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# Heat Shielding: A Novel Method of Colonial Thermoregulation in Honey Bees

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**Abstract** Honey bees, *Apis mellifera*, maintain constant colony temperatures throughout the year. Honey bees fan their wings to cool the colony, and often spread fluid in conjunction with this behavior to induce evaporative cooling. We present an additional, previously undescribed mechanism used by the honey bee to maintain constant colony temperature in response to localized temperature increases. Worker bees shield the comb from external heat sources by positioning themselves on hot interior regions of the hive's walls. Although honey comb and brood comb were both shielded, the temperature-sensitive brood received a greater number of heat shielders and was thus better protected from overheating. Heat shielding appears to be a context-dependent adaptive behavior performed by worker bees who would previously have been considered "unemployed."

## Introduction

Honey bees, *Apis* spp., are an ideal system for the study of adaptive behavior. Effectively sterile workers build, maintain, defend, and forage for their colony. The most thoroughly studied worker behaviors are those related to foraging (i.e., waggle and round dances; Frisch 1967) and colonial thermoregulation (Heinrich 1980, 1985). Honey bees maintain constant hive temperature by primarily biomechanical means; to decrease hive temperature bees "fan" the colony by buzzing wings, and to increase hive temperature bees isometrically contract wing muscles (Heinrich 1980, 1985). The ability to maintain constant colony temperature allows the honey bee colony to rear brood when the ambient temperature is exceedingly low or high (Seeley 1985, 1995), and elevated temperatures defend against brood infections (Deans 1940; Bailey 1967). Thus, maintaining hive temperature is vital to the survival of a honey bee colony.

Although workers perform many functions, fewer than half of the workers in a colony are considered to be "working" at any given time (Seeley 1995). Bees that are not performing overt tasks, typically called "unemployed," may be obtaining information about the status of the colony (e.g., amount of honey and pollen reserves) that will prove beneficial as they switch to employed status (Seeley 1995). It is not clear, however, that the presence of unemployed workers in the hive serves no purpose other than to gather information. Since maintenance of constant brood temperature is vital, these workers may insulate the brood comb against temperature loss. We hypothesize that workers also shield the brood against external heat sources by absorbing excess heat. While workers can survive temperatures up to 50°C (Coelho 1991), temperatures above 36°C for any appreciable length of time are harmful to brood and may result in developmental abnormalities or death (reviewed in Winston 1986).

We examined the "heat shielding" hypothesis by observing the spatial location of honey bees after applying a heat source to the outer wall of observation hives. If honey bees shield the combs from external heat sources, individuals should aggregate at this source and may preferentially shield brood comb to protect the temperature-sensitive larvae.

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## Methods

### General Methods

In May 1998 ten honey bee colonies (*Apis mellifera* ligustica) were collected from an apiary outside Ithaca, NY, and placed indoors in observation hives of two different sizes (inner dimensions: small, 43.0 × 40.0 × 4.5 cm, $n=6$; large, 73.5 × 45.2 × 4.0 cm, $n=4$). Two colonies, both in small hives, suffered a great decrease in population due to the loss of the queen. Electric heating pads ($n=2$; Four Paws 6-W heater) were used to increase the temperature on glass sections of the observation hives. Temperature was recorded with an IT 660 electrotherm digital thermometer (Electromedics) from two probes, one located within the brood comb of the small observation hives and the other between heating pads and observation glass. All descriptive statistics are presented as means ± standard error.

### Spatial Location of Workers

On 31 July and 1 August 1998, four 5.5 × 5.5 cm regions were drawn on the glass surface of the eight observation hives containing healthy colonies: two squares each within the brood-comb and honey-comb areas. The paired areas were similar in bee number and either brood development or honey stores. Over two of the four squares, either in the brood-comb or honey-comb area, we placed a pair of heating pads. The observation hive's Styrofoam insulation was replaced, and one of the pads was allowed to heat for 15 min. After each session the number of bees perched upon the observation glass (i.e., tarsal segments on glass) within each square was counted ($n=16$ total pairings). In addition, the total number of bees within the marked region, not only those perched on the glass, was recorded before and after treatment for 11 pairs. We were unable to gather this data in the remaining five pairs due to a high density of bees.

Heating-area attractiveness was analyzed by comparing the proportional increase in the total number of bees within treatment (heated) and control (unheated) squares ($n = 11$ each). The number of individuals perched upon the glass of the observation hive was compared between heated and unheated squares ($n = 8$ pairs each for brood comb and honey comb). Due to continuity problems (one cannot divide by zero), the number of individuals perched on the glass surface before and after heating was increased by one prior to calculating proportions. These data were used to compare between individuals in the brood comb and honey comb. All tests on behavioral data are Wilcoxon paired tests.

### Heat Pad Effect

On 29 and 30 July 1998, heat pads were attached to the exterior glass walls of the small observation hives containing a small (approx. 100 worker bees; $n = 2$) and large number of bees (approx. 3750 bees; $n = 4$). Temperatures of the brood comb before and after 15 min of heating were recorded along with the glass temperature under the heating pad at the end of the heating period. The relative brood-comb temperature increase was calculated as the increase in brood-comb temperature divided by number of degrees above the starting brood-comb temperature that the heating pad reached. This is conservative with respect to the heat shielding hypothesis since the average difference between the starting brood-comb temperature and the final heating-pad temperature was greater for colonies with a small number of bees (7.13 ± 0.60° C) than for colonies with a large number of bees (5.93 ± 0.40° C). Data were gathered in pairwise fashion, with small colonies paired to large colonies. Temperature data were analyzed with paired and unpaired *t* tests.

