Empty Comb Stimulates Honey Production[1, 2]

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HOARDING behavior measurement is a recently proposed technique for predicting the honey production ability of stocks of honey bees (Kulincevic and Rothenbuhler, 1973; Kulincevic *et al.,* 1974) which is still being evaluated for its usefulness to bee breeders. This technique involves putting a small number of bees in a laboratory cage supplied with a piece of comb and then measuring the rate at which the bees remove sugar syrup from a gravity feeder and place it in the comb.

A LABORATORY EXPERIMENT

While working with the hoarding test, we conducted an experiment evaluating the effect of different amounts of empty comb on hoarding rate. For this experiment, laboratory hoarding cages were fitted with one, two, or three pieces of dark brood comb having totals of 46.75, 93.50, and 140.25 cm^2 of exposed surface area, respectively. Each cage was supplied with 50 adult worker bees, ages 1-24 hr., a gravity feeder containing 50% sugar syrup, a second feeder containing water, and a third containing a pollen substitute (Rinderer and Elliott, 1977). The cages were inspected daily for 7 days; the milliliters of sugar syrup removed from the feeder were measured; and all feeders were replenished. After 7 days, the bees were removed from the cages, and the numbers of empty cells and cells containing stored sugar syrup were counted. Finally the data on the volume of sugar syrup removed during 7 days, the time required for removal of 20 ml. of syrup, and the numbers of cells used for storage were submitted to statistical analysis.

The analysis showed that greater surface areas of comb caused greater hoarding (Table 1). Bees supplied with 46.75, 93.50, and 140.25 cm^2 of comb surface area consumed or stored 20 ml. of sugar syrup in an average 5.4, 4.6, and 3.9 days, respectively. Each rate was statistically different from the others. When the hoarding rate was calculated as milliliters of sugar syrup taken per bee per day, the same trends were apparent. One, two, and three pieces of comb resulted in hoarding rates of 0.105, 0.135, and 0.188 ml. per bee, and each rate was statistically different from the others.

The appearance of the combs after the 7-day hoarding period highlighted the observed effect. One, two, and three pieces of comb contained averages of 180, 360, and 537 cells containing hoarded sugar syrup. Converted to percentages, these numbers represent 77, 54, and 51% of the available cells. The 77% of cells containing stored syrup that occurred with the one-comb treatment was statistically higher than 54 or 51% that occurred with the other treatments. However, in all cases there was ample space left for additional syrup storage. Therefore, the differences in hoarding that we observed were not caused by lack of space.

We found these results quite exciting. Not only had we learned more about conducting a hoarding experiment, we also learned that empty comb might possibly stimulate nectar gathering and honey production. We decided to test this possibility with a field experiment.

A FIELD EXPERIMENT

Twenty colonies of bees were chosen from our laboratory's colonies on the basis of approximately equal numbers of bees, equal size brood nests, and equal honey and pollen stores. Each colony was derived from open-mated stock common to southern Louisiana. These colonies were moved to an apiary location near St. Gabriel, La., prior to the spring (April 1977) nectar flow. Half of the colonies (selected at random) were given empty honey supers containing 2.03 m^2 of comb surface area, and half were given empty supers containing 0.94 m^2 of comb surface area. Each colony was weighed prior to the nectar flow. (Early in the experiment one colony became queenless and was dropped from the study.)

After 10 days of nectar flow, the colonies were inspected and all were judged to have ½-¾ of all the storage combs filled with nectar and ripening honey. At this inspection, each colony was given additional supers containing comb equal to that already supplied. These supers were placed just above the brood nests. Thus, in one group of colonies each colony was given supers containing a total of 4.06 m^2 of comb surface area, and in the other group each colony was given supers containing a total of 1.88 m^2 of comb surface

Table 1. — Laboratory hoarding measurements and comb-space usage of bees provided with three surface areas of empty comb.

