Worker-Bee Crowding Affects Brood Production, Honey Production, and Longevity of Honey Bees (Hymenoptera: Apidae)

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ABSTRACT This study measured the effects of hive volume on the productivity and growth of colonies of honey bees, *Apis mellifera* L., in Baton Rouge, LA. In a winter experiment, populations of 5,000, 10,000, and 15,000 bees were installed in hives to produce population densities of 150 or 550 bees per liter of hive volume (3 by 2 factorial, $n = 60$). More crowded bees consumed less honey (6.8 ± 1.9 mg per bee/d [mean ± SD] versus 12.2 ± 2.6 mg per bee/d) but produced less brood (0.34 ± 0.20 versus 0.72 ± 0.31 cells per bee) and had a shorter life span than less crowded colonies. In spring, summer, and autumn, experiments were conducted with initial populations of 9,600 bees per colony. At 100, 200, 300, and 500 bees per liter ($n = 32$), more crowded bees produced more honey. Average honey production was −70, −17, +28, and +67 g/d for the least to most crowded bees, respectively. More crowded bees produced less brood, but the difference was less marked than in winter. A final experiment measured the effects of adding hive space that did not contain comb ($n = 27$). Of three treatments, colonies with five combs in a 25-liter hive produced the most honey (105 g/d), and colonies with additional space and combs (10 combs in a 47-liter hive) produced the least (29 g/d). Colonies with combless space (five combs in a 47-liter hive) were intermediate (62 g/d). The treatment with combless space produced more brood than the more crowded treatment but less than the treatment with 10 combs.

KEY WORDS *Apis mellifera*, density, space

THIS WORK is part of a study to define management variables that affect the growth and productivity of honey bee colonies. These variables include such things as size and color of hives, size of combs, and the number of worker bees in a colony. The results not only affect general bee management but identify management variables that can impede the genetic selection of honey bees, *Apis mellifera* L., in field colonies.

Management variables can mask genetic differences between stocks of honey bees (Harbo 1988). Thus, it is not enough to simply make test colonies uniform; test colonies need to provide optimal conditions that promote the full expression of heritable traits.

The objective of this work was to measure how the volume of a hive affects honey production (consumption in winter), brood production, and longevity of worker bees. In this study, the relationship between the population of honey bees and the volume of the hive is calculated in bees per liter and is called bee density. The first two experiments measured the effects of bee density in winter; the last two measured similar effects during periods of potential honey production in the spring, summer, and autumn.

The effect of bee density (more or less crowding) on population growth has not been measured, and the effect on honey production has been inconsistent. Because hives are normally filled with combs, bees at a lower density will have more comb than bees at a higher density. Rinderer (1981) concluded that volatiles from empty comb stimulate bees to collect nectar and that colonies with more empty comb store more honey during major nectar flows but less during minor flows (Rinderer 1982). Szabo et al. (1992) concluded that empty comb had no effect on honey production.

Materials and Methods

General Design. These experiments were conducted in Baton Rouge, LA, before 1988, so the bees were not infested with tracheal or Varroa mites (*Acarapis woodi* (Rennie) and *Varroa jacobsoni* Oudemans, respectively).

All experiments used the same basic procedure (Harbo 1986). This procedure was designed to provide equal test colonies and precise measurements of honey weight and bee populations. Within each trial, worker bees for each colony were taken from a single population of bees that had been put into a large screened cage and stored for 1 or 2 days before the experiment began. The bees in this cage came from many different sources, so when the bees were subdivided into test populations, the test populations were uniform (one to another) but were genetically diverse within each colony. To maintain this uniformity between populations, trials were ended the day before any adult progeny emerged from the brood cells. This limited population growth to the production of immature workers, all of which were counted at the end of an experiment by measuring brood area on the combs with a wire grid (6.5 cm^2 per square) and converting to absolute numbers using 3.7 cells per cm^2.

