Insectes soc. 49 (2002) 50–55
0020-1812/02/010050-06 $ 1.50+0.20/0

Insectes Sociaux

Research article

Effects of colony food shortage on social interactions in honey bee colonies

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Received 20 April 2001; revised 17 September 2001; accepted 29 October 2001.

Summary. The age of onset of foraging in honey bee colonies is affected both by inhibitory social interactions among nestmates and starvation. We determined whether starvation affects worker-worker interactions by quantifying the frequencies of five social interactions (trophallaxis, begging, offering, antennating, and grooming) in colonies that either were starved or well-fed. We hypothesized that bees in starved colonies engage in fewer social interactions than bees in colonies with ample food stores. In all three trials, starved colonies had significantly greater numbers of foragers than well-fed colonies, as in a previous study. In three of three trials, starved bees showed a significantly higher frequency of begging behavior than well-fed bees. Begging in starved colonies increased exponentially with time as the starvation presumably grew more severe. Immediately following the onset of foraging in starved colonies, the frequency of begging declined dramatically. No consistent differences for other observed social behaviors were found. Our results under starvation conditions do not provide support for the hypothesis that precocious forager development must be associated with a decrease in social interactions. Perhaps factors that influence precocious foraging under starvation conditions differ from those under conditions of ample food stores. We speculate that the duration and specific nature of the social contact may be important. Furthermore, we speculate that begging itself may be a cue associated with precocious forager development.

Key words: Division of labor, behavioral development, starvation, begging, trophallaxis.

Introduction

Honey bee colonies have an age-related division of labor: younger bees perform tasks inside the hive such as feeding larvae, while the oldest bees in the colony forage for nectar and pollen in the environment. Foraging is a matter of utmost importance, as both the survival of adults working inside the hive and the developing larvae are dependent on food brought back to the colony by foragers. According to a study of one colony, this task is performed by less than 50% of the worker population (Thom et al., 2000), but foragers are sensitive to changes in the needs of the entire colony (reviewed by Seeley, 1995).

Regulation of foraging in response to changing colony needs can take place in two ways: modulating the foraging effort of committed foragers, and an increase in the size of the foraging force by accelerating the behavioral development of pre-foragers. The existing foragers in a colony counter depletion of pollen stores by increasing pollen load size and by switching from nectar to pollen foraging (Fewell and Winston, 1992). Foragers apparently can determine colony need for pollen (Free, 1967; Barker, 1971; Free and Williams, 1971); this may operate via social interactions with nurse bees (Camazine, 1993), direct assessment of pollen stores by pollen foragers (Calderone, 1993; Pankiw et al., 1998; Dreller et al., 1999; Dreller and Tarpy, 2000), or perhaps both. Nectar foragers alter their intensity of foraging and recruitment of idle foragers based on socially mediated assessment of colony stores and inflow (reviewed by Seeley, 1995). The time it takes for returning foragers to be unloaded by food-storer bees is an indicator of colony nectar inflow (Seeley, 1989).

Less is known about how changes in colony need cause new foragers to develop. Huang and Robinson (1992; 1996) have shown that the presence of foragers in a colony inhibits the development of younger bees into foragers, even when the foragers are prevented from bringing fresh food into the hive. This inhibition apparently requires direct contact among individuals; when young bees were isolated from nestmates in a hive by double-screened cages, they showed precocious behavioral development (Huang et al., 1998), just as when they were reared in isolation in the laboratory

(Huang and Robinson, 1992). These results indicate that certain types of social interactions with older bees delay the age at onset of foraging for younger colony members, but the nature of these interactions is not known.

Schulz et al. (1998) showed that starving a colony causes young bees to develop into foragers faster than well-fed bees. Bees in colonies fed *ad libitum* from a feeder but exposed only to empty honeycomb did not show accelerated behavioral development, showing that empty comb is not a cue mediating precocious foraging (Schulz et al., 1998). These experiments were performed in small colonies composed of approximately 1000 one-day-old adult workers called "single-cohort colonies." It is possible that in more typical colonies the response to starvation also relies on modulation of activity by already committed foragers.

It is not known how starvation leads to precocious forager development. It has been suggested that individuals are informed of the nutritional state of a colony via frequent trophallaxis (Wilson, 1971; Ribbands, 1952). One possibility is that starvation causes a decrease in trophallaxis among individual workers, reducing the inhibitory signal suggested by Huang and Robinson (1992). Foragers interact with in-hive pre-foragers by giving them freshly collected nectar (Nixon and Ribbands, 1952; Wilson and Eisner, 1957). A single-cohort colony with no foraging force and no food for trophallaxis would be expected to engage in reduced rates of these possibly inhibitory interactions.