Surface area of empty comb (cm^2)	Time to remove 20 ml from feeder (days)	ml per bee per day	Cells with stored syrup	
			Total No.	%
46.75	5.4[a]	0.105[a]	180.7[a]	77.14[a]
93.50	4.6[a]	0.135[a]	360.4[a]	54.19
140.25	3.9[a]	0.188[a]	537.7[a]	51.21

[a] Statistically different from measurements for all other surface areas of empty comb.

area. After 5 additional days the nectar flow stopped: colonies were again weighed, and all honey supers were removed.

All colonies were then transported to a new location near Welsh, La. where there was an ongoing nectar flow. Treatments in the two groups of colonies were reversed. Those colonies that previously had initially received supers with 0.94 m^2 of comb surface area were given 2.03 m^2 of comb surface area. Those that had received 2.03 m^2 of comb surface area were given 0.94 m^2 of comb surface area. Each colony was again weighed. After 3 days of nectar flow, the colonies were inspected. Since all combs were ½-¾ filled with nectar and ripening honey, additional supers were supplied such that one group of colonies received combs having a total of 4.06 m^2 of surface area, and the other group received combs having a total of 1.88 m^2 of surface area.

After 7 additional days of nectar flow at the Welsh 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 available empty comb were vague. At this time, the colonies were again weighed.

Calculations were made of net weight gain for each of the colonies in both locations (total weight minus original weight minus weight of additional equipment). These calculations were submitted to statistical analysis.

We found that greater empty comb surface area resulted in greater net weight gain (Table 2). At the St. Gabriel apiary location, those colonies receiving 4.06 m^2 of comb surface area had an average of 51 kg. of weight increase while those receiving 1.88 m^2 of comb surface area had a smaller average increase of 36 kg. The same effect occurred at the Welsh apiary location. Those colonies with more supers averaged 58 kg. of increase, while those with fewer supers averaged 47 kg. of increase. Statistical analysis showed that such differences would occur by chance only 8 in 10,000 times (Table 3).

The origins of the observed differences were illuminated by colony observations. During the colony inspections which resulted in supplying additional supers to the colonies, all combs, regardless of how many were present, were ½-¾ 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 fewer supers. Clearly, the bees responded differently to the different amounts of comb available.

We concluded that large amounts of comb, at least under strong nectar flow conditions such as we encountered, result in increased nectar gathering by bees and consequently generate greater honey production.

Table 2. — Surface area of empty comb available to field colonies of honey bees tested at two 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
		St. Gabriel apiary location	
1	9	4.06	50.82
2	10	1.88	36.14
		Welsh apiary location	
1	9	1.88	47.45
2	10	4.06	57.91

[a] The differences associated with the two levels of comb are statistically different.

Table 3. Hoarding response of bees caged with one of two amounts of comb for 3 days.

Surface areas of comb (cm^2)	Numbers of replicates	Ml per bee sugar syrup per day	Average cells with sugar syrup solution
46.75	24	0.111[a]	12.0
140.25	24	0.145	21.5

[a] Differences associated with the different levels of comb are statistically different.

A SECOND LABORATORY EXPERIMENT

On the basis of the results of the field experiment, we suspected that the past experience bees had with empty comb might influence foraging rate. To test the effect of past experience with comb and to further test the hypothesis of the stimulation of empty comb, we transferred bees from one level of comb to another in a laboratory test. Our thought was that if empty comb does stimulate hoarding behavior, then bees transferred from one level of comb to another would show predictable changes in hoarding behavior. Also, if the experiment was properly controlled, any effect of past experience would become apparent.

Twelve hoarding cages, fitted with one piece of dark comb (46.75 cm^2 of surface area) and twelve cages fitted with three pieces of dark comb (140.25 cm^2), were each stocked with fifty 1-day-old bees. These cages were observed for hoarding rate for 3 full days.

The bees were then transferred to freshly prepared cages. Four classes of transfers were made: from cages with three combs to cages with three combs (3-3), from three combs to one comb (3-1), from one comb to three combs (1-3), and from one to one comb (1-1). These transfers were made by hand, after the bees had been chilled for 10-20 min. in a -20° C freezer. After transfer, the bees in the fresh hoarding cages were observed for hoarding rate for 4 full days. This experiment was repeated with bees from different colony sources.

