



Condition-dependent timing of comb construction by honeybee colonies: how do workers know when to start building?

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(Received 9 June 1997; initial acceptance 10 September 1997;
final acceptance 19 December 1997; MS. number: A7949)

ABSTRACT

Colonies of honeybees, *Apis mellifera*, initiate new comb construction only when two conditions are met: (1) they are currently collecting nectar and (2) they have filled their available comb beyond a threshold level with brood and food. In this study I explored how the individual workers responsible for building might use readily accessible local cues to acquire this global information on colony and environmental state. In particular, I tested the hypothesis that comb is built by nectar receivers (bees specialized to receive nectar from foragers and store it in comb cells) that experience increased distension of their crops. Crop distension could serve as a cue that both conditions for building have been satisfied, because the bees' crops will fill up as they receive nectar from successful foragers and have difficulty finding comb in which to store it. However, two findings led to rejection of this hypothesis. First, very few nectar receivers participated in comb building. Most builders came from another, unidentified subpopulation of workers. Second, potential builders showed no increase in crop size correlated with the onset of new comb construction or with the development of conditions that favour comb building. This was true both for identified nectar receiver bees and for bees belonging to the age cohort at which wax secretion and comb building reach their peak levels. The behavioural repertoire of comb-building bees suggests that these builders come from a pool of underemployed bees that may evaluate colony state by direct inspection of comb cells.

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Insect colonies are capable of remarkably swift and well-coordinated shifts in behaviour, mobilizing large labour forces to handle sudden feeding opportunities, defensive emergencies, or other contingencies. At the individual level, these shifts require workers to modify their behaviour appropriately as the task demands change. For this a worker needs accurate and timely information about colony and environmental state. In a large-colony species like the honeybee, the great difference in scale between a worker and the society as a whole can make acquisition of such information a daunting challenge. Bees and other social insects circumvent this problem in part by relying on subtle local cues correlated with global conditions, rather than directly assaying colony or environmental state (Seeley 1995). A honeybee colony's water collectors, for example, determine their colony's need for water by monitoring the time delays experienced in finding willing receiver bees, and the number of times receivers refuse to accept their loads (Lindauer 1954; Kühnholz & Seeley 1997). Analysis of

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other, less well-understood behavioural coordination phenomena should profit from identifying and testing analogous cues.

One such poorly understood phenomenon is a honeybee colony's control of the timing of new comb construction. Honeybees nest in cavities which they fill with sheets of comb whose cells serve both as brood-rearing chambers and as storehouses for pollen and honey. The bees' honey hoard fuels thermoregulation and brood rearing in the middle of winter, permitting them to field large foraging forces in late spring and to hasten the creation of reproductive swarms (Seeley & Visscher 1985). Colonies do not build all their comb at once, but rather add to it in pulses coinciding with periods of nectar intake (Hepburn 1986). The initiation of these building pulses depends on two conditions being satisfied: (1) the colony is currently collecting nectar and (2) the colony has filled its available comb beyond a threshold level with brood and food (Pratt 1997). Once building has started, it will continue as long as nectar intake persists, regardless of comb fullness (Pratt 1997). This strategy appears to enhance fitness by optimizing the trade-off between two costs: (1) the opportunity cost

of lacking sufficient empty comb to store rich but temporally unpredictable nectar flows; and (2) the energetic cost of investing prematurely in expensive wax secretion and comb construction.

The proximate mechanism by which this strategy is implemented is unknown. Monitoring both nectar intake and comb fullness is not a trivial feat for a worker bee. Nectar intake depends on external environmental features directly encountered only by foragers, whose work largely keeps them away from the storage comb. Moreover, foragers have inactive wax glands and do not normally participate in comb construction (Rösch 1927). On the other hand, the bees working inside the nest (from which the builders are drawn) lack direct experience of nectar conditions, but are in a better position to monitor comb state. Even so, they are faced with a potentially difficult and time-consuming task in a nest that can contain over 12 000 cm² of comb (Seeley & Morse 1976).

