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Heat shielding: a task for youngsters

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Heat shielding is a recently identified mechanism used by worker honey bees (*Apis mellifera*) to help maintain constant hive temperatures. Only workers perform this behavior; in our experiment, drones actively avoided heated hive regions. Observations of marked day-old cohorts within broodcomb regions indicate that heat shielding is performed by young bees to preferentially protect advanced stage larvae and pupae. As expected, the number of heat-shielders significantly increased with both the temperature of the heat source and the size of the colony. Of the young bees observed to perform the behavior, those aged 12–14 days were significantly more likely to heat-shield than expected. Combined, these data suggest that classifications of age-based tasks in honey bees should include heat shielding, and that the behavior is an adaptation designed to protect temperature-sensitive brood. *Key words:* age polyethism, *Apis mellifera*, honey bees, thermoregulation. *[Behav Ecol]*

Honey bees have been shown to use temperature to thwart disease (Starks et al., 2000) and predators (Ono et al., 1995). But perhaps the most impressive temperature-related characteristic of honey bees is simple maintenance: honey bees (*Apis mellifera*) maintain colony temperatures throughout the year (Heinrich, 1980, 1985; Seeley, 1985). Honey bees are hardly alone in this regard as many social animals produce structures within which temperature control is important (e.g., stingless bees: Engels et al., 1995; yellowjackets: Coelho and Ross, 1996; paper wasps: Jeanne and Morgan, 1992; wood ants: Horstmann and Schmid, 1986, Rosengren et al., 1987; army ants: Franks, 1989; forest ants: Banschbach et al., 1997; termites: Korb and Linsenmair, 2000; caterpillars: Ruf and Fiedler, 2000). The honey bee distinguishes itself, however, in the degree to which it controls fluctuations in temperature.

Honey bees isometrically contract muscles to heat the colony and fan their wings to cool the colony—often spreading fluid in conjunction to induce evaporative cooling. Maintaining elevated and constant broodcomb temperatures is clearly adaptive as it shortens brood development times and maximizes brood health (Heinrich, 1980, 1985; Seeley, 1985). An additional mechanism used by the honey bee to maintain constant colony temperature has recently been identified: heat shielding (Starks and Gilley, 1999).

In response to localized temperature increases, worker bees shield the comb from the external heat source by positioning themselves on the hot interior region of the hive's walls. Heat shielding reduces the transfer of heat from outside to inside the hive (Starks and Gilley, 1999) and thus may serve to reduce incidences of over-heating. This behavior—placing the ventral surface directly on heated surfaces—appears to be similar, albeit with the opposite effect, to that reported by Bujok et al. (2002). These researchers observed honey bees with elevated thoracic temperatures position themselves directly over capped brood (i.e., over pupae or older larvae preparing for pupation) in order to elevate the temperature, or maintain elevated temperatures, on specific regions of the hive.

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Although no queens or drones were observed to heat-shield in Starks and Gilley (1999), it is unclear if the behavior is opportunistic—that is, if any individual will do it—or if the behavior is specific to a class of honey bee workers. Because the ontogeny of a honey bee worker takes it through a series of tasks (for review, see Jassim et al. 2000), it is possible that one stage includes heat shielding as an additional function. Alternatively, heat shielding could represent a behavior performed regardless of age. If the latter case is true, this would represent a somewhat rare occurrence in honey bee colonies with normal age distributions. Examining heat shielding in colonies containing bees marked at eclosion will allow us to determine if a given age class is more or less likely to perform the behavior.

In addition, although both honeycomb and broodcomb were shielded, in the previous study the temperature-sensitive brood received a greater number of heat-shielders and thus appeared better protected from overheating (Starks and Gilley, 1999). As the behavior appears to be expressed preferentially over the broodcomb, it is reasonable to posit that the behavioral response will also vary in strength within the broodcomb as a function of comb characteristics (e.g., the age of the developing brood). In a design similar to Starks and Gilley (1999), we examined the identity of heat-shielders and the possible fine-grained context dependence of the expression of the behavior.