We hypothesized that bees in starved colonies engage in less social interactions than in colonies with ample food stores. We tested this hypothesis by quantifying five social behaviors in starved and well-fed colonies: trophallaxis, begging, offering, antennating (without trophallaxis), and grooming. These behaviors were chosen as the most obvious and easily observed social behaviors. The lack of an existing foraging force during the first few days of the life of a single-cohort colony allowed us to examine factors related only to the development of new foragers.

Materials and methods

Bees and colonies

Experiments were performed during the summer of 1997 at the University of Illinois Bee Research Facility. Each trial of an experiment was performed with two colonies, one starved and one well-fed. Bees were typical of North American populations of *Apis mellifera* L. (a mix of predominantly European subspecies; see Phillips, 1915; Pellet, 1938).

Single-cohort colonies were established by taking frames of honey comb containing old pupae from large colonies in our apiaries ("source colonies"). These frames were placed in an incubator at 33 °C until adults emerged. Both single-cohort-colonies (starved and well-fed) in each trial were established with matched numbers of bees from two source colonies. Different source colonies were used for each trial of the experiment. New colonies were established for each trial for a total of 6 single-cohort colonies. Bees were marked on the thorax either with a small plastic number tag (n = 200) or with a spot of Testor's enamel paint (n ≈ 800), a different color for each single-cohort colony. The tagged bees were used for behavioral observations. In trials 2 and 3, these focal bees also were paint-marked on the abdomen to facilitate observations of bees with their heads in cells (Seeley and Kolmes, 1991). Each colony was provided with a caged, unrelated queen to prevent any influences of brood on behavioral development (Pankiw et al., 1998a; LeConte et al., 2001).

Colonies were housed in a temperature-regulated room at 29 °C and were connected to a hole in a wall that provided access to the outdoors for flight. Bees in each colony were confined to one side of a single frame observation hive to allow behavioral observations by a single individual. A grid of 2″ × 2″ squares was drawn on the glass to facilitate in-hive behavioral observations. Food was given to each colony as described below.

Starved and well-fed colonies

The purpose of this experiment was to compare social interactions in paired colonies that differed in their amount of stored food. Colonies were prepared as in Schulz et al. (1998). Well-fed colonies were given a full frame of honey in cells that were not capped over with wax to provide an easily accessible and plentiful food supply. Starved colonies were given only about a 2–3 day supply of honey, pipetted into cells of an empty frame of honeycomb (as in Schulz et al., 1998). Two days of food is the minimum necessary for bees to survive to an age at which they can forage (Schulz et al., 1998). Frames used in both starved and well-fed colonies contained no pollen.

Foraging observations

Observations also were made to determine the number of foragers and age at initiation of foraging in each colony. These were done to determine whether starvation caused more bees to become precocious foragers at younger ages, as in Schulz et al. (1998). Observations continued for 3 days after the start of foraging by either colony in a trial. Entrances of both hives were observed alternately for 2–3 five-minute periods during the 30 min intervals between in-hive observations. Hive entrances were blocked with a mesh screen and foragers identified as bees returning with pollen on their corbiculae or with abdomens distended by a full crop. Foragers were then paint-marked on the abdomen, counted, and allowed to return to the hive.

Observations of social behaviors

Social behaviors were recorded whenever a focal bee was involved in a social interaction, regardless of whether it was the initiator or recipient of the behavior. Three categories of social behaviors were recorded: trophallaxis, grooming, and antennating (see Table 1). Trophallaxis was broken down into successful (food exchange), begging with no food exchange, and offering with no food exchange. Begging behavior was recorded when a tagged bee extended her proboscis toward another bee but received no food. Offering was recorded when a tagged bee opened her mandibles but made little or no contact with another bee. Successful trophallaxis was recorded when one bee extended her proboscis to receive food and contacted another bee whose mandibles were opened to give food for greater than 2 sec (Korst and Velthuis, 1982). Bees either donating or receiving food were recorded as performing trophallaxis. If a focal bee was engaged for less than 2 sec with another bee, she was recorded as either performing begging or offering accordingly. Antennation was only recorded when the focal bee rapidly touched the antennae or body of another bee without trophallaxis, even though successful trophallaxis often includes antennation (Free, 1956).