A cueing mechanism that could make their work easier is suggested by the age of building bees. Honeybees, like most social insects, exhibit a correlation between task performance and age (Rösch 1925, 1927; Ribbands 1952; Sakagami 1953; Seeley 1982). Young bees typically perform brood-related tasks, middle-aged bees work at the nest periphery in food storage and nest construction, and old bees fly outside the nest to forage. Wax secretion and building behaviour reach peak frequencies among bees 5–20 days old, overlapping the 10- to 20-day age range of nectar receiver bees (Rösch 1927; Seeley 1982, 1989; Hepburn et al. 1991; Muller & Hepburn 1992). These bees unload nectar from successful foragers and then either store it in comb cells or regurgitate it to other bees. This behaviour puts them in a good position to monitor both nectar intake (through their interactions with foragers) and comb fullness (through their experiences searching for storage locations). Moreover, they might be able to assay both conditions simultaneously by monitoring a single cue: the distension of their crops. Ribbands (1952) proposed that bees acting as nectar receivers may be required to hold incoming nectar in their crops if comb space is insufficient for storage. Although he did not specify a mechanism by which crop nectar could trigger wax secretion and comb construction, a reasonable hypothesis is that the bees are cued by increased stimulation of stretch receptors in the abdominal wall. Such receptors have not been described for bees, but are well known in several insect taxa (Dethier 1976; Chapman 1982).

Consistent with this mechanism, Hepburn & Magnuson (1988) found a positive correlation between the amount of wax secreted by house bees and the amount of nectar stored in their crops. More direct tests of this hypothesis have not been performed, hence I tested two of its specific predictions: (1) nectar receiver bees should participate heavily in comb construction and (2) an increase in the crop size of builders should precede the onset of construction. I also compiled a behavioural repertoire of building bees to identify other opportunities available to them for gathering information about comb fullness and nectar intake.

METHODS AND MATERIALS

Study Site, Colonies and Nests

All experiments were performed at Cornell University's Liddell Laboratory near Ithaca, New York (42°26'N, 76°30'W). Small colonies (4000–6000 workers) of largely Italian stock (*Apis mellifera ligustica*) were housed in three-frame observation hives (4.5 × 46.5 × 77.5 cm or 4.5 × 46 × 70.5 cm). The hives were kept in laboratory buildings but their entrances were fitted into wall apertures, giving the colonies' foragers access to the outside. To facilitate observation of interactions between returning foragers and nectar receiver bees, the hive entrance was fitted with a wedge which forced all traffic to enter and leave from one side of the comb. The glass wall on this side of the hive was divided into three, independently removable parts. This allowed me to remove and replace individual frames of comb with minimal disturbance to the colony. The hives contained frames of two standard sizes (shallow depth: 45 × 14 cm, and full depth: 45 × 23 cm) in combinations varied for each experiment, as described below.

Experiment 1: Marking Nectar Receiver Bees

Each experimental hive contained one full-depth frame of comb filled with brood, honey and pollen (the brood comb) and one shallow-depth frame of fully drawn but largely empty comb (the food storage comb). Above these frames was either an empty frame in which the bees could build new comb (replicate 1) or an empty space with no frame at all (replicates 2 and 3). The colony was enclosed in a cage (described below) to permit controlled feeding without interference from foreign bees.

The experiment began after the colony had gone several days without building any comb. Using the technique of Seeley (1989), I paint-marked large samples of the colony's nectar receivers. I marked 600 bees in the first replicate, 450 in the second and 280 in the third. (The variation across colonies reflects variation in the time spent marking. I did not attempt to identify all of the receivers in the colony or to mark a consistent proportion, but simply to mark a large enough sample to allow statistical inferences about their subsequent participation in comb construction.) I then replaced the storage comb with a full comb (replicate 1) or with an empty frame in which the bees could build new comb (replicates 2 and 3; in replicate 1 the colony already contained a building frame). The resulting combination of high nectar intake and scarce empty storage comb created circumstances likely to spur new comb construction (Pratt 1997).