METHODS

Subjects

On 17 June 2003, workers and two combs of brood were collected from eight *A. mellifera* L. colonies maintained at our Grafton, Massachusetts, apiary. Care was taken to ensure that we did not collect the queen from these colonies. The workers and one comb from each colony were placed within a two-frame observation hive (inner dimensions: 53 × 48 × 5 cm). The upper and lower frames were separated with queen excluder; the upper frame contained foundation for honeycomb production. These hives contained a new queen, initially constrained within a plastic queen cell with sugar plug. Seven of the eight queens were accepted by the workers, and these queenright colonies were used in our experiments. The additional frame of broodcomb was placed first within an individually marked cloth bag and then within an incubator maintained at approximately 33°C. All observation hives were

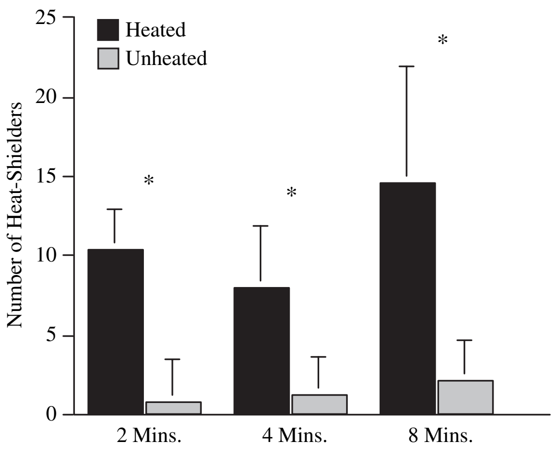

Figure 1
Change in number of bees observed on heated and on unheated glass after heating periods. Data are from seven observation hives. Columns represent means, and error bars represent standard errors. * $p < .01$.

installed at the Tufts University International Social Insect Research Facility, and the honey bees were allowed to forage naturally.

One-day-old bees were given specific paint marks indicating day of eclosion: bees were marked on 10 consecutive days (18–27 June 2003), and thus, we could identify 10 individual age cohorts. All marked bees were added to their original colonies, although many of these animals were not accepted but rather were expelled by other workers. An exhaustive colony census was taken on 8 July by recording the total number of bees, the number of each class (queen, drone, unmarked worker, marked worker, color of marked worker), and the comb characteristics (capped brood, uncapped brood, capped honey, uncapped honey, and empty cell) within multiple small sections (9 × 13 cells each; 24 sections per comb) of the hive. Each section covered approximately 117 cells. This procedure was repeated until each section of the colony was censused. Our experimental hives contained 1432 ± 92.2 worker bees (mean ± SE), and 84.7 ± 30.9 of these workers were marked dorsally and ventrally on the thorax with Testors enamel paint.

Temperature data

Small electric heating pads ($n = 2$; 10 × 12.5 cm, Repti Therm Mini 4-W heater) were used to increase the temperature on Plexiglas sections of the observation hives. By using a hand-held digital thermometer and type K (nickel-chromium and nickel-aluminum) Teflon-insulated thermocouples sensitive to 0.1°C, temperature data was recorded from within the hive and from under the heating pad both before and after heating periods. To ensure that the bees were not attracted to electrical current instead of heat, a few trials were made using Thermacare chemical-based heating pads. Bees perched on warm sections significantly outnumbered bees on unheated sections (24.0 ± 4.0 versus 4.7 ± 0.9; paired t test; $t_2 = 4.4$, $p < .05$); thus we felt comfortable continuing our experiments with electric heating pads.

Test 1: identity of heat-shielders

On 3 July 2003, black construction paper with two 9.5 × 12-cm rectangular cutouts in the broodcomb area was secured to the Plexiglas of each experimental colony. Cutout areas were covered with the heating pads for periods of 2, 4, and 8 min. One of the two heating pads was active, and the other, the control, was maintained at room temperature. Before and after each session, the number of bees perched on the observation Plexiglas (i.e., tarsal segments on glass) within each square was counted ($n = 21$ total pairings). The presence of marked bees with tarsal segments on the Plexiglas was noted at this time. Each hive was allowed at least 30 min to cool between trials, and the "hot" section was staggered between trials to ensure against an undetected preference for a given hive location.