The initial bee populations for each colony were calculated by weighing small cages (packages) before and after they received bees from the source cage. Subsamples were weighed to calculate number of bees. Each package was then added to a hive that contained preweighed combs and a caged queen. A sheet of queen excluder was placed over the opening of the package so that drones and any dead workers would remain inside. Intercolony movement of flying bees was minimized by confining bees (keeping entrances screened) until the next day. After the entrances were opened, the packages were removed, and the drones and dead bees inside the packages were counted and subtracted from the estimate of the initial population. A drone was counted as 1.6 workers.

The final bee populations were estimated on the last day of the experiment by screening the entrance of each colony before sunrise (when all the bees were inside), weighing colonies with the bees inside, then subtracting the weight of the equipment without bees. A sample of bees was collected from each colony, and the combs were taken to the laboratory to measure brood and honey.

The weight of honey in each colony was measured at the beginning and end of each trial by weighing combs and bees. Bees store honey in combs, but a significant amount is sometimes stored in the foreguts of adult bees. Therefore, initial and final comb weights were combined with foregut weights of the initial or final population (mean foregut weight × the number of workers) to obtain a precise measure of honey consumed by each colony. The samples used for estimating populations were also the source of foreguts to weigh. Ten foreguts were weighed from each sample. After weighing >1,000 foreguts from worker bees, I established a correlation between the mean weight of bees and the mean weight of their foreguts (Fig. 1). Thereafter (these experiments included), I used the regression equation from this correlation to calculate foregut weight from the fresh weight of worker bees.

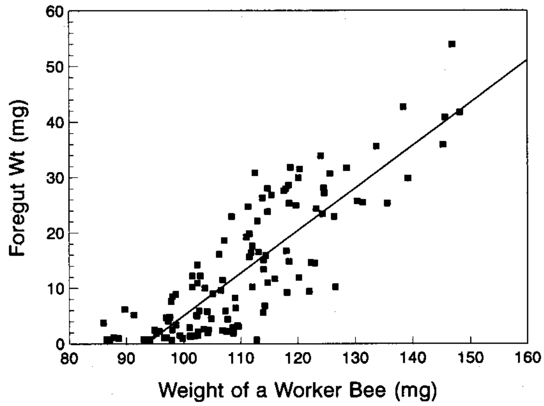

Fig. 1. Predicting weight of foregut from weight of whole bees. Each of the 115 points represents a mean from a sample of 7–10 worker bees; each sample came from a separate population.

Experiment 1. This experiment measured the effect of hive space on honey consumption and longevity of worker bees in broodless colonies during winter. Initial populations of 6,300 or 16,000 bees were each compared at different densities but not compared with each other. Each trial consisted of two populations of either 6,300 or 16,000 bees evaluated at 200 and 600 bees per liter of hive space. Each colony was evaluated for 20 d during which time the queen in each colony was kept caged; the colonies therefore produced no brood.

The effects of bee density on honey loss and adult survival were analyzed with a paired t test for each population size. The experiment consisted of 20 colonies.

Experiment 2. The purpose of this experiment was to measure the effects of different population sizes (5,000, 10,000, and 15,000 bees) and different hive densities (150 and 550 bees per liter of hive space) on honey consumption, brood production, and worker longevity. This 3 by 2 factorial design consisted of six treatments per trial (see Fig. 2) with the bees for each trial derived from a single big cage. The experiment consisted of 60 colonies (five different test periods between 5 December and 6 March with two trials during each period). SAS software was used in the analysis of variance (ANOVA)(SAS Institute 1979).

The 12 colonies that were tested during each time period were placed at least 10 m apart and at least 0.5 k from the nearest apiary. All colony entrances faced southeast and were protected with robbing screens and fencing (Fig. 2A). The robbing screens were adopted after some crowded colonies had recorded a net gain of honey in December when there was no nectar forage. The gain was proportional to abnormally