Construction began 1 (replicate 1) or 2 (replicates 2 and 3) days after the marking of nectar receivers. The start of construction was easily detected by the appearance of a large festoon of bees hanging from the top of the previously empty building frame. I removed the frame and festoon, enclosed them in a plastic bag, and placed them in a freezer to kill the bees. After dark on the same day, when all of the foragers had returned to the nest, I froze

the hive itself to kill the remaining bees. I then counted the bees to determine the total colony population, the total number of marked bees and the numbers of marked and unmarked builders. I used *G* tests (Sokal & Rohlf 1981) to compare the number of marked bees observed among the builders to that expected if all the builders were recruited from the population of nectar receivers. The expected value was based on the assumption that the percentage of builders bearing marks should equal the percentage of receivers bearing marks. Calculation of the latter value required an estimate of the number of receivers in the colony. I used both a low and a high estimate (20 and 50% of the colony's total worker population) based on published data for colonies experiencing moderate and high nectar intake, respectively (Seeley 1995). This experiment was performed three times: 15–16 June 1994, 20–22 July 1994 and 5–7 June 1995.

Experiment 2: Tracking Crop Distension of Potential Builders

Potential builders were chosen from two groups: nectar receiver bees that were identified as described above, and bees that were known to belong to the age range during which wax secretion and building behaviour are most frequently observed. This allowed me to detect a role for crop size in triggering comb building even if the results of experiment 1 showed that nectar receivers are not the builders. Known-age bees were identified as follows. Several frames of capped brood taken from another colony were kept in an incubator at 35°C. From 18 to 27 August 1995, 170–200 freshly eclosed bees were removed from the incubator each day, given a distinctive paint mark and introduced to the observation hive through a hole in its entrance tube.

Beginning on 26 August, the colony was provided with 2.5 molar sucrose *ad libitum* every day. From 28 August to 2 September, 50–60 nectar receivers were paint-marked each day between 1100 and 1200 hours. At approximately 1400 hours on each of these days, 60 bees were removed from the colony: 30 of the receivers identified on that day and 30 bees from the marked cohort which had just reached 10 days of age. They were collected by removing the glass covering of the hive and scooping up each bee in a separate scintillation vial. I immediately refrigerated the vials and then rapidly dissected the crops from the cold-immobilized bees. At the end of each day, I measured the relative fullness of the colony's comb by noting the contents of 100 randomly sampled cells (for a description of the sampling technique see Pratt 1997). Daily measurements of comb fullness and crop sizes continued through to 2 September as the colony gradually filled its comb and eventually began to build new comb.

Experiment 3: Behavioural Repertoire of Builders

The experimental hive contained one full-depth brood comb, one full-depth food storage comb packed with honey and one empty frame in which the bees could

build new comb. On 1 July 1994, I fed the colony to induce construction and then paint-marked 80 bees that were seen actively building (chewing and working wax at the growing edge of the comb). To reduce building activity, I shut off the feeder and replaced the honey-filled storage comb with a completely empty comb. Reduced construction during this period improved the likelihood of observing the behaviour of building bees when they were not building.

To choose bees for observation systematically, I covered the front of the hive with a sheet of glass on which was drawn a five by eight square sampling grid. I successively sampled each square, closely examining it for the presence of marked bees. If I found a bee, I followed her for 3–5 min, recording every behaviour and the time at which it occurred. The behavioural categories into which worker actions were classified are given in Table 2. Most of these are readily understood from their names, but some require further explanation. 'Hang in festoon' refers to the large cluster of inactive bees surrounding the site of new comb construction. 'Build comb' includes both working at the growing edge of new comb and shaping, repairing or extending old comb. 'Chew cell caps' refers to bees scraping the wax caps of covered brood or honey cells, perhaps to thin the caps or collect wax for use elsewhere in the hive. Bees often crawled into cells where their actions could not be directly observed. I inferred their behaviour from the type of cell using the techniques of Sakagami (1953): long cell inspections (greater than 10 s in duration) were classified as 'Store honey', 'Pack pollen', or 'Attend larva'. When I could not determine the type of cell, I described the behaviour as 'Unknown long inspection'. 'Brief cell inspection' includes any insertion of the entire head into a cell for 10 s or less, regardless of the type of cell. 'Walk' includes any motion through the hive while not doing anything else. 'Stand' refers to complete motionlessness. 'Plane' consists of scraping the mandibles across a wood or glass surface (hive wall or frame). 'Fan' consists of standing still and fanning the wings to ventilate the hive. All observations were made 2–4 July 1994.