Test 2: context dependence of heat shielding

On 7 July 2003, we modified the design above by locating our rectangular cutouts to cover a range of comb characteristics within the general broodcomb region: in this way we could determine fine-grained differences in heat-shielding preferences (e.g., above capped brood, uncapped brood). Cutout areas were covered with active (i.e., hot) heating pads for periods of 4 and 8 min ($n = 28$ total heating periods). Before and after each session, the number of bees perched on the observation Plexiglas within each square was counted. Each hive was allowed at least 30 min to cool between trials.

Statistical methods

Paired t tests were used to compare the change in number of individuals perched upon the glass of the observation hive on heated and unheated squares. An F test was used to examine differences across samples. Chi-square tests were used to determine if marked bees were more likely than expected to perch on hot regions. Multiple linear regression analysis was used to examine the context dependence of heat shielding. Unless otherwise noted, all descriptive statistics are presented as mean ± SE. All statistics were performed by using DataDesk 6.1.

RESULTS

Detection of heat shielding

This initial study represents only those trials that included both a heated section and an unheated control. Mean temperature of the outer Plexiglas before activation was 28.94 ± 0.21 °C and after heating was 40.39 ± 0.36 °C; this latter value is well outside normal broodcomb temperatures. The change in number of heat-shielding bees on heated Plexiglas was significantly greater than was the change in number of heat-shielding bees on unheated Plexiglas for each time period (2 min: $t_6 = 4.48$, $p < .01$; 4 min: $t_6 = 5.08$, $p < .01$; 8 min: $t_6 = 4.11$, $p < .01$) (Figure 1). No difference in the increase in heat-shielders was detected across time periods ($F = 1.99$, $p = .17$). These results were mirrored with respect to marked bees (2 min: $t_6 = 3.27$, $p < .02$; 4 min: $t_6 = 2.71$, $p < .04$; 8 min: $t_6 = 3.24$, $p < .02$; $F = 1.16$, $p = .33$). These data suggest that heat shielding is a robust behavior observed in response to temperature increases, but that the duration of heat may not be important.

Context dependence of heat shielding

Multiple linear regression of the effect of colony size, heating pad temperature, and number of capped brood on the total number of heat-shielders indicates a significant and positive impact of all three variables (Table 1). Although the impact of colony size is an unsurprising result (i.e., larger colonies should have more heat-shielders), uncovering positive relationships between total number of heat-shielders and both

Table 1
Multiple linear regression

Source	SS	df	*F*
Regression	2307.4	3	17.7
Residual	1043.06	24	

Heat-shielders (Y)	Coefficient (SE)	*p*	R^2
Colony size (X_1)	0.032 (0.006)	<.0001	.689
Temperature (X_2)	2.617 (0.005)	.0006	
Capped Brood (X_3)	0.019 (0.007)	.016	

The relationship between the total number of heat-shielders and colony size, heating pad temperature, and number of capped brood. The number of uncapped brood and food cells were omitted from the final analysis because neither showed a significant relationship. X represents the independent variables; Y, the dependent variable. See also Figure 2.

temperature and number of capped brood are more interesting (Figure 2). These data support the hypothesis that heat shielding is a context-dependent behavior performed to preferentially shield temperature-sensitive developing brood.

Identity of heat-shielders

Because no difference between time periods for marked and unmarked heat-shielders was observed (see above), data from across time periods was combined in the examination of marked versus unmarked heat-shielders. For the 3 July examination, there was a significant difference between the increase of marked and unmarked heat-shielders after the application of heating pads ($\chi^2_1 = 16.30$, $p < .001$) (Figure 3a). Although only 5.9% of all workers were marked, 13.7% of all heat-shielders were marked. As the unmarked population must have had bees within the 7–16-day age range, these data are likely conservative. Of the marked workers, those 12–14 days old were significantly more likely than expected to perform the behavior ($\chi^2_9 = 33.37$, $p < .001$) (Figure 4).