## Results

### Effect of Heat on Spatial Location of Workers

Heating the glass surface of the observation hive increased the total number of bees in heated sections; indeed, heating appeared to draw bees from unheated sections (proportional change unheated, 0.93 ± 0.06; heated, 1.32 ± 0.17; Wilcoxon paired test, $P < 0.0001$). The number of bees on the heated glass surface was significantly greater for both the honey-comb and brood-comb regions (Fig. 1). The proportional increase in the number of bees on heated surfaces was greater for brood-comb than for honey-comb regions (Fig. 2). Workers did not appear to buzz their wings, and no drone or queen was observed on heated glass surfaces.

### Effect of Heat on Hive Temperature

Heating pads reached average temperatures of 38.01 ± 0.77° C (range 32.5–42.5) but were significantly hotter for colonies with a large number of workers (40.69 ± 0.40° C) than for colonies with a small number of workers (35.50 ± 0.69° C; *t* test, $t_{14} = 6.52$, $P < 0.001$). Despite this, colonies with a large number of workers had a significantly lower relative brood-comb temperature increase than did colonies with a small number of workers (large, 0.21 ± 0.02; small, 0.47 ± 0.07; paired *t* test: $t_7 = 3.65$, $P < 0.01$). The brood-comb temperature in both large and small colonies increased due to the presence of the heat pad (large, before 34.62 ± 0.08° C, after 35.90 ± 0.20° C; small, before 28.38 ± 0.70° C, after 31.50 ± 0.81° C).

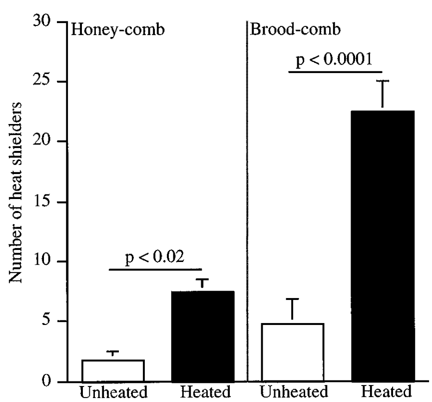


Fig. 1. Number of bees observed on heated and unheated glass after 15 min of heating for both honey-comb and brood-comb regions. Data are from eight observation hives. *Columns* means; *error bars* standard errors

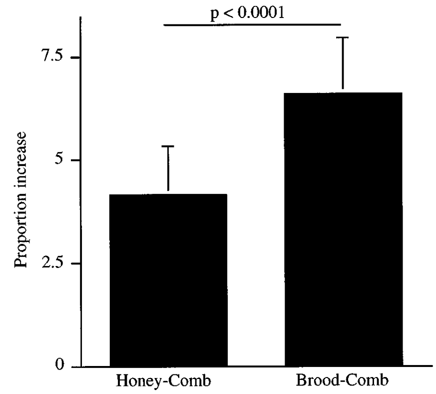


Fig. 2. Proportion increase in the number of bees on the surface of the observation hive from before to after heating for both honey-comb and brood-comb regions. Data are from eight observation hives. *Columns* proportions; *error bars* standard errors

## Discussion

Honey bee workers were attracted to the heated glass and positioned themselves on the heated surface (Fig. 1). In colonies with a large number of workers the effect of heat on internal hive temperature was dampened. Since the bodies of honey bee workers can absorb heat (Coelho 1991), we propose that workers position themselves on hot surfaces to limit heat from passing from external sources to the comb inside the hive. Since individual bees were more likely to shield the temperature-sensitive brood comb than they were to shield the honey comb (Fig. 2), heat-shielding appears to be a context-dependent adaptively beneficial behavior.

An alternative explanation for the increase in number of bees on the heated glass is that bees recognize brood comb by means of its elevated temperature and thus mistakenly identified the heat source as a brood-comb surface. However, the following reasoning argues against this hypothesis: (a) instead of an increased proportion of heat shielders over the brood comb (Fig. 2), there should be no difference in the proportion of bees on heated glass over brood-comb and honey-comb regions; (b) instead of being attracted to the heat, workers typically vacate the brood comb when it reaches the temperatures generated in this study (Winston 1986); and (c) worker bees have excellent comb recognition abilities (Breed et al. 1988, 1995, 1998), and are thus unlikely to mistake a smooth, glass surface for the deeply textured brood comb.

A second alternative explanation is that the worker bees were "basking" in the radiation of the heat pads in order to maintain a high body temperature rather than to shield the colony. We do not favor this hypothesis for the following reasons: (a) the examined colonies were strong both in bee number and honey stores, and therefore were not energetically stressed by the experimental design; (b) since brood-comb temperatures were high (approx. 34.6° C), the bees within the brood-comb region were warmer than those in honey-comb region, and hence bees in the honey comb, not the brood comb, should have been more likely to seek hot surfaces on which to elevate body temperature (see Fig. 2); and (c) these experiments were conducted in the warm months of July and August when honey bee colonies in temperate regions are not subjected to excessively cold weather.

Our results suggest that honey bee workers can shield their combs from external heat sources. In the natural environment, heat shielders may act as mobile insulation for nest cavity walls that are particularly thin and exposed to sunlight. Such insulation would augment the efficiency of other thermoregulatory behaviors. It is widely known that honey bee workers insulate the colony from the cold of winter (Winston 1986). However, this is the first report indicating that bees insulate the colony from heat sources. Heat shielding appears to be an adaptive behavior performed by individuals that would previously have been considered "unemployed" worker bees.

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