Effect of Empty Comb on Hoarding Behavior and Honey Production of the Honey Bee[1,2]

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ABSTRACT

J. Econ. Entomol. 71: 757–759 (1978)

Honey bees, *Apis mellifera* L., in laboratory cages supplied with either 46.75, 93.50, or 140.25 cm² of comb surface area (CSA) hoarded 0.105, 0.135, and 0.188 ml of sucrose solution/bee/day. These differences are highly significant.

Field colonies of honey bees were supplied with empty honey storage combs having either 4.06 or 1.88 m² of CSA. Resultant colony weight gains were 51 and 36 kg, respectively. The colonies were then moved to a 2nd apiary location and the CSA treatments were reversed using fresh storage combs. At the 2nd apiary location, 4.06 and 1.88 m² of CSA resulted in 58 and 47 kg of colony weight gain, respectively. Analysis of variance showed the difference in response to treatment was highly significant. Under both laboratory and field conditions greater CSA resulted in greater nectar gathering by honey bees. These experiments support the hypothesis that empty comb functions as a stimulus of nectar-foraging behavior.

Hoarding behavior in honey bees, *Apis mellifera* L., has been explored in laboratory cages (Kulinčević and Rothenbuhler 1973) and honey production measurements from field colonies were significantly correlated with such laboratory tests (Kulinčević et al. 1974). Work at our laboratory (Rinderer, unpublished data) suggested that a greater surface area of comb available to bees in laboratory cages resulted in a greater rate of hoarding. The experiments reported here were designed to further explore this effect of empty comb on bees in laboratory cages and also to explore the effect of empty comb on the behavior of field colonies.

Materials and Methods

Laboratory cages (Kulinčević et al. 1973) were fitted with 1, 2, or 3 pieces of dark comb having totals of 46.75, 93.50, and 140.25 cm² of exposed surface area, respectively. While comb position has no apparent effect on hoarding behavior (Rinderer, unpublished data), comb pieces were arranged at random among the 3 places available for comb in the cages. Each hoarding cage was supplied with one feeder that contained 50% (wt/wt) sucrose in water solution; a 2nd feeder contained water; and a 3rd contained a pollen substitute (Rinderer and Elliott 1977).

Each hoarding cage received 50 worker bees that ranged in age from 1–24 h. This total was composed of ca. equal numbers of bees from each of 3 colonies produced by naturally mated queens. Combs of emerging adults from these colonies were held in 35° C incubator, and bees of appropriate age were collected from them.

Each hoarding cage was inspected daily for 7 days; dead bees were counted and removed, the amount of sucrose solution removed from the feeder was measured, and all feeders were replenished. After 7 days, the bees were removed from the cages, and numbers of empty cells and cells containing stored sucrose solution were counted.

Data on the volume of sucrose solution removed during 7 days, the time required to remove 20 ml of solution, and the numbers of cells used for storage were submitted to analysis of variance and least significant difference tests.

For the field experiments, 20 colonies of bees were chosen from our laboratory's colonies on the basis of ca. equal numbers of bees, equal size brood nests, and equal honey and pollen stores. Each colony was derived from a queen of open-mated stock. These colonies were moved to an apiary location near St. Gabriel, LA, prior to the spring (Apr. 1977) nectar flow. Based on random selection, half of the colonies were given empty honey storage combs with 2.03 m² of comb surface area (CSA) and half were given storage combs with 0.94 m² CSA. Each colony was weighed prior to nectar flow. After 10 days of nectar flow, colonies were inspected and all were judged to have 1/2–3/4 of all the storage combs filled with nectar and ripening honey. At this inspection, each colony was given additional storage combs with a CSA equal to that already supplied. These combs were placed just above the brood nest. Thus, in one group of colonies each colony was given a total of 4.06 m² of CSA, and in the other group, each colony was given a total of 1.88 m² of CSA.

After 5 additional days, the nectar flow stopped; colonies were again weighed, and all storage combs were removed from the colonies. All colonies were then transported to a new location near Welch, LA, with an ongoing nectar flow. Treatments on the 2 groups of colonies were reversed. Those colonies that previously had initially received 0.94 m² of CSA were given 2.03 m² of CSA. Those that had received 2.03 m² of CSA were given 0.94 m² CSA. Each colony was again weighed.

After 3 days of nectar flow, the colonies were inspected. Since all combs were 1/2–3/4 filled with nectar and ripening honey, additional CSA was supplied such that one group of colonies received a total of 4.06 m² CSA and the other group received a total of 1.88 m² CSA. After 7 additional days of nectar flow at the Welch location, all comb space in all colonies was filled with nectar and ripening honey to the extent that distinctions between larger and smaller amounts of empty CSA available in the colonies were vague. At this time, the colonies were again weighed.

Early in the experiment, one colony became queenless and was dropped from the experiment. Calculations were made of net weight gain for each of the other colonies in both locations (total weight minus original weight minus

[1] Hymenoptera: Apidae.

[2] In cooperation with Louisiana Agricultural Experiment Station. Received for publication Apr. 25, 1978.

Table 1.—Laboratory hoarding measurements and comb-space usage of bees provided with 3 surface areas of empty comb at 35° C, 50% RH.

Surface area of empty comb (cm^2)	Time to remove 20 ml from feeder (days)	ml/bee/day	Cells with stored sucrose	
			Total no.	%
46.75	5.4±0.16[a]	0.105±0.007[a]	180.7±3.0[a]	77.14±5.33[a]
93.50	4.6±0.16[a]	0.135±0.010[a]	360.4±4.0[a]	54.19±3.82[a]
140.25	3.9±0.18[a]	0.188±0.006[a]	537.7±6.2±a	51.21±2.18[a]

[a] $P < 0.01$.

weight of additional equipment). These calculations were submitted to analysis of variance.