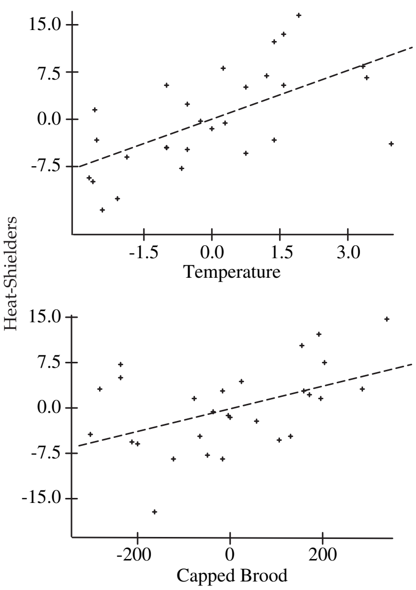

Figure 2
The relationship between the number of heat-shielders and the temperature of the heating pad and the number of capped brood under the heat source. Data are presented as residuals, and the relationship was determined by using a multiple linear regression (which also included colony size; see Table 1). Accordingly, these positive relationships are observed even when controlling for the effect of other variables.

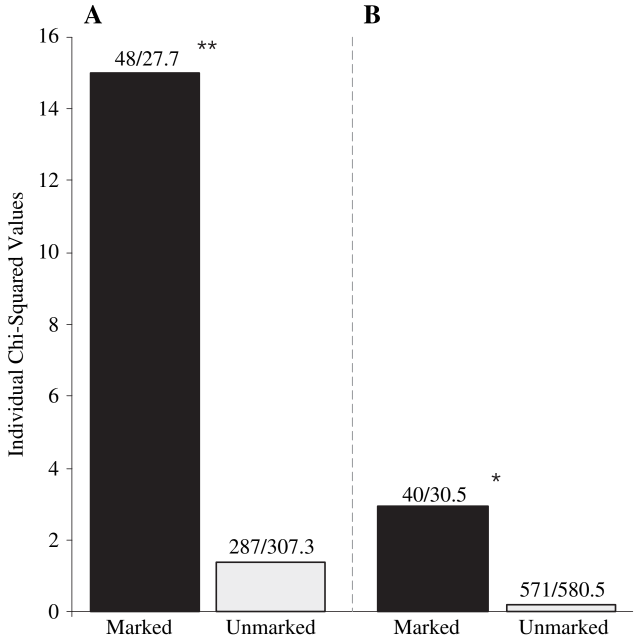

Figure 3
Although fewer in number, marked bees were significantly more likely than were unmarked bees to be attracted to heated hive regions. (A) Data from 3 July. (B) Data from 7 July. $*p < .05$; $**p < .001$. Observed and expected values are given.

Marked workers were overrepresented for the 7 July examination as well ($\chi^2_1 = 3.08$, $p < .05$) (Figure 3b). The effect of age class, however, was not significant for this sample ($\chi^2_9 = 11.25$, $p > .25$). Although this result suggests that our age class data should be cautiously interpreted, we believe that failure to find a significant age effect in this second sample is an artifact of our marking protocol. Because of the uneven distribution of eclosing workers, a full 35% of marked workers in our first sample were 12–14-day-old bees. As the animals

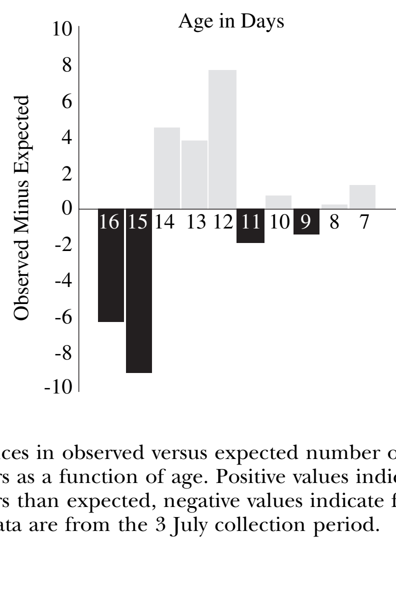

Figure 4
The differences in observed versus expected number of marked heat-shielders as a function of age. Positive values indicate more heat-shielders than expected, negative values indicate fewer than expected. Data are from the 3 July collection period.

aged between data collection periods, only 5% of marked workers in our second sample were 12–14-day-old bees. Accordingly, our sample of 12–14-day-old marked workers may have been too small to detect a proclivity toward heat shielding.

During our trials, only 23 males were observed in the heat-shielding position, and of these only three were found on heated sections of Plexiglas ($\chi^2_1 = 10.63$, $p < .01$). As such, males appear to significantly avoid performing the behavior. Combined these data strongly suggest that drones avoid heat shielding, and although individuals of many ages heat-shield, bees between 12 and 14 days old are most likely to perform the task.

