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Effect of Population Size on Worker Survival and Honey Loss in Broodless Colonies of Honey Bees, *Apis mellifera* L. (Hymenoptera: Apidae)[1]

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ABSTRACT About 7 kg of honey bees were caged, stored for 2 days, and subdivided into 3 populations: ca. 4,400, 8,900, and 34,000 bees. The bees then were placed in hives that had no brood and a known quantity of honey. The resulting colonies had ca. 2 liters of space and one caged queen per 1,000 bees. Worker survival, honey loss per bee, colony temperature, and survival of caged queens were compared in six replicates. Each replicate covered 20 to 27 days during winter in Baton Rouge, La. Population size had no effect on survival of workers or caged queens. However, larger populations were significantly warmer than smaller populations when the ambient temperature was <13°C ($P < 0.05$). Honey loss per bee per day was significantly greater for 4,400 bees (mean ± SD = 6.7 ± 1.5 mg) than for 8,900 (4.5 ± 1.7 mg) or 34,000 (4.2 ± 0.7 mg) bees ($P < 0.05$).

Honey bees, *Apis mellifera* L., never live alone but exist in populations ranging from about 1,000 to 70,000 bees. Larger populations produce more honey per bee (Farrar 1937), rear fewer cells of brood per bee (Moeller 1961), and during winter consume less honey per bee (Free and Racey 1968) than smaller colonies.

This study compared broodless populations of different sizes and began a systematic approach to the storage of queens and the maintenance of worker populations in winter. It was designed to measure the effect of absolute numbers of bees (always 500 bees per liter and one queen per 1,000 workers) on (1) honey loss, (2) colony temperature, (3) queen survival, and (4) worker survival.

Materials and Methods

Work was done between 10 November 1981 and 17 February 1982 in Baton Rouge, La. There was no nectar flow during this period, and the colonies were not opened or disturbed during the 20- to 27-day test interval.

A randomized complete block design was used. Each block (replicate) consisted of a population of about 7 kg of worker bees and 44 caged queens. The workers and queens were confined in a screened cage measuring 47 by 27 by 53 cm. The bees were fed 50% (wt/wt) sugar syrup for 2 days and were then subdivided into three populations (treatments): 0.5, 1.0, and 4.0 kg of bees. There were six replicates.

Source of Bees

The bees and queens for the cage came from a variety of sources. The bees were taken from normal queenright colonies of various sizes and from queenless colonies that had been cell builders or queen storage colonies. The queens were mated, and most were less than 6 months old.

About 1 h after the 7 kg of bees were put into the cage, queens were randomly placed on queen storage boards and put into the cage with the worker bees. Four queens were put on a board destined for the 0.5-kg population, eight queens on a board for the 1.0-kg population, and 32 queens on two boards for the 4.0-kg population (Fig. 1).

After subdividing the cage of bees, each of the three populations was kept in a screened box until it was hived (1 to 2 h). The boxes were made from empty hive bodies that would fit on top of their respective hives.

Hives for the Experiment

Hives for the boxes were widely spaced to prevent drifting and robbing. They were placed 25 to 80 m apart (most were about 60 m apart) and at least 500 m from the nearest apiary. Hives were randomly assigned to one of the chosen sites in the field, all were set on concrete blocks, all were painted white, and all entrances faced southeast. Bees in the 0.5-kg box (4,400 bees) were put into a 10-liter hive, those in the 1.0-kg box (8,900 bees) were put into a 16-liter hive, and those in the 4.0-kg box (34,000 bees) were put into a 64-liter hive. Volumes were that of the empty hive (no combs, bees, or queen board). All hives contained preweighed frames of honey and their respective queen board(s) when the boxes of bees were added (Fig. 1).

The bees were added to the hives about 4 p.m. The boxes had the same length and width as the hives, so they were merely opened, placed on top of the hive, and then allowed to enter the hive. A queen excluder at the opening of the box kept drones and dead workers in the box. Boxes were taped to the hive, and the hive entrances were screened shut. Thus, no bees were allowed to leave the hives until the next morning when the entrances were opened. The boxes were removed after 2 or 3 days. The number of drones and dead bees remaining in the boxes were counted and subtracted from the estimated population.