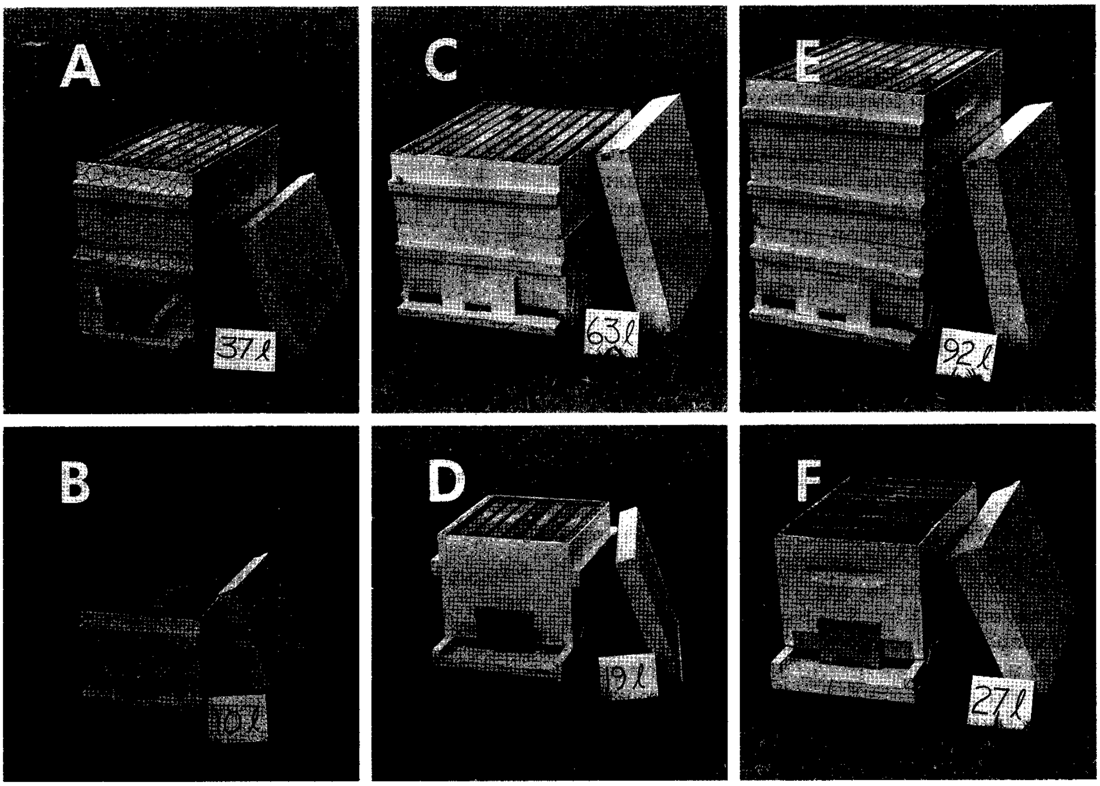

Fig. 2. Hives used in experiment 2. Hive volumes (written in liters next to each hive) and the density of worker bees in a hive were calculated from inside dimensions of the empty hive box and did not subtract the space occupied by frames of comb. Hives A and B contained 5,000 bees, C and D contained 10,000, and E and F contained 15,000. Therefore, the top row had 150 bees per liter; the bottom row had 550. All colonies had entrances modified to prevent robbing, and all were fenced (shown only in A) to keep skunks and opossums from eating bees at the entrance. Comb sizes were 13 × 43 cm for hives A, C, and E; 13 × 19 cm for hive B; and 20 × 23 cm for hives D and F.

high losses that occurred in less crowded colonies. Therefore, four trials without robbing screens were not included in the analysis of honey loss.

Experiment 3. The objectives of this experiment were to measure the effects of hive volume on honey production, brood production, and adult longevity during the spring, summer, and fall. The four experimental treatments were 500, 300, 200, and 100 bees per liter. Comb sizes were 20 by 23 cm for 500 bees per liter and 20 by 43 cm for the others. The hive for 500 bees per liter is shown in Fig. 2D; the other hives had volumes of 31, 47, and 90 liters and held 6, 10, and 20 standard combs, respectively. All hives were fenced as shown in Fig. 2A.