Flight Cages

For experiments 1 and 2, the colony had to be confined within a flight cage to control its nectar intake. Cages consisted of large (3.5 × 6.5 × 1.8 m) frames of electrical conduit supporting walls of nylon mesh (Pedersen et al. 1950). This design allowed foragers to see the sky and surrounding landscape and the cues these provide for normal flight and orientation, but prevented them from accessing the abundant nectar and pollen sources nearby. All of their food instead came from artificial feeders placed within the cage (for feeder design see Seeley 1995). The cages also prevented robbing of these feeders by foragers from nearby colonies.

Pilot studies suggested that caging the foragers in this manner sometimes inhibits comb construction. Hence, the bees were not confined when it was necessary to assay their inclination to build. For the first two replicates of experiment 1, the bees were caged only on the day when

Table 1. Results of three replicates of an experiment testing whether a colony's builders are recruited from among its nectar receivers

Date	Colony population	Estimated number of nectar receivers (20% of total population)	Number (%) of marked nectar receivers	Number of builders	Expected number (%) of marked builders	Observed number (%) of marked builders	G
16 June 1994	7637	1527	532 (34.8)	1449	504 (34.8)	43 (3.0)	906
22 July 1994	2416	483	380 (78.7)	123	97 (78.7)	2 (1.6)	357
7 June 1995	3716	743	227 (30.6)	279	85 (30.6)	13 (4.7)	119

G tests revealed significant differences between observed and expected values in all three replicates ($P \leq 0.001$).

nectar receivers were marked. For experiment 2 and the third replicate of experiment 1, the bees were caged throughout, but the cage roof was perforated with approximately 10 square holes 5–10 cm wide. Foragers could escape through these holes and forage in the countryside, but the cage still prevented foreign bees from discovering any feeders placed within it. Foragers that left the cage in this way were able to return to the nest through a small hole in the side of the tunnel connecting the hive entrance to the cage. Because foragers had free access to natural nectar sources, this technique did not allow complete control of the colony's food intake. It did, however, permit the maintenance of a minimal food intake and the paint-marking of foragers, requirements for both experiments 1 and 2.

RESULTS

Experiment 1: Marking Nectar Receiver Bees

Marked bees appeared in the building festoon in all three replicates, indicating that some nectar receivers switched to comb construction. In all cases, however, the proportion of marked bees among the builders was significantly less than the proportion expected under the null hypothesis that all of the builders were former nectar receivers (Table 1). This was true for both the high and low estimates of the total number of receivers in the colony (G test: $P < 0.001$). Rejection of the null hypothesis becomes less likely with increasing values of this total number. However, the differences were still present under the assumption that 75% of the colony's workers were nectar receivers (G test: $P < 0.05$). Proportions this high have not been reported and seem quite unlikely. Given that 25% of a colony's population may be engaged in foraging under favourable conditions (Seeley 1995), such an extreme value would leave no workers available for other vital tasks such as brood care. Thus, while it is clear that some of the builders were recruited from among the nectar receivers, most probably came from some other subpopulation within the colony.

Experiment 2: Tracking Crop Distension of Potential Builders

As the experimental colony collected nectar at a high rate and filled its storage comb, the number of empty cells gradually declined (Fig. 1). On 2 September, with fewer than 5% of cells completely empty, the colony began to construct new comb. The crop size of both 10-day-old bees and nectar receivers showed considerable variation across days of the experiment (Fig. 1). Both bee group and day had significant effects on crop weight (ANOVA: bee group: $F_{1,283} = 14.92$, $P < 0.0001$; day: $F_{5,283} = 2.83$, $P < 0.05$; interaction: $F_{5,283} = 0.19$, NS). Nectar receivers had consistently larger crop sizes than 10-day-old bees. However, no trend could be found relating daily variation in crop size to either level of comb fullness (correlation: 10-day-old bees: Pearson's $R = -0.006$, NS; receiver bees: Pearson's $R = -0.07$, NS) or size of nectar intake (correlation: 10-day-old bees: Pearson's $R = 0.14$, NS; receiver bees: Pearson's $R = 0.10$, NS). Also, no evidence was found for increasing crop size over time as the colony filled its comb and began to build (linear regression: 10-day-old bees: $F_{1,156} = 0.053$, NS, $R^2 = 0.00036$; receiver bees: $F_{1,135} = 0.59$, NS, $R^2 = 0.0044$).

