulatory Behavior

More workers performed incubation than fanning (colony A: 62% of 50 workers incubated, 48% fanned, $\chi^2 = 1.98$, $df = 1$, $p > 0.10$; colony B: 68% of 31 workers incubated, 32% fanned, $\chi^2 = 7.81$, $df = 1$, $p < 0.005$). Workers' total per-scan rates of fanning and incubation were positively correlated (Spearman correlation, colony A: $r = 0.42$, $p < 0.005$; colony B: $r = 0.42$, $p < 0.05$). Most of the workers that thermoregulated performed both fanning and incubation (colony A: 67% of workers performed both tasks; colony B: 55% of workers performed both tasks). A few workers performed both fanning and incubation in the same observation period (colony A: once each by three workers; colony B: once each by two workers). Furthermore, on several occasions single workers either fanned or incubated during a scan when two or more nest-mates were performing the other task (this occurred four times in colony A and three times in colony B).

Nest-mate workers varied in the range of temperatures at which they performed incubation (Table 1) and fanning (Table 2). More individuals incubated

Table 2: Individual variation in rates of fanning at different temperatures for *B. bifarius* workers. Format of table and criteria for including workers as in Table 1

Worker ID	Ambient temperature range (°C)					
	16.4–18.3	18.4–20.3	20.4–22.3	22.4–26.3	26.4–28.3	28.4–32.5
*Colony A						
o/ol	0.14	0	0	0	0	0.42
og	0	0.05	0.04	0	0.14	0.67
p/r	0	0.05	0	0	0.14	0.58
o/p	0	0	0.05	0.07	0.05	0
blg	0	0	0.07	0	0	0
lgw	0	0	0	0.43	0.14	0.42
b/o	0	0	0	0.19	0.14	0
go	x	0	0	x	0.07	0.25
lg/y	0	0	0	0	0.14	0.33
ob	x	0	0	0	0.14	0.17
or	0	0	0	0	0.14	0.33
po	0	0	0	0	0.10	0.25
wo	0	0	0	x	0.14	0.43
w/og	0	0	0	0	0.07	0
bo	0	0	0	0	0.07	0
y/o	0	x	0	0	0.29	x
lgp	0	0	0	0	0.19	0
o/olg	0	0	0	0	0.14	0
o/w	0	0	0	0	0.14	0
oo	0	0	0	0	0.05	0
p/o	0	0	0	0	0.05	0
r/r	0	0	0	0	0	0.07
ro	0	0	0	0	0	0.36
w/olg	0	0	0	0	0	0.57
Mean	0.14	0.05	0.05	0.23	0.12	0.37
Pr (workers active)	0.05	0.09	0.13	0.14	0.79	0.57
†Colony B						
w/w	0	0.07	0	0	0	0.05
yr	0	0	0	0.03	0.06	0.21
g/p	0	0	0	0	0.17	0.63
lgr	0	0	0	0	0.06	0.47
pg	0	0	0	0	0.06	0.05
lgb	0	0	0	0	0.14	0
bp	0	0	0	0	0	0.26
lg/p.b	0	0	0	0	0	0.08
lg/r	x	0	x	0	0	0.14
ylg	x	0	x	0	0	0.14
Mean	0.00	0.07	0.00	0.03	0.10	0.23
Pr (workers active)	0	0.10	0	0.10	0.50	0.90

*An additional 21 workers were present at four or more temperature intervals but never fanned.

†An additional 13 workers were present at four or more temperature intervals but never fanned.

at lower temperatures, and more fanned at higher temperatures (correlations of proportion of workers performing tasks with temperature; fanning: colony A, $r = 0.86$, $p < 0.05$; colony B, $r = 0.89$, $p < 0.05$, incubating: colony A, $r = -0.91$, $p < 0.05$, colony B: $r = -0.84$, $p < 0.05$). Most workers that incubated at higher temperatures also performed this task at a range of lower temperatures; the converse was true for fanning (Tables 1 and 2). Furthermore, workers' total per-scan incubation rates were correlated with the temperature range over which they incubated (colony A: $r = 0.81$, $n = 29$, $p < 0.001$; colony B incubation: $r = 0.83$, $n = 18$, $p < 0.001$; only workers that were alive for at least 5 observation days or 35 scans were included). Similar patterns held for fanning, but the correlation was not significant in colony B (colony A fanning: $r = 0.60$, $n = 23$, $p < 0.005$; colony B fanning: $r = 0.25$, $n = 10$, $p > 0.25$). Workers' mean per-scan rates of incubation and fanning did not increase consistently at more extreme temperatures, although mean per-scan fanning rates were greatest at the highest range of temperatures (Tables 1 and 2).