The 32 test colonies in this experiment were evenly divided into four trial periods (each 21 d) that began 8 March, 23 May, 3 July, and 19 September. Each trial consisted of two replicates of four treatments. The initial worker population in each colony was ≈10,000 bees (actual average was 9,600) because this was found to be an optimal size for stock evaluation (Harbo 1986). Results were analyzed with analysis of variance (ANOVA) and LSD mean separation (SAS Institute 1979). The interaction served as the error term for treatment and in calculating LSD values.

Experiment 4. This experiment attempted to separate the effects of comb and space. In experiments 1–3, all space in a hive contained combs, as shown in Fig. 2. In this experiment, one of the treatments had only 5 combs in a 47-liter hive (standard Langstroth size) that could hold 10. The other two treatments were a 25-liter hive with 5 combs and a 47-liter hive with 10. All combs were 20 by 43 cm.

As in experiment 3, this experiment was conducted during periods of potential honey production with initial populations of 9,600 bees. The 27 test colonies were divided into three trials (each 16 d) that began 10 April, 17 April, and 9 October. Each trial consisted of three replicates of three treatments. Results were analyzed with analysis of variance (ANOVA) and LSD mean separation (SAS Institute 1979).

Explanation of Terms Used in Tables. *Total weight gain* was the weight gained or lost in the combs and in the foreguts of worker bees during the experiment. This did not include the weight of bees, but it did include the weight of the brood and pollen.

Brood production is presented in cells per bee. This was the number of cells of brood (eggs, larvae, and pupae) that were present in a colony at the end of the experiment divided by the mean population (the midpoint between the initial and final populations) for each colony.

Honey gain removed the weight of the brood from *total weight gain*. The number of brood cells in each colony was measured at the end of the experiment, and the weight of the brood (an average weight of 93 mg/cell for all stages [80 mg in experiment 4]) was subtracted from the final comb weight (Nelson & Sturtevant 1924). Thus, *honey gain* or *honey loss* estimated the change in the weight of the honey reserves in a colony. *Honey gain* is presented in mg/d per bee by dividing honey gain by the duration of the experiment and the mean population of a colony.

Adult survival was calculated for each colony by dividing the final population by the initial population.

Results and Discussion

General Results. This study has led to two major conclusions. The first is that more crowded bees produce more honey than less crowded bees. The second is that less crowded bees produce more brood. The trends were similar in all experiments, regardless of nectar availability or season. Crowded colonies conserved more honey in winter and produced more honey at other times of the year; less crowded bees produced more brood and lived longer than more crowded bees.

Regression analysis showed that total body weight is a reliable indicator of the weight of the contents of the foregut (Fig. 1). The linear relationship between bee weight (X) and foregut weight (Y) (both in mg) was $Y = 0.76X - 70.4$ ($F = 254$; df = 1, 113; $P < 0.0001$; $r = 0.83$). Major causes of variation were probably size of bees and the amount of material in the hindgut.

Experiment 1. More crowded bees (600 bees per liter) consumed less honey per bee than bees given more space (200 bees per liter), regardless of population size ($t = 3.9$, df = 4, $P < 0.02$ for populations of 6,000 bees; $t = 4.8$, df = 4, $P = 0.01$ for 16,000 bees) (Table 1).

Survival of adult bees did not show a common trend. With the smaller population, bees lived longer when they were crowded ($t = 3.9$, df = 4, $P = 0.02$). Crowding had no significant effect on longevity of bees in populations of 16,000 ($t = 2.0$, df = 4, $P = 0.12$), but the tendency was for less crowded bees to live longer (Table 1).

Table 1. Comparing bees maintained in outdoor hives that contained caged queens and no brood (experiment 1)

Initial population	No. bees per liter	Honey loss, mg/bee/day	% Adult survival
6,300	200	9.64 ± 1.85a	88.1 ± 11.5a
6,300	600	5.56 ± 1.15b	94.5 ± 8.2b
16,000	200	6.06 ± 1.07a	83.8 ± 20.5ns
16,000	600	4.76 ± 0.72b	79.3 ± 23.3ns

See text for definitions of terms. Data in each row are means ± SD of five colonies.