Experiment 3: Behavioural Repertoire of Builders

Despite my efforts to discourage construction, building continued intermittently and at a low rate throughout the observation period. This may have reflected continued nectar intake from natural sources, judging by the presence of waggle dancers and a small increase in the number of honey-filled cells in the initially empty storage comb. Moreover, another colony at Liddell, whose hive rested on a scale, gained no weight on the first and second days, but gained 0.05 kg on the third day. (A weight gain of zero indicates a light nectar intake, since the colony would otherwise lose weight.) None the less, construction was much reduced compared to the period during which the builders had been marked.

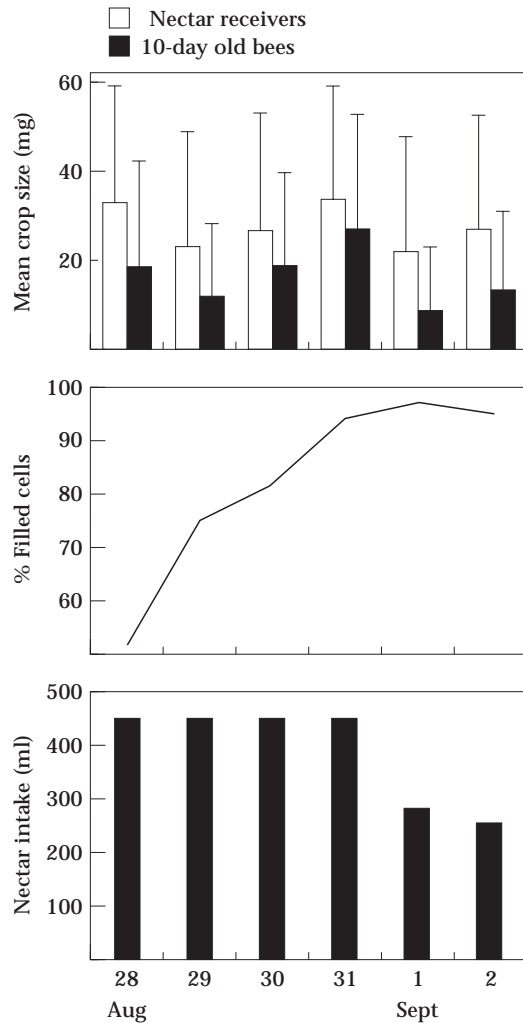


Figure 1. Results of experiment 2 tracking changes in crop weight of nectar receiver bees and 10-day-old bees as a colony gradually filled its comb with honey. The bees began building comb on 2 September.

Marked bees were observed over 3 days for a total of 8.3 h. **Table 2** shows the cumulative number of minutes the sampled bees performed each activity, as well as the relative proportion of time spent in each activity. Bees spent most of their time (54.6%) standing still or walking through the nest, performing no obvious task. Among tasks, building behaviours were by far the most frequent, taking up 14.7% of the bees' time. Food storage and general nest-maintenance activities each comprised 5.7%. Brood care and foraging were both quite rare (1.7% and 0.2%, respectively), although the foraging measure is likely to be an underestimate because foragers spend much of their time outside the nest and thus elude observation. [Lindauer's \(1952\)](#) continuous observation of a single forager showed that she spent only 25% of her time inside the nest on her busiest foraging day. Thus the actual proportion of time spent in foraging tasks may be 1.0% or more.

Although the cumulative time spent in brief cell inspections was low (1.3% of total observation time), these

Table 2. Behavioural repertoire of comb-building bees, including both the absolute time builders were observed performing each behaviour and each behaviour's percentage of the total observation time

Behaviour	Time (min)	Percentage
Build		
Hang in festoon	16	3.1
Build comb	49	9.9
Chew cell caps	8	1.7
Store food		
Pack pollen	16	3.2
Store honey	5	1.0
Regurgitate	4	0.8
Receive food	4	0.7
Brood care		
Attend larva	9	1.7
Forage		
Waggle dance	1	0.2
Groom		
Groom self	74	14.8
Groom other	3	0.5
Other		
Walk	234	46.8
Stand	39	7.8
Plane	14	2.7
Fan	13	2.7
Brief cell inspection	6	1.3
Unknown long inspection	4	0.8
Handle trash	2	0.3
Total	500	

occurred fairly often. A total of 148 brief inspections were seen in the 8.3 h of observations, a rate of about one inspection every 3.5 min. Each inspection lasted no longer than 10 s and was typically much shorter. Every kind of cell (honey, pollen, brood, empty) received brief inspections.