Each observation period consisted of 3 complete scans of the frame. Each scan was initiated from the upper left corner and continued from left to right until a tagged bee was observed. The bee's number and behavior were recorded and the scan continued row by row from the left to right until the bottom right corner was reached. Starved and well-fed colonies were observed consecutively each observation period by the same observer (MJV). There were four observation periods per day at approximately the same time each day, two in the morning and two in the afternoon with approximately 30 min between observation periods. Bees clumped together until the afternoon of the day following colony establishment (day 2) making only one observation period possible that day. Nine observation periods were completed for trial 1 on days 2–4, up until the onset of foraging. Thirteen observation periods were completed for trial 2 on days 2–5, including the first day of foraging (day 5). Sixteen observation periods were completed for trial 3, which included two days of foraging (days 5 and 6), with only three observation periods on day 6. Observations were extended in trials 2 and 3 to determine whether there were starvation-related differences in behavior after foraging began. In total, at least 4 hours were spent observing each colony each day. Because it was easy to determine which colony was starved or well-fed during behavioral observations, it was not possible to conduct this study blind with respect to treatment.

Colony censuses

Before the beginning of behavioral observations on days 1–4, all dead focal bees were recorded and removed from the observation hive to determine whether differential mortality occurred between the starved and well-fed colonies in each trial. The number of focal bees remaining was calculated each day by taking the starting number (n = 200) and subtracting the number of dead bees removed from each hive. This was expected to provide a complete count of mortality; no flight was observed prior to day 4 in any colony, so dead bees could not have been removed by undertakers. At the end of each experiment, a census was performed to determine the number of foragers and non-foragers remaining in each colony. This was done to assess whether differences in food stores changed the distribution of foragers and non-foragers in starved and well-fed colonies. The bees were anaesthetized with carbon dioxide, killed by freezing, and then individually examined for the appropriate thoracic and abdominal paint marks.

Statistical analyses

Differences in the distribution of foragers and non-foragers between starved and well-fed colonies were examined with 2 × 2 G-tests. Differences in the frequency of observed social behaviors prior to the onset of foraging were determined by Mann-Whitney U-tests performed on the total counts for each behavior in each trial. Because begging was found to be the only behavior that differed consistently between starved and well-fed colonies, regression analysis was used to test for the possible correlation between begging and the amount of time the bees were starved (prior to the onset of foraging). Although the data were collected over time, because each observation period was separated by at least 30 min (while the act of begging lasts only seconds), we assumed that observations in different periods were independent and thus appropriate for regression analysis. An exponential regression ($y = ab^x$) was found to best fit the distribution of occurrences of begging as a function of starvation duration, and this function was used for regression analyses.

Results

In three out of three trials, starved colonies produced significantly more foragers than well-fed control colonies (Fig. 1). These results are consistent with those of Schulz et al. (1998) and indicate that more bees in starved colonies experienced accelerated behavioral development.

In three out of three trials, differences in social interactions consistently were seen for begging behavior. The frequency of begging was significantly higher in starved colonies than in well-fed colonies prior to the onset of foraging (Table 1; Fig. 2). No other behavior consistently differed in frequency between starved and well-fed colonies (Table 1; Fig. 3).

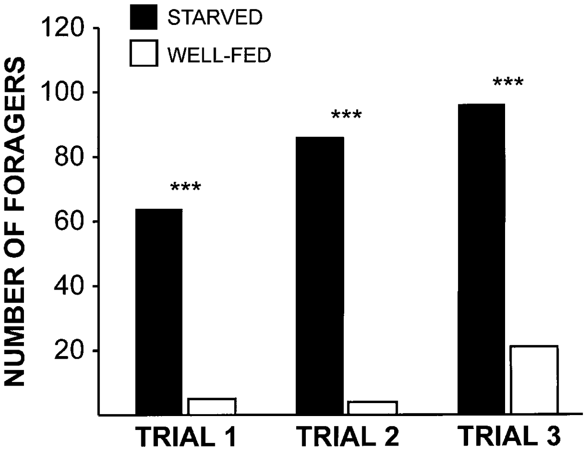

Figure 1. Number of foragers in starved and well-fed colonies after 3 days of observation, starting the day a forager was seen in either colony. *** indicates a significant difference in distributions of foragers and non-foragers between colonies ($p < 0.001$, 2 × 2 G-test)

Table 1. Differences in frequency of social interactions between starved and well-fed colonies (Mann-Whitney U-tests performed on the total counts for each behavior in each trial)

Behavior	Trial 1	Trial 2	Trial 3
Antennating	NS	starved ($p < 0.05$)	NS
Trophallaxis	NS	NS	NS
Grooming	NS	NS	NS
Offering	NS	NS	NS
Begging	starved ($p < 0.001$)	starved ($p < 0.001$)	starved ($p < 0.001$)

(starved = starved > well-fed; for all others there were no significant differences [NS]).