Effects of bee density were compared within each population size using paired t tests (df = 4). Means followed by different letters were different at the $\alpha = 0.05$ level; ns, not significant.

Experiment 2. Bee density affected all three variables: honey loss, adult survival, and brood production (Tables 2 and 3). In all three population sizes, bees with more space in their hive (150 bees per liter) ate more honey, produced more brood, and lived longer than bees that were more crowded (550 bees per liter).

Bees with more hive space tended to live longer than crowded bees ($P < 0.0005$) (Table 3). However, experiment 1 suggested that there may be an interaction between population size and crowding. In experiment 1, 6,000 bees survived better when they were more crowded; 16,000 bees did not. Experiment 2 was able to test for this interaction; the trend was the same but the result was not significant ($P = 0.22$) (Table 3). However, experiment 2 showed that population size had a significant effect on adult survival ($P = 0.043$) (Table 3). The significant difference was caused by lower adult survival in two treatments (crowded hives with 10,000 or 15,000 bees); adult survival was nearly equal among the different population sizes when bees were less crowded (Table 2).

The data indicate that crowding reduced the life span of bees in the larger populations but had a weaker effect on smaller populations. Thus, there may be a population threshold below which crowding has no effect or a beneficial effect (as in experiment 1). A major difference between the two experiments was that the colonies in experiment 1 contained no brood, whereas those in experiment 2 were rearing brood. Brood-rearing may intensify the effects of crowding by placing a population of immature bees in the center of a colony.

The effect of crowding on brood production was very definite ($F = 203$; df = 1, 25; $P < 0.0001$) (Table 3). Bees given more space (150 bees per liter) often produced two or three times more brood than more crowded bees (550 bees per liter). This was not caused by insufficient space in the more crowded colonies because in late March, initial populations of ≈10,000 bees (experiment 3) averaged >16,000 cells of brood in the same 19-liter hives. This was four times

Table 2. Effects of population size and hive space on bee colonies during 22-d test periods

Initial population	No. bees per liter	No. colonies	Honey loss, (mg/bee/day)[a]	% Adult survival	Brood production, cells/bee
5,300 ± 600	150	10	14.6 ± 1.3	86.9 ± 7.2	0.90 ± 0.34
5,300 ± 500	550	10	8.8 ± 1.3	84.0 ± 9.5	0.31 ± 0.21
10,200 ± 600	150	10	11.9 ± 1.8	83.4 ± 9.6	0.74 ± 0.29
10,200 ± 600	550	10	6.2 ± 1.8	77.9 ± 9.1	0.38 ± 0.22
15,400 ± 1000	150	10	10.1 ± 2.5	87.4 ± 5.9	0.53 ± 0.19
15,400 ± 1100	550	10	5.5 ± 0.6	78.1 ± 12.1	0.32 ± 0.17
5,300[b]	Both	20	11.7 ± 3.3a	85.5 ± 8.3a	0.61 ± 0.41a
10,200	Both	20	9.1 ± 3.5b	80.7 ± 9.5b	0.56 ± 0.32a
15,400	Both	20	7.8 ± 3.0b	82.8 ± 10.4ab	0.43 ± 0.21b
All	150[c]	30	12.2 ± 2.6	85.9 ± 7.7	0.72 ± 0.31
All	550	30	6.8 ± 1.9	80.0 ± 10.3	0.34 ± 0.20

Each of 10 replicates consisted of six colonies shown in Fig. 2. Data are means ± SD (experiment 2). See text for definitions of terms.

[a] Data in this column came from only 30 colonies because robber-preventing entrances (Fig. 2) were not used in the earlier replicates. Thirty colonies do not provide enough degrees of freedom to analyze the complete model as was done for the other two variables in Table 3.

[b] Population size had a significant effect on both adult survival and brood production (Table 3). LSD mean separation was used to detect significant effects among the three populations. Means followed by different leters are different at the $\alpha = 0.05$ level.