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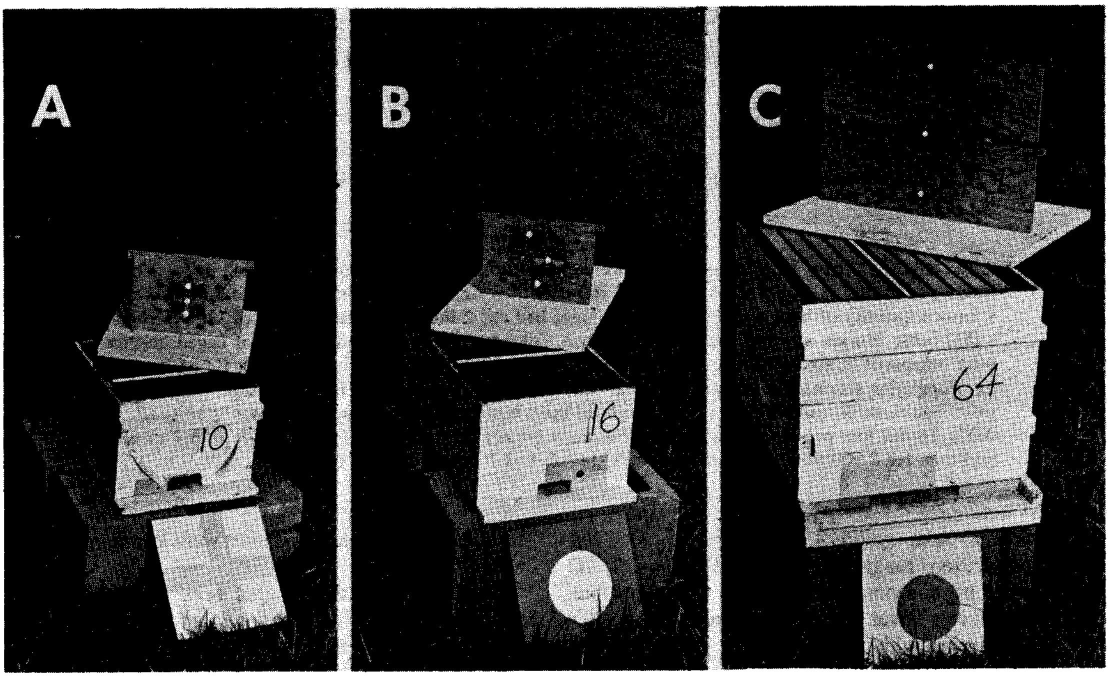

FIG. 1. Hives and queen boards. All hives were painted white, all had plywood lids (19 mm thick), and all entrances faced southeast. The length by width by height of the hives (ID) were 23 by 23 by 19 cm for the 10-liter size, 40 by 23 by 18 cm for the 16-liter size, and 47 by 38 by 36 cm for the 64-liter size. The boards for queen storage (shown above their respective hives) were the same size as the frames. Frames and boards in the 10- and 16-liter hives were 21 by 16 cm, and those in the 64-liter hive were 45 by 16 cm (length by height). The boards were placed in the hives where the white bars are drawn. The upper queen board in the 64-liter hive was directly above the other. Boards were made of 13-mm plywood; holes for queens were 24 mm in diameter, and passage holes were 13 mm in diameter. Screen was 10-mesh per 25 mm on one side of the board and 8-mesh per 25 mm on the other. White dots on the queen boards show the positions of the thermocouples.

Data Collection and Calculation

Original populations were estimated by weighing the empty and full boxes of bees. Just before the original cages were subdivided into three boxes, three samples of about 100 bees each were collected in preweighed mailing tubes, weighed, and then placed in a freezer. After the bees were frozen, they were counted, and a mean weight per bee was calculated. With this estimate, the number of bees in the three boxes was calculated.