There was a significant relationship between the frequency of begging and the duration of starvation. In three out of three trials, begging in starved colonies increased exponentially with time (Trial 1: $y = 1.455 \cdot 1.457^x$; $R^2 = 0.967$, $p < 0.0001$; Trial 2: $y = 3.857 \cdot 1.343^x$, $R^2 = 0.96$, $p < 0.0001$; Trial 3: $y = 5.264 \cdot 1.259^x$, $R^2 = 0.867$, $p < 0.001$). No such increase was seen in well-fed colonies (Trial 1: $y = 4.329 \cdot 1.042^x$; $R^2 = 0.0825$, $p = 0.454$; Trial 2: $y = 1.319 \cdot 1.124^x$; $R^2 = 0.189$, $p = 0.242$; Trial 3: $y = 3.316 \cdot 1.103^x$; $R^2 = 0.184$, $p = 0.250$). In trials 2 and 3, where observations were extended beyond the onset of foraging, begging behavior dramatically decreased as the foragers began to bring in fresh food (Figs. 2B and 2C).

There were fewer bees in starved colonies than well-fed colonies at the end of the experiment (Table 2). This could reflect higher mortality of bees in starved colonies. Alternatively, perhaps more bees from starved colonies “drifted” into other nearby colonies where food was more plentiful. However, there was no evidence for drifting between the experimental colonies, and during the pre-foraging observation

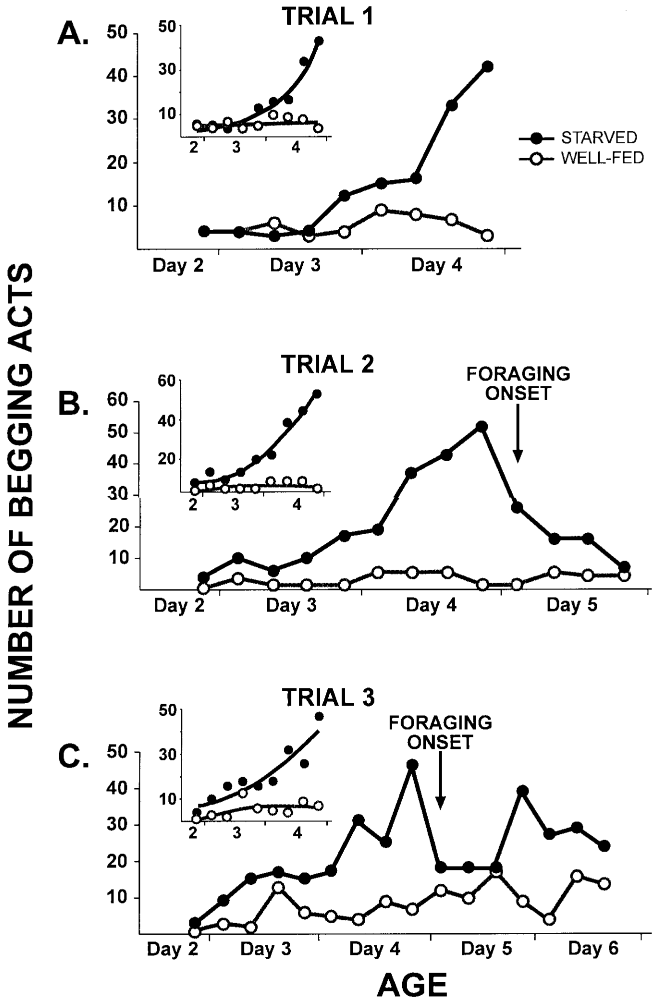

Figure 2. Number of observed begging acts in starved and well-fed colonies. The time course of the experiment in days is provided below each x-axis. Each data point represents the results of one observation period. When possible, four observation periods were completed each day. Arrows in Fig 2B and 2C indicate the day of onset of foraging in starved colonies. *Inserts* show exponential regressions of begging incidents with time prior to the onset of foraging (see Results for regression statistics). These inserts share the same data points and axes as their respective larger graphs for days 2–4