[c] Bee density had a significant effect on all three variables (Table 3).

more brood than identical colonies and twice as much as less crowded colonies had produced in winter with the same adult population.

Brood production showed a strong population by density interaction (Table 3). Smaller populations tend to produce more brood per bee than larger populations (Free & Racey 1968, Harbo 1986), but that trend was evident in this experiment only in the colonies that were given space. The smallest population tripled brood production when given more space; the largest population increased brood production by only 66% (Table 2). When crowded, all three populations produced ≈0.34 cells of brood per bee.

Table 3. Factorial ANOVA to evaluate the effects of bee density and population size on adult survival, brood production, and honey consumption (experiment 2)

Source	df	Mean square	F	$P > F$
Adult survival				
Time	4	638.4	19.7	0.0001
Replicate (time)	5	29.2	0.9	0.497
Population size	2	115.7	3.6	0.043
Density	1	524.5	16.2	0.0005
Population × density	2	51.9	1.6	0.222
Population × time	8	39.3	1.2	0.332
Density × time	4	79.3	2.5	0.072
Population × density × time	8	41.4	1.28	0.299
Error	25	32.4	—	—
Brood production				
Time	4	0.613	55.9	0.0001
Replicate (time)	5	0.012	1.1	0.381
Population size	2	0.173	15.8	0.0001
Density	1	2.235	203.8	0.0001
Population × density	2	0.184	16.8	0.0001
Population × time	8	0.014	1.3	0.308
Density × time	4	0.070	6.4	0.0011
Population × density × time	8	0.017	1.5	0.198
Error	25	0.011	—	—
Honey loss				
Replicate	4	3.5	1.4	0.273
Population size	2	40.5	16.2	0.0001
Density	1	217.1	86.7	0.0001
Error	22	2.5	—	—

The result of honey consumption is consistent with the results of experiment 1. In all three populations, bees consumed more honey when provided with excess hive space. As expected (Free & Racey 1968, Harbo 1986), larger populations consumed less honey per bee than smaller populations.

Increased honey consumption by bees in less crowded hives was not caused by increased brood production in those colonies. Of course, some of the increased honey consumption was caused by the increase in brood rearing, but bees in less crowded hives ate more honey when no brood was produced (as in experiment 1). Crowded conditions probably retained heat better, so bees in less crowded hives needed to eat more honey to generate enough heat in their colony. I noted that bees in spacious hives appeared active, whereas crowded bees appeared lethargic.

Experiment 3. Crowded bees produced more honey than bees that were less crowded (Table 4). ANOVA for weight gain and honey gain were both highly significant (Table 5).

Adult survival and brood production were greater in less crowded colonies (Table 4; ANOVA, Table 5). Unlike honey production, differences in brood production and adult survival did not continue throughout the range of the treatments (Table 4), and any advantage in providing extra space tended to diminish or level off at 200 bees per liter.

Therefore, the least crowded treatment (100 bees per liter) can be eliminated as a practical density for general beekeeping or colony evaluation. It was equal to or worse than 200 bees per liter in every category.

Table 4. Results of experiment 3 where colonies that began with 9,600 bees were evaluated for 21 d in spring, summer, or fall in four different sizes of hive

No. bees per liter	Total weight gain, g	Honey gain, mg/bee/day	% Adult survival	Brood production (cells/bee)
100	−1,480a	−15.8a	69.1a	1.9a
200	−352b	−10.2b	66.8a	2.1a
300	582c	−3.7c	59.8b	1.9a
500	1,404d	1.9d	59.1b	1.6b
LSD[a]	689	4.4	6.6	0.22

Means followed by different letters are different at the α = 0.05 level. n = 8 for each treatment.

[a] LSD mean separation was used to detect significant effects among the four treatment means in each column. The LSD value for each column was calculated from the MSE of the interaction (the error term in this ANOVA).

The other extreme (500 bees per liter) is also impractical except under rare conditions. The combination of earlier death for adults and lower brood production would severely reduce population growth in the most crowded size, and its advantage in honey production would be nullified by a lack of storage space for honey. A possible use for this density would be with small populations (≈5,000 bees) when there is no need to stimulate brood rearing.