Estimating field populations after the duration of the experiment was a similar process. The entrances of the hives were closed when it was too early or too cold for flight. Then the hives were weighed to the nearest gram on a balance that was set up in a van. Another hive without combs was placed on the location, and all the bees were brushed and shaken into it. Three samples of bees were then taken from the bees in the hive before new combs were added. The original combs and equipment (now without bees) were reweighed (to find the

Table 1. Honey consumption (mg per bee per day) in three sizes of broodless colonies in Baton Rouge, La.

Date of expt. (replicate no.)	10-liter hive (ca. 4,400 bees)[a]	16-liter hive (ca. 8,900 bees)[a]	64-liter hive (ca. 33,600 bees)[a]	Mean ambient temp (°C)
12 Nov.–9 Dec. (1)[b]	—	—	—	14.9
18 Nov.–10 Dec. (2)	5.3	3.3	3.6	14.8
25 Nov.–17 Dec. (3)	5.7	4.3	4.2	13.5
2–23 Dec. (4)	9.1	2.9	4.1	11.5
21 Jan.–10 Feb. (5)	6.8	5.0	3.8	10.9
28 Jan.–17 Feb. (6)	6.6	7.2	5.2	10.5
Mean ± SD	6.7 ± 1.5a[c]	4.5 ± 1.7b	4.2 ± 0.7b	

[a]Mean initial population. See Table 4 for the initial and final populations of each colony.
[b]Honey consumption for replicate 1 was omitted because bees in the 10-liter hive were starving.
[c]Means followed by different letters are different at the $P < 0.05$ level.

Table 2. Colony temperature (°C) at the warmest of three places on the queen boards (usually the center position); measurements were used only when the colony had been established for at least 3 days and when the ambient temperature was <13°C

Replicate no.	Date	Ambient temp (°C)	10-liter colonies	16-liter colonies	64-liter colonies
1	20 Nov.	10.6	18.2	27.5	26.4
1	1 Dec.	12.8	13.1	20.3	30.8
2	1 Dec.	12.8	17.9	16.9	26.8
2	10 Dec.	6.1	19.4	29.1	28.8
4	11 Dec.	6.1	21.8	22.6	25.9
4	16 Dec.	6.1	24.3	22.7	26.0
4	23 Dec.	10.0	22.2	25.4	20.4
5	26 Jan.	8.2	18.0	20.6	28.6
5	27 Jan.	6.6	22.1	22.1	27.9
5	1 Feb.	11.7	22.8	27.5	27.1
6	1 Feb.	11.7	28.5	29.4	29.8
Mean			20.8a[a]	24.0b	27.1c

[a]Means followed by different letters were different at the $P < 0.05$ level.

Table 3. Survivorship of caged, mated queens in colonies described in Tables 1 and 4; the colonies in replicate 3 were omitted because many queens died during the 2 days before the experimental period while stored in the 7-kg package.

Replicate no.	No. of surviving queens/initial no. of queens: 10-liter hive	16-liter hive	64-liter hive
1	3/4	3/8	31/32
2	3/4	8/8	31/32
4	3/4	6/8	25/32
5	4/4	7/8	32/32
6	4/4	3/8	17/32
Total	17/20 (85%)	27/40 (68%)	136/160 (85%)

total weight of the bees) and then returned to the laboratory where the combs of honey were weighed.

To calculate total honey loss, I included honey stored in the combs and that stored in the foreguts of the bees. The foreguts of at least 14 bees from the original cage and 14 from each colony were weighed to estimate the amount of honey carried by the bees. To measure honey loss in the combs, each frame was weighed (without bees on it) before and after the experiment. Initial weight included the initial weight of the combs plus the total weight of the foreguts of the initial population. Final weight was the final weight of combs plus the total weight of the foreguts in the final population. Thus, both foreguts and combs were considered honey reservoirs for a colony.

To calculate honey loss per bee per day, I assumed a linear decline in the number of bees from the original to the final population. Thus, the net honey loss (original minus final weights described above) was divided by the sum of the original and final populations divided by 2; this equals the honey used per bee for the duration of the experiment. This value divided by the number of days in the experiment yielded honey loss per bee per day.