Discussion

Our data indicate that wing fanning and brood cell incubation by *B. bifarius* workers were complementary and nearly exclusive responses to changes in nest temperature. Ambient air temperature explained significant variation in colony-wide rates of both fanning and incubation. Furthermore, daily variation in the rates of performance of these tasks was highly correlated between the colonies (see also O'Donnell et al. 2000). Our data indicate a shift between fanning and incubation at ambient temperatures of approximately 25°C in colony A and 27°C in colony B (Fig. 2).

Colony needs for compensatory thermoregulatory behavior increase at extreme temperatures. As bumble bee nest temperatures reach extreme levels (either high or low), development of the brood can be compromised or terminated. Heinrich (1979) suggested that developmental anomalies can result in bumble bee broods below comb temperatures of approximately 30°C. In our study, the primary behavioral response to extreme temperatures was a change in the number of workers thermoregulating. Individuals' rates of fanning and incubation did not vary consistently with temperature, although the highest temperatures (above 28.4°C) elicited the highest mean fanning rates. We conclude that changes in workers' probabilities of fanning and incubating, and therefore in the number of bees performing these tasks, were important in regulating *B. bifarius* nest temperature. Changes in individuals' work rates were less important to the colonies' thermoregulatory responses.

Most workers did not specialize exclusively on one thermoregulatory task, but instead switched between fanning and incubation depending on colony conditions. However, individual workers varied in how they responded to different temperature levels within the nest. Few workers showed evidence of different temperature preferences for the performance of thermoregulatory tasks. Instead, workers varied in the range of temperatures at which they thermoregulated.

These results suggest that workers differed in their thresholds of response to colony need for temperature control. Most workers fanned only at higher temperatures and incubated only at lower temperatures, suggesting that relatively few individuals had low thresholds of response to temperature. The fact that workers occasionally fanned or incubated during observation periods when many of their nest-mates were performing the complementary task further demonstrates that workers did not respond identically to colony needs for temperature adjustment. The simultaneous performance of tasks with opposite effects is predicted by the threshold of response models, especially at intermediate or transitional environmental conditions (Bonabeau et al. 1998).

Our data suggest that *Bombus* workers' thermoregulatory behavior was probabilistic, rather than deterministic, over their active temperature range. Responses to other colony needs, such as food storage, may prevent workers from thermoregulating at every temperature within their response threshold. However, at the colony level, thermoregulatory behavior was a relatively predictable response to variation in ambient temperature. Predictable colony responses are often derived from probabilistic worker behavior in insect societies (Oster & Wilson 1978; Jeanne 1986).

The threshold of response models are attractive to insect sociobiologists because they can account for both worker idiosyncrasy and flexibility in behavior (Robinson & Page 1989; Theraulaz et al. 1998). Threshold effects on task performance have been documented in ants with morphological worker castes (Wilson 1985; Detrain & Pasteels 1991, 1992), and in species with monomorphic worker castes such as bumble bees, honey bees and social wasps (this study; Robinson 1987; Page et al. 1995; O'Donnell 1998a). However, little is known about the mechanisms which underlie individual differences in response thresholds. Repeatable individual differences in task performance based on genotypic variation within colonies have been documented in a number of insect societies (reviewed in O'Donnell 1998b), but have not been tested in bumble bees. Queens mate with multiple males in some *Bombus* species, including *B. bifarius*. Multiple mating increases genotypic variation within colonies, and genotypic differences may be associated with workers' thresholds of response (Robinson & Page 1989).

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