I concluded that bees should not be given excess space during a weak nectar flow or during periods of nectar dearth. These conditions exist most of the time. Moderate crowding in the spring, summer, or autumn can benefit honey production (or conserve honey) when the nectar flow is weak and does little to reduce population growth. Autumn in Louisiana is an example of a period when moderate crowding (300–400 bees per liter) may be beneficial. In late winter, when crowding has its strongest influence on brood rearing and when a beekeeper wants to maximize population growth, less crowding (≈200 bees per liter) may be better.

Table 5. Analyses of variance for experiment 3

Source[a]	df	Mean square	F	$P > F$
		Adult survival		
Time	3	130	7.9	0.002
Density	3	201	5.9	0.017
Time × density	9	34	2.1	0.10
Error	16	16		
		Brood production		
Time	3	3.26	246	0.002
Density	3	0.33	8.8	0.005
Time × density	9	0.038	2.9	0.03
Error	16	0.013		
		Total weight gain		
Time	3	11,009,800	41	0.0001
Density	3	12,317,606	33	0.0001
Time × density	9	370,933	1.4	0.28
Error	16	270,516		
		Honey gain		
Time		340	39	0.0001
Density		479	31	0.0001
Time × density	9	15.2	1.8	0.15
Error	16	8.6		

[a] Time × density is the error term for density.

Table 6. Results of experiment 4 where colonies that began with 9,600 bees were evaluated for 16 d in spring or fall in three different arrangements of hives and combs

No. bees/liter (no. of combs)	Total weight gain, g	Honey gain, mg/bee/day	% Adult survival	Brood[a] production, cells/bee
200 (10)	1509a	3.3a	78a	1.51a
200 (5)	1922a	7.3b	78a	1.36b
400 (5)	2523b	12.3c	77a	1.24c
LSD[b]	—	—	6.5	0.09
Tmt F	14.0	43.9	0.1	37.0
$P > F$	0.016	0.002	0.90	0.003

LSD mean separation was used to detect significant effects among the three treatment means in each column. Means followed by different letters were different at the α = 0.05 level. Because of unequal variances among the three time periods, the data for total weight gain and honey gain were transformed by ranking the values within each of the three time periods. Therefore, the LSD values were not listed for the first two columns because they would be meaningless with respect to the actual means listed in the table. All four variables were analyzed with ANOVA with the interaction (time × treatment) serving as the error term for treatment; thus, df = 2, 4. n = 9 for each treatment.

[a] Duration of brood production was 14 d in this experiment.

[b] LSD values were calculated from the MSE of the interaction.

My data with populations of 10,000 bees suggest that crowded bees produce more honey than less crowded bees during all periods, even during periods with a heavy nectar flow. Periods of heavy nectar flow are often periods when a bee colony is reaching its maximum size (as many as 45,000–60,000 bees), and it is possible that results with 10,000 bees may not extend to large populations. Regardless, bees should not be kept crowded during a heavy nectar flow unless one is willing to remove honey at frequent intervals. Otherwise, the combs could become filled or full enough to suppress honey production. Rinderer & Baxter (1978) produced more honey from colonies kept in six hive bodies than in colonies kept in four. The treatment with six hive bodies provided 50% more hive space than the treatment with four (≈250 versus 375 bees per liter). In a Canadian field test at bee densities that I estimate at 160, 90, and 65 bees per liter, hive space had no significant effect on honey production (Szabo et al. 1992). However, the trend was for more crowded bees to produce more honey.

Experiment 4. Both combs and combless space in a hive affected honey production and brood rearing. Colonies with combless space produced less honey and more brood than colonies with the same amount of comb but less space (Table 6). However, the effect was stronger when the space contained combs.

This experiment also supports the conclusions of experiment 3. With data from only two treatments in experiment 4 (those treatments with the hive filled with combs), one has a small version of experiment 3. The results were the same, more crowded bees produced more honey and less brood.

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