DISCUSSION

The data presented here do not support the hypothesis that comb is built by nectar receivers that detect the need for new comb via cues derived from the increasing size of their crops. Two findings in particular contradict the hypothesis. First, while some nectar receiver bees participated in comb construction, the number building was very small and far less than would be expected if all builders were recruited from the ranks of nectar receivers. Second, potential builders showed no increase in crop size correlated with the onset of new comb construction or with the development of conditions known to favour comb building. This was true both for identified nectar receiver bees and for bees known to belong to the age cohort at which wax secretion and comb building reach their peak levels.

Who Are The Builders?

The paucity of nectar receivers among the comb builders seems to contradict previous findings that these tasks are performed by bees of the same age caste ([Rösch](#)

1927; Seeley 1982, 1989; Hepburn et al. 1991; Muller & Hepburn 1992). However, earlier studies measured the relative frequency of behaviours among aggregates of bees over large age ranges. The age ranges of building and food storage overlap extensively, but not completely. Food storage commonly occurs somewhat later, and is frequently the last in-nest task a bee performs before she flies out to finish her life as a forager. This was apparent in the fact that many bees showed up at the nectar feeder within 1 day, or even within a few hours, of being marked as nectar receivers. Moreover, even among bees of the same age, some may specialize on food storage and others on comb building, without affecting the aggregate behavioural frequencies of the age cohort.

From the perspective of the colony's functional design, the low frequency of nectar receivers among builders is perhaps not surprising. Because colonies start building only when they are collecting nectar, diverting labour from food storage to construction could reduce the colony's nectar intake rate. To avoid this, builders may instead be drawn from a pool of inactive or underemployed reserves. While direct evidence for this hypothesis is lacking, it is consistent with the observation that builders spent most of their time away from construction sites simply standing still or walking through the hive (Table 2). It is also consistent with Kolmes' (1985) observations of the effect of comb construction on the frequencies of other behaviours in the colony. He compared colonies in hives fully stocked with comb to matched colonies whose workers were required to build some of their comb. The wax-deprived bees, in addition to devoting more time to comb building, spent more time walking and less time grooming and standing still. No other behavioural differences were detected. These results make sense if builders were recruited from reserves engaged primarily in standing and grooming, rather than bees working at other tasks, such as food storage or brood care.

Other observers of social insects have noted high levels of inactivity consistent with the presence of labour reserves. (Lindauer 1952; Herbers & Cunningham 1983; Hölldobler & Wilson 1990). This is somewhat puzzling, since maintenance of reserves does not seem compatible with a colony's maximization of ergonomic efficiency (Kolmes 1986). Indeed, Oster & Wilson (1978) saw reserves as an energetically expensive precaution against environmental unpredictability used by colonies with many highly specialized and behaviourally inflexible castes. They contrasted this strategy with reliance on a smaller number of less specialized castes whose members can switch tasks when confronted with environmental contingencies. More recent theoretical and empirical work has underscored the prevalence of dynamic task switching by flexible generalists as the means by which a colony adaptively allocates labour (Calabi 1988; Gordon 1989, 1996; Sendova-Franks & Franks 1993; Tofts 1993; Bourke & Franks 1995). Rather than specializing on a few tasks and remaining idle when those tasks are not in demand, workers can remain constantly productive by switching between behaviours as needed. Given this kind of flexibility, why should a colony maintain reserves?

Part of the answer may lie in circumstances under which switching active workers between tasks imposes energetic expenses exceeding the cost of reserves. For example, many species, including the honeybee, rely on short-lived and unpredictable food bonanzas. These windfalls are likely to cause large changes in the total labour demand placed on the colony. Unlike shifts in the relative demands for different tasks, these absolute increases cannot readily be addressed by task switching. A colony unprepared for pulses of intense labour demand will miss out on major feeding opportunities. The need for mobilization of excess labour will be especially high in cases where more than one critical task is simultaneously in demand, such as comb building and nectar storage.