In case the concentration of honey was different in the foreguts before and after the experiment, the contents of the foreguts were checked for percent dissolved solids, using an AO refractometer. The foregut contents of at least five workers from the initial and at least five from the final population of replicates 1, 2, 5, and 6 were measured.

Table 4. Worker survivorship in broodless populations containing one caged queen and 2 liters of space per 1,000 workers; each replicate consisted of a large population that was subdivided into three populations

Replicate no.[a] (duration)	Final population/original population (% survival): 10-Liter hive	16-Liter hive	64-Liter hive	20-Day survival rate[b]
1 (27 days)	2,609/4,761 (55%)[c]	5,730/8,881 (65%)	25,107/37,092 (68%)	72%
2 (22 days)	4,080/4,600 (89%)	8,668/11,000 (79%)	31,996/34,800 (92%)	88%
3 (22 days)	3,294/4,130 (80%)	6,340/8,020 (79%)	25,431/32,600 (78%)	81%
4 (21 days)	4,080/4,958 (82%)	7,289/9,663 (75%)	30,326/35,500 (85%)	82%
5 (20 days)	4,138/4,212 (98%)	8,042/8,300 (97%)	31,521/31,400 (100%)	98%
6 (20 days)	3,588/3,705 (97%)	7,635/7,795 (98%)	30,471/30,056 (101%)	99%
Mean population[d] (20 days)	3,572/4,402 (85%)	7,500/8,943 (84%)	29,850/33,575 (89%)	

[a]See Table 2 for dates for each replicate.
[b]The mean for each replicate was calculated by averaging the corrected 20-day survival rates of the three colonies (equal weight per colony rather than per bee).
[c]Colony almost starved on day 27.
[d]Since the time periods were not equal among replicates, all final populations were adjusted to 20 days when calculating mean final population.

Temperature Measurements

Three thermocouples were placed on the queen board(s) of each colony. One was located at the top edge of the uppermost row of queen cages, one was near the center of the queens, and one was at the bottom edge of the bottom row of queen cages (Fig. 1). Thermocouple wires outside the hives were numbered and fitted with plugs that could connect to a Batt 8 digital thermometer.

Average ambient temperature was calculated by using data collected at a weather station located 400 m from the colonies. Temperatures at 2-h intervals were used to calculate the mean temperature for an experimental period.

Statistical Analyses

Analysis of variance (randomized complete block design) was used to compare worker survival and honey consumption among the three treatments. Randomized block analysis of variance was also used to compare temperatures, but because of expected variations caused by time and ambient temperature, each measurement of a replicate served as a block in the analysis. Duncan's multiple range test was used for mean separation.

The other statistical measures compared treatments without separating block effects. Concentrations of sugar in the foreguts of the initial vs. final population of workers were compared with a t test. Queen survival was analyzed with chi-square. The significance level for all analyses was $\alpha = 0.05$.

Results and Discussion

Sugar Concentration in the Foreguts

Sugar concentration in the foreguts of bees fed 50% sugar syrup at the beginning of the experiment was only 3% lower than the concentration in the foreguts of bees at the end of the experiment. After feeding bees 50% (wt/wt) sugar syrup in a cage for 2 days, the sugar concentration in their foreguts was 69.7 ± 4.1% (mean ± SD) ($n = 47$). When taken from colonies at the end of the experiment, bees had 72.5 ± 3.5% ($n = 64$) dissolved solids (probably sugar) in their foreguts. The replicates were significantly different ($P < 0.01$), but a difference of only 3% was not enough to include in the calculations. Capped honey in the colonies averaged 81% dissolved solids; uncapped averaged 76.5%.

Honey Loss

Honey loss per bee per day was greater for colonies with 4,400 bees than for those with 8,900 or 34,000 bees ($P < 0.05$). Populations of 4,400 bees used 6.7 ± 1.5 (mean ± SD) mg of honey per bee per day, 8,900 bees used 4.5 ± 1.7 mg per bee per day, 34,000 bees used 4.2 ± 0.7 mg per bee per day (Table 1).

The relationship between population and honey loss was similar to that reported for queenright, overwintered colonies in England (Free and Racey 1968). Their study extended 6 months, so the colonies had brood part of the time and may have foraged some.