Before transfer, the bees caged with three pieces of comb hoarded more sugar syrup than the bees caged with one piece and used almost twice as many cells for storage (Table 3). At the end of the three days there was ample room for more storage in all combs. Thus, lack of storage space did not cause the observed differences. After transfer, the bees transferred to three pieces of comb hoarded more than those bees moved to one (Table 4). Bees in group 1-3 hoarded more sugar syrup than bees in any other treatment group as judged by statistical analysis. Bees in group 3-3 continued a relatively high rate of hoarding. The

Table 4. Hoarding response for 4 days of bees after their transfer from one level of comb surface area to another.

Transfer type (cm^2 of surface area of comb)	Number of replications	Average Ml of sugar syrup consumption	Cells with stored sugar syrup	Per cent of cells with stored sugar syrup
46.75 to 140.25 cm^2	12	15.0[a]*	61.4[a]	11.4[a b]
140.25 to 140.25 cm^2	12	11.7[b]	53.8[a]	9.9[b]
140.25 to 46.75 cm^2	12	9.7[b c]	34.3[b]	19.1[a]
46.75 to 46.75 cm^2	12	8.8[c]	29.5[b]	16.4[a b]

* Numbers in each category not collected by common letters are statistically different.

hoarding of group 3-3 was numerically but not statistically higher than that of bees in group 3-1, and it was statistically higher than that of group 1-1 bees. Group 3-1 bees hoarded numerically but not statistically more than group 1-1 bees.

Overall, the results of these experiments supplied further evidence for the hypothesis that empty comb stimulates hoarding behavior. The data collected in this experiment are similar to the data of the first laboratory experiment even though different sources of bees and a different technique were used. Furthermore, the transfer of bees from high or low amounts of comb resulted in a raising or lowering of the hoarding rate that was consistent with the comb stimulation hypothesis.

The results of this experiment also support the hypothesis that past experience with comb will affect hoarding behavior. Bees in group 3-1 tended to hoard more than bees in group 1-1. This may indicate a time lag of response to stimulus generated by any of a number of possible mechanisms. Also, those bees in group 1-3 hoarded more than the bees in group 3-3. These results indicate that bees may be additionally stimulated by large amounts of empty comb after a period during which they had limited experience of empty comb.

AN INTERPRETATION OF NECTAR GATHERING

The results of these experiments provide a basis for the conclusion that empty comb functions in a hive as a stimulus of nectar-foraging behavior. With empty comb accepted as a stimulus, certain features of nectar foraging can be better understood. First, the nature of what von Frisch (1967) termed "scout bees" becomes clear. "Scout bees" are those bees with a threshold to empty comb low enough that empty comb stimulates them to seek nectar sources. Upon their return to the hive they dance and recruit additional 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 the honey in the colony was interpreted as the stimulus for this activity. With the information supplied by our experiments 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 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 and as stimuli for other activities become available to a greater or lesser extent.

MANAGEMENT IMPLICATIONS

The results of these experiments suggest ways that commercial honey bee colonies might be effectively managed. The ideal management system may involve restricting the space in bee colonies until just before a nectar flow and then supplying the colonies with an abundance of empty supers. Of course, this ideal requires compromise based on time considerations, available equipment, and the need for swarm control.

Both nectar flows experienced during our field experiment were exceptionally strong, and the strength of nectar flows may well influence response to large amounts of empty comb by bee colonies. Nectar flows of less strength may result in combs only half filled with honey or full combs in the center of stacked supers with empty combs to the sides. Thus, while extra supering may prove useful in some honey production areas, it may not prove useful in others. This is especially likely in areas with poor nectar flows. With this caution in mind, beekeepers who have practiced restriction of super space in an effort to crowd the honey crop into a minimum number of well filled combs, might profitably experiment with supplying extra comb space during promising nectar flows. In this way they could gain information about how the technique integrates with their own management style as well as with the nectar flow conditions in their own beekeeping area. Such information would provide them with a meaningful basis on which to make sound management decisions.

FOOTNOTES

[1] In cooperation with Louisiana Agricultural Experiment Station.

[2] This article summarizes the research reported in Rinderer, T. E. and J. R. Baxter, 1978a, 1978b.

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