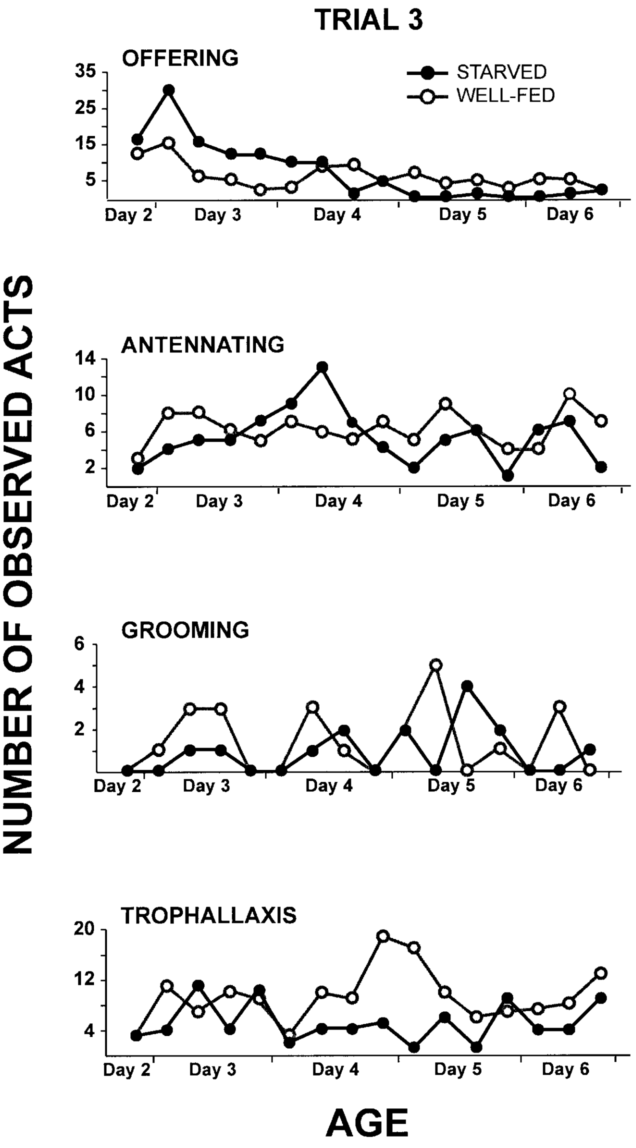

Figure 3. Number of observed acts of social behaviors other than begging in starved and well-fed colonies. Results from Trial 3 only as a representative data set. Each data point represents the results of one observation period. When possible, four observation periods were completed each day. No consistent differences were seen between starved and well-fed colonies in this or the other two trials (see Table 1)

periods, mortality of marked focal bees was similar and very low in both colony types (Table 2).

Discussion

The principal significance of these results is that they reveal patterns of change in one social behavior, begging, under starvation conditions that are known to accelerate behavioral development. This difference apparently does not occur as part of an overall change in social activity under starvation conditions; no other observed behaviors changed in frequency, including related behaviors such as offering food and successful trophallaxis. Furthermore, begging became more frequent as starvation presumably became more severe, and begging declined dramatically once foraging began in these colonies. It is not known whether the increase in begging is a causal factor in determining age of onset of foraging, or simply correlated with age of onset of foraging.

Huang and Robinson (1992; 1996) showed that foragers inhibit the development of precocious foragers, regardless of whether or not fresh food is being brought into colonies by foragers, and this effect requires some form of direct social contact (Huang et al., 1998). Furthermore, queen pheromone

Trial	Colony	Focal Bees Remaining in Hive			Total Bees Recovered (at end of experiment)
		day 2	day 3	day 4	
1	starved	197	196	185	539
	well-fed	199	197	197	861
2	starved	189	189	187	500
	well-fed	191	189	189	772
3	starved	192	191	190	663
	well-fed	198	198	197	766