My estimate of 4.2 mg per bee per day seems to be a reasonable estimate of honey loss for a large, broodless colony (>15,000 bees) during winter months in Louisiana. It is difficult to cite supporting evidence because others did not measure populations before and after and did not weigh honey separate from equipment and bees. Nevertheless, by estimating the populations at 25,000 bees in November, decreasing to 15,000 bees in 60 days, I converted colony weight data from Louisiana (Oertel 1958) and Arkansas (Warren 1960) to 4.0 and 3.7 mg honey used per bee per day, respectively. From Wyoming data (Corkins 1930), I estimated that colonies used about 4 mg of honey per bee per day during the 3 winter months.

Colony Temperatures

Larger colonies were warmer. When the ambient temperature was between 6 and 13°C, the warmest of three points on the queen board (almost always the center) averaged 20.8°C in 10-liter colonies, 24.0°C in 16-liter colonies, and 27.1°C in 64-liter colonies. Differences were significant at the 0.05 level (Table 2).

In spite of the warmer temperatures, neither queen nor worker survival was greater in the large colonies. Thus, temperature did not seem to affect survival in a queen bank.

Queen Survival

Queen survival was not a function of population when the concentration of bees was equal. Both 10- and 64-liter colonies had 85% survival after the 20- to 27-day storage interval (Table 3). Queens in the 16-liter hive had a survival rate of 68% which was significantly lower ($P < 0.05$) than that of the 10 and 64 liter hives (chi-square analysis). Perhaps the more cubical shape of the 10- and 64-liter hives was advantageous. There was no linear correlation between queen survival and population size. However, queens can survive well in storage colonies during the winter (Griffin 1966, Levinsohn and Lensky 1981), so variables such as feeding, the presence of brood, or bee density may be important.

Worker Survival

Worker survival in broodless colonies was independent of population. Mean survival for a 20-day period was 85% for 4,400 bees, 84% for 8,900 bees, and 89% for 34,000 bees (Table 4).

Among replicates, however, there were considerable differences in worker survival. For comparison, worker survival was reduced to a 20-day period by assuming a linear loss of bees. Based on the mean survival of the three colonies in a replicate, replicate 1 had the lowest survival (72%), replicates 2 to 4 had intermediate survival (88, 81, and 82%), and replicates 5 and 6 had the highest survival (98 and 99%) (Table 4).

Replicates 2 to 6 fit the survival rates of winter bees as described by Sakagami and Fukuda (1968). They found that throughout the first 50 days, winter bees had 85% survival per 20-day period. This is very similar to what

I found in replicates 2 to 4 in November and December. Sakagami and Fukuda called this the prewintering period. From day 50 to 220, Sakagami and Fukuda reported a much higher survival for winter bees, 97% survival per 20-day period. They called this the wintering period and it fit the survival of replicates 5 and 6 in January and February. The lower survival rate of replicate 1 may indicate that this replicate contained a large proportion of physiologically nonwintering bees.

When considering population loss, honey loss per bee, and queen survival, this study showed that there was very little advantage in maintaining broodless populations with more than about 8,000 bees. This supports Jeffree and Allen (1956), who suggested that there may be an optimal (most efficient) autumn population for a honey bee colony. They reported that a November population of 8,000 to 15,000 bees was optimal because populations within that range had the highest proportion of bees the following March (spring population/autumn population). Free and Racey (1968) estimated honey loss as well as population and came to a similar conclusion; they found no advantage having autumn populations larger than 18,000 bees.

Although populations >18,000 bees may not always be most efficient, these larger populations have many advantages. For example, larger autumn populations provide safety because they are less likely to decline in numbers to an inefficient level (<8,000 bees) or to a level that threatens survival. Furthermore, large winter populations may be needed in areas that have colder winter temperatures than England or the southern United States, where these measurements were made. Larger broodless populations maintained a higher cluster temperature while consuming less honey per bee. This higher temperature did not affect queen or worker survival, but it may enable larger populations to have more mobility in cold weather. This mobility may affect movement within the hive and may make the bees more responsive to marginal or brief opportunities for flight or foraging.

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