DISCUSSION

Data presented here suggest that males avoid heat shielding, that workers bees 12 to 14 days-old are most likely to heat-shield, and that the behavior is very sensitive to context, specifically temperature and the number of capped cells in broodcomb regions. Given that the behavior shows a graded response with respect to both temperature and number of capped brood, it is highly unlikely that the results are artifacts of the experimental design. Indeed, given that the colony sizes were unique and our analysis controlled for this factor, it is also unlikely that our results were driven by inherent differences between hives.

Preferentially protecting brood that has reached the penultimate developmental stage makes evolutionary sense both in terms of total investment (higher in older brood) and in potential for developmental failure: transitioning between the larval and pupal stages is a highly sensitive time especially with respect to some broodcomb diseases (e.g., chalkbrood; Bailey and Ball, 1991). In addition, exciting new data suggest that workers that develop in different temperature regimens differ in foraging abilities (Tautz et al., 2003), which further emphasizes the importance of temperature maintenance in the broodcomb for many aspects of honey bee biology. Accordingly, heat shielding appears to be an adaptation not only to maintain consistent hive temperature but also to maximize the health of future workers.

Although males were not observed heat shielding in the original description of the behavior (Starks and Gilley, 1999), our data suggest that males may actively avoid performing the task. These results imply that high body temperatures are especially detrimental to drones, which may be the case if sperm production is suboptimal at elevated body temperatures. As drones have a nonzero probability of successfully mating, this behavior may be too costly for a potential reproductive to perform. Workers, alternatively, are sterile and are released from such constraints.

Our data on workers suggests that bees between the ages of 12 and 14 days are most likely to perform the behavior. This result makes intuitive sense as this age class of bees performs the majority of their work within broodcomb regions of the hive (Winston, 1986). It must be noted that there is significant plasticity regarding the performance of particular behaviors. Although a honey bee worker normally progresses through a series of different tasks while it ages (for review, see Jassim et al., 2000), the performance of each task at a specific age is not developmentally fixed. For example, by creating colonies containing bees of a single age class, researchers have done excellent work examining precocious foragers (see Schulz and Robinson, 2001). Given that our observation hives were likely to contain workers of all age classes, however, our data are likely to represent the normal progression through worker tasks.

Even with such compelling data, it is unclear how often the behavior is performed by feral *A. mellifera* colonies. Although heat shielding is likely to occur when the sun directly strikes a bark-free section of a tree cavity housing a honey bee colony, it is not clear how often such a section would be directly over a broodcomb region. It is possible, however, that this is an ancestral behavior. Other species within the *Apidae*, such as the giant honey bee (*A. dorsata*) and the dwarf honey bee (*A. florea*), form colonies outside of enclosed cavities. As such, these species may experience higher levels of temperature fluctuation at the extreme end of the temperature gradient. Although other colony cooling behaviors would certainly be used (e.g., fanning, induced evaporative cooling), heat shielding—in terms of increased density of bees over a heated region—may also help shield temperature sensitive brood. Clearly there is much to be discovered regarding the natural context of this behavior.

In addition to the natural context, in the future researchers should examine how heat-shielders handle the increased body temperature. When the honey bee's body temperature reaches the temperature of the external heat source—most likely through the increase first of thoracic temperature, then head, and finally abdomen temperature (Schmaranzer, 2000)—the bees will no longer hinder the transfer of heat. Indeed, as extreme heat is detrimental to the honey bee (Coelho, 1991), honey bees must have a method of releasing the heat. Although only a hypotheses, heat release is likely to take place outside the hive, in the honeycomb, or in the periphery of the broodcomb.

In conclusion, what is known of this recently identified behavior is that (1) the broodcomb is preferentially shielded over the honeycomb (Starks and Gilley, 1999), (2) capped brood is preferentially shielded over uncapped brood and cells that contain food within the broodcomb, (3) males avoid heat shielding, and (4) bees between the ages of 12 and 14 days are significantly more likely to perform the behavior than are younger or older bees. Accordingly, data presented here suggest that classifications of age-based tasks in honey bees should include heat shielding and that the behavior is an adaptation designed to protect temperature-sensitive brood.

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