Table 2. Number of focal bees in the hive each morning prior to observations. Each census was taken by counting dead focal bees inside the hive and subtracting them from the number of live focal bees from the previous day. Total Bees Recovered indicates the total number of all bees, focal and unmarked, recovered at the end of the experiment after foraging observations ceased

is known to inhibit the development of foragers (Pankiw et al., 1998b) and is transferred from worker to worker via trophallaxis (Naumann et al., 1991). Because precocious forager development is inhibited by worker-worker interactions, and because starvation promotes precocious forager development, we predicted an overall decrease in the number of social interactions in starved colonies compared to well-fed colonies. However, our results show that frequencies of social behaviors that require direct contact between individuals (i.e. successful trophallaxis, antennating, grooming) did not significantly differ in well-fed and starved colonies. The sample sizes for these behaviors were relatively low, but there are not even any hints of a change in total social interactions with starvation, except for the marked increase in begging. The only behavior that differed between starved and well-fed colonies, begging, consists of minimal social contact. Our results under starvation conditions do not provide evidence to support the general hypothesis that precocious forager development must be associated with a decrease in social interactions. Perhaps the duration and specific nature of the social contact may be important, but they were not studied here. Another possibility is that the factors that influence the age at onset of foraging in honey bee colonies under starvation conditions are different than when colonies have ample food supplies. Perhaps performing the experiment more times to employ a more powerful factorial design may have revealed subtler differences in other behaviors associated with starvation, but the results obtained to date provide no encouragement to do so.

We speculate that begging may be a cue associated with precocious forager development. Lindauer (1961) suggested that continuous and more vigorous solicitation of food from foragers by nurse bees induced potential foragers to leave the hive and forage. Honey bee foragers often beg for food from nestmates in the hive before leaving on a foraging trip (Nunez, 1970), perhaps to gain information on the colony's nutritional needs by assessing the "communal stomach" (Wilson, 1971) via trophallaxis. Effects of begging are also seen for fire ant (*Solenopsis invicta* Buren) foragers; starved nurses alter the amount and type of food being brought into a colony by actively soliciting the foragers (Sorensen et al., 1985). Thus begging itself may act as a signal of colony needs. The modality of this signal may be chemical or mechanical, and the number of failed solicitations could be an important factor. If a bee attempts to gain food from a nestmate and fails multiple times, this may be a signal either to the solicitor or the bee being solicited that foraging is required. This is similar to the recruitment of food-storer bees by nectar foragers performing the tremble dance (reviewed by Seeley, 1995). Foragers with a crop full of nectar that experience lengthy delays before engaging in trophallaxis with a food-storer bee will perform tremble dances to recruit new food storers (Seeley, 1992; Kirchner and Lindauer, 1994). Another example of encounter rate being associated with task performance has been shown for *Pogonomyrmex* ants; the probability of becoming a midden worker is correlated with the number of social contacts with midden workers (Gordon and Mehdiabadi, 1999). We speculate that begging could be involved in forager development in a similar manner; the number of times a bee solicits food and is rejected may be used as a cue that foraging is needed. To test this speculation requires manipulation of begging behavior; it is not immediately apparent how such manipulations can be accomplished.

Alternatively, it is possible that begging behavior is not a cue associated with colony food shortage, but simply a "symptom" that starvation conditions exist. Individual bees may be affected physiologically by starvation, leading to a change in rate of forager development, regardless of their social environment. Anecdotal evidence suggests that starved bees have increased brain levels of octopamine (Kaatz et al., 1994), a neurochemical known to affect division of labor in honey bee colonies (Schulz and Robinson, 2001). Therefore, bees may be becoming foragers due to an individual physiological response to starvation, and not a social cue.

Gathering information about colony needs via worker-worker interactions is well known in social insect colonies (see also Wilson, 1971; Seeley, 1995; Jeanne, 1996). Differences in begging behavior between starved and well-fed honey bee colonies were detected in this study, although it is not clear whether this has any functional significance for the regulation of precocious foraging. The solitary ancestors of social insects did not rely on social cues to react to changing needs such as starvation. In social insect colonies, food gathering (foraging) and food consumption have been uncoupled, and therefore it is difficult to know whether individual starvation is directly associated with foraging. In this study, the needs of the individual and colony were equivalent; both were starved. Thus future experiments must find ways to uncouple the needs of the individual and the needs of the colony to determine how behavioral development is regulated in honey bee colonies.

Acknowledgments

This manuscript is based on the dissertation of Maria Vermiglio, submitted in partial fulfillment of the requirements for a Master's of Science in Biology, University of Illinois at Urbana-Champaign. We thank J. Kuehn, A. Ross, and R. Kim for technical assistance, and also thank A. Barron, S. Beshers, G. Bloch, M. Elekonich, J. Sullivan, C. Whitfield, and two anonymous reviewers for comments that improved this manuscript. This research was supported by NIH grant DC03008 and HD07333 (administered by the Neuroscience Program, University of Illinois at Urbana-Champaign).

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