Moreover, task switching might sometimes be too slow to handle rapidly changing labour demands. If the development of traits required to perform a task well takes longer than the time frame during which need for the task typically arises, it may pay a colony to keep underemployed specialists on hand to spring into action when their work is needed in large amounts. Comb construction, for instance, relies on an adequate number of bees with functional wax glands. The normal development of these glands in young bees takes place over approximately 1 week (Rösch 1927). Also, when old bees whose wax glands have degenerated are induced to resume construction by isolating them in groups lacking comb and young bees, wax secretion and comb construction resume only after 4–5 days of glandular regeneration (Boehm 1965). Even 12-day-old bees whose glands are at peak activity require 24–48 h to make a medium-sized wax flake (Hepburn & Muller 1988; Hepburn et al. 1991).

What is the Proximate Mechanism Triggering Construction?

The discovery that few builders also work as nectar receivers does not in itself preclude a role for crop size cues in triggering construction. Nectar receivers pass on much of their nectar loads to other hive bees rather than storing it immediately in comb cells (Seeley 1989). Crop distension experienced by these 'downstream' bees may stimulate some of them to begin building. However, the results of experiment 2 suggest that this is not the case. Even among bees 10 days old, near the peak of the age distribution of comb builders (Rösch 1927; Hepburn et al. 1991; Muller & Hepburn 1992), mean crop size did not increase as a colony collected nectar, filled its comb and started to build. Crop size varied between days and may have been influenced by the size of the nectar intake, judging by the especially low mean crop weights on the last 2 days of the experiment, when nectar intake was reduced (Fig. 1). None the less, increases in crop size did not reflect the conditions that trigger building: simultaneous nectar intake and suprathreshold comb fullness. This result seems to contrast with the observations of Hepburn & Magnuson (1988), who found a correlation between engorgement and wax secretion. However, this correlation does not demonstrate a causal relationship between the two phenomena. An alternative explanation is suggested by the high rate of absconding noted in the

earlier study. The observed engorgement and wax secretion may have reflected preparation for swarming, after which the bees would need both food stores in their crops and ample wax with which to build a new nest.

Closer examination of the threshold level of comb fullness at which building typically starts indicates why crop size may be an inadequate cue. The bees should not experience a greater need to use their crops for storage until they are running short of empty comb in which to store incoming nectar. The results of experiment 3 seem to confirm this, since building did not start until less than 5% of the available comb was empty. Nectar collection from the feeder declined at this point, perhaps indicating reduced storage efficiency. (An alternative explanation is increased competition from natural nectar sources. Because intake from flowers was not measured, it is impossible to distinguish these hypotheses.) However, more detailed studies have shown that colonies do not usually wait for such congestion, but rather start building even when ample empty comb is still present (Pratt 1997). That is, while they must surpass a threshold fullness before beginning construction, this threshold is quite low. In balancing the energetic costs of wax secretion and the opportunity costs of missing out on rich but brief nectar flows due to a lack of storage space, the bees seem to lean more toward avoiding the latter costs (Pratt 1997).

This leaves unanswered the question of how potential builders assay the conditions at which building is appropriate. One possibility is that nectar-bearing bees measure how long it takes them to find a cell suitable for honey deposition (Kelley 1991). Another hypothesis is suggested by the results of the behavioural repertoire presented here. Potential builders may directly assay comb state by frequent brief inspection of cell contents. As they wander through the hive inspecting cells, they may continually modify their current perception of the state of comb fullness. If they can independently assay the presence of nectar intake (e.g. through the frequency with which other bees solicit them to receive nectar), they will have access to both necessary pieces of information. Thus, the apparently aimless meanderings of bees through the hive may have real utility for the colony, as the workers monitor colony state until they perceive conditions demanding further action (Lindauer 1952). Neither of these intriguing hypotheses has been subjected to experimental test.

Acknowledgments

I thank Tom Seeley, Kern Reeve, Cole Gilbert, Nick Calderone, Scott Camazine and an anonymous referee for comments on the manuscript. I am grateful to Roger Morse for providing the flight cages used in experiments 1 and 2. Funding for this project was provided by the United States Department of Agriculture (Hatch grant NY(C)-191407) and by a grant from the Cornell University chapter of Sigma Xi. I was also supported by a training grant from the National Institute of Mental Health.

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