Results and Discussion

In the laboratory experiment, greater surface areas of comb caused greater hoarding (Table 1). Bees with 46.75, 93.50, and 140.25 cm^2 of comb surface consumed or stored 20 ml of sucrose solution during means of 5.4, 4.6, and 3.9 days, respectively. Each response level is significantly different from the others. When hoarding is calculated as ml of sucrose solution/bee/day, the same trends were noted. One, 2, and 3 pieces of comb caused significantly different ($P < 0.01$) hoarding rates of 0.105, 0.135, and 0.188 ml/bee/day, respectively.

The appearance of the combs after the 7-day hoarding period highlighted the observed effect. Treatments of one, 2, and 3 pieces of comb caused significantly different ($P < 0.01$) averages of 180, 360, and 537 cells containing hoarded sucrose solution. In the 3 treatments, 77, 54, and 51% of the available cells contained stored sucrose solution. While the 77% filled cells associated with the one-comb treatment was significantly higher than 54 or 51%, in all cases ample space was left for additional storage. Thus, response differences were not caused by lack of space.

In the field experiment, greater empty CSA resulted in greater net weight gain (Table 2). At the St. Gabriel apiary location, colonies that received 4.06 m^2 of CSA had an avg of 51 kg of weight increase while those receiving 1.88 m^2 of CSA had a smaller avg of 36 kg. The same treatment effect occurred at the Welch apiary location. Colonies with the greater CSA averaged 58 kg of increase while those with the lesser CSA averaged 47 kg.

Table 2.—Surface area of empty comb available to field colonies of honey bees tested at 2 locations and the resultant weight increase as a consequence of nectar hoarding.

Colony group	No. of colonies	Total m^2 of comb surface supplied for nectar storage	Avg kg[a] of weight increase/colony±SE
	St. Gabriel apiary location		
1	9	4.06	50.82±4.50
2	10	1.88	36.14±3.77
	Welch apiary location		
1	9	1.88	47.45±4.55
2	10	4.06	57.91±5.00

[a] Analysis appears in Table 3.

The striking differences associated with different levels of empty CSA were highly significant ($P < 0.008$) (Table 3). The origins of these differences were illuminated by colony observations. During the colony inspections which resulted in supplying additional CSA to the colonies, all combs, regardless of colony treatment or location, were ½–3/4 filled with nectar and ripening honey. Furthermore, at all times during the experiment, every colony had empty storage space available. Thus, differences did not occur as a result of lack of storage space in those colonies that received less CSA. Clearly, the bees responded differently to the different amounts of CSA.

Analysis of variance revealed that significant differences in colony weight gain arose from location differences (Table 3). Average weight gain differences between the 2 locations were significant ($P < 0.05$), probably as a consequence of differences in nectar flow conditions. Such differences in nectar flow conditions routinely occur and stem from differences in floral sources, weather, soil types, etc.

No significant interaction between amounts of CSA and apiary locations occurred in the experiment (Table 3). However, both nectar flows were strong. Other nectar flows might result in observed interactions.

We conclude that large amounts of CSA, at least under strong nectar flow conditions, result in increased nectar gathering by bees and consequently generate greater honey production.

Results of these experiments provided strong evidence that empty comb functions in a hive as a stimulus of nectar-foraging behavior. With empty comb accepted as a stimulus, a model explaining features of nectar foraging can be developed. First, the nature of what von Frisch (1967) termed "scout bees" becomes clear. Scout bees are those with a threshold to some quality of empty comb low enough that empty comb stimulates them to seek nectar sources. Upon their return to the hive they dance and recruit addi-

Table 3.—Results of a 2-way analysis of variance of colony weight increase data presented in Table 2.

Source of variation	df	F value	Probability
Apiary location	1	4.03	0.052[a]
Comb treatment	1	7.87	0.008[b]
Location by treatment	1	0.25	0.622[c]

[a] Significant.
[b] Highly significant.
[c] Not significant.

tional foragers. The number and intensity of dances has been seen to increase in colonies with a small amount of honey (Wittekindt 1961). The amount of honey in the colony was interpreted as the stimulus for this activity. With the information now available, empty comb appears as the more likely stimulus. Second, empty comb may predispose the recruits to be more receptive to the dance of returning scout bees and thus result in more candidates for recruitment. Third, empty comb may provide a continuing source of stimulation which elicits a continuing high level of nectar foraging. This stimulation may either operate directly on foraging bees or indirectly through nonforaging bees which receive nectar loads from returning foragers.

Clearly, other stimuli, e.g., the presence of unsealed brood (Doull 1971), tend to draw bees into a variety of other activities. Nectar foraging can be seen to vary in intensity as the stimulus of empty comb becomes more or less available in the colony.

The field experiment has specific limitations when the technique is considered for practical application. Both nectar flows experienced during the experiment were exceptionally strong, and the strength of nectar flows may well influence response to large amounts of storage CSA by bee colonies. Nectar flows of less strength may result in many combs only half filled with honey or full combs in the centers of stacked storage chambers with empty combs to the sides. While the overall production increases may still be greater with more CSA, the technique may not prove to be economic in areas with poor nectar flows.

Acknowledgment

J. Harbo, Research Entomologist, and E. Jensen, Biological Technician, at our laboratory, facilitated this research; L. Mornhinveg and C. Carter Jr., student workers, assisted with the beekeeping; and J. Perry, commercial beekeeper, generously supplied access to the Welch, LA, apiary location.

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JOURNAL OF ECONOMIC ENTOMOLOGY