Effect of Comb Size on Population Growth of Honey Bee (Hymenoptera: Apidae) Colonies

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ABSTRACT Population growth was compared in 21 colonies of honey bees, *Apis mellifera* L., during the period of maximal population growth in Louisiana. Each colony began with 1.25 kg of bees, no brood, and 40 liters of hive space (measured empty). Colonies differed in comb size (13 by 19, 13 by 43, 20 by 43, or 26 by 43 cm), but each hive had the same comb surface area (1.1 m^2). Bees were put into hives on 12 March, queens were released 15 March, and hives were expanded to 1.4 m^2 of comb surface area and 48 liters on 10 April. Colonies with the largest combs produced more brood and had more adult workers on 13 May than colonies with the two smallest combs. At the end of the experiment, mean adult populations were 19,300, 22,900, 23,600, and 28,400 in colonies with the smallest to largest combs, respectively. A second experiment compared comb effects versus queen effects by measuring the amount of brood produced in 10 d by colonies with instrumentally inseminated or naturally mated queens on either the largest or smallest comb sizes. Comb effects were significant, queen effects were not. Small combs reduced brood production and diminished differences among queens; therefore, one must use large combs when evaluating queen fecundity.

KEY WORDS Insecta, *Apis mellifera*, population, comb size

POPULATION GROWTH of a colony of honey bees, *Apis mellifera* L., combines brood production and adult survival. Brood production in Louisiana ranges from about 2,200 bees per day for large colonies in spring to no brood production in most of November and December (Harbo 1986a). Adult survival also shows a seasonal trend. Winter bees have an average life span of 154 d (Sakagami & Fukuda 1968), whereas during spring and summer, average life spans are reported to be 25 d (Woyke 1984) and 28 d (Free & Spencer-Booth 1959, Sakagami & Fukuda 1968, DeJong & DeJong 1983).

My objective was to determine if comb size affects the growth rate of a honey bee population. Based on management preferences, Dadant (1918) and Adam (1975) recommended large combs (26 by 43 cm) and Farrar (1968) recommended small combs (13 by 43 cm). However, an intermediate size (20 by 43 cm), called the Langstroth frame, is the most commonly used brood comb in the United States. In field experiments in the USSR, Battalov (1963) compared colonies with frames measuring 23 by 43.5 and 30 by 43.5 cm. By allowing space for the wooden frame, these sizes were probably very similar to the comb sizes (20 by 43 and 26 by 43 cm) mentioned above. Battalov found that colonies produced more brood and developed a greater population on the smaller comb size.

Experiment 1 in this study compared the population growth of colonies having one of the above three comb sizes or a smaller size (13 by 19 cm) that is sometimes used in small colonies. The results showed that colonies with larger combs produce more brood, so experiment 2 was conducted to measure the interaction between two variables, comb size and queen insemination, both of which affect brood production. Colonies with instrumentally inseminated (II) queens do not produce as much brood as colonies with naturally mated (NM) queens (Harbo & Szabo 1984, Harbo 1986b), so I wanted to determine if larger combs would increase oviposition rates of II queens, thus making them more competitive with NM queens.

Materials and Methods

Experiment 1. This test compared the effects of four comb sizes (Fig. 1) on the growth of honey bee populations. The experiment covered 59 d (15 March–13 May 1985), a period of maximal colony growth in Baton Rouge, Louisiana.

Twenty-one colonies were established on 12 March, each with a naturally mated sister queen and 1,250 g of worker bees. The caged queens were released 15 March. There were 6, 4, 5, and 6 colonies with the smallest to largest combs, respectively. All hives had volumes of 40 liters and frames containing foundation rather than drawn combs (Fig. 1). Colonies had equal amounts of crimp-wired, beeswax foundation (1.1 m^2 of surface area on 12 March, enlarged to 1.4 m^2 and 48 liters of hive space on 10 April), and were fed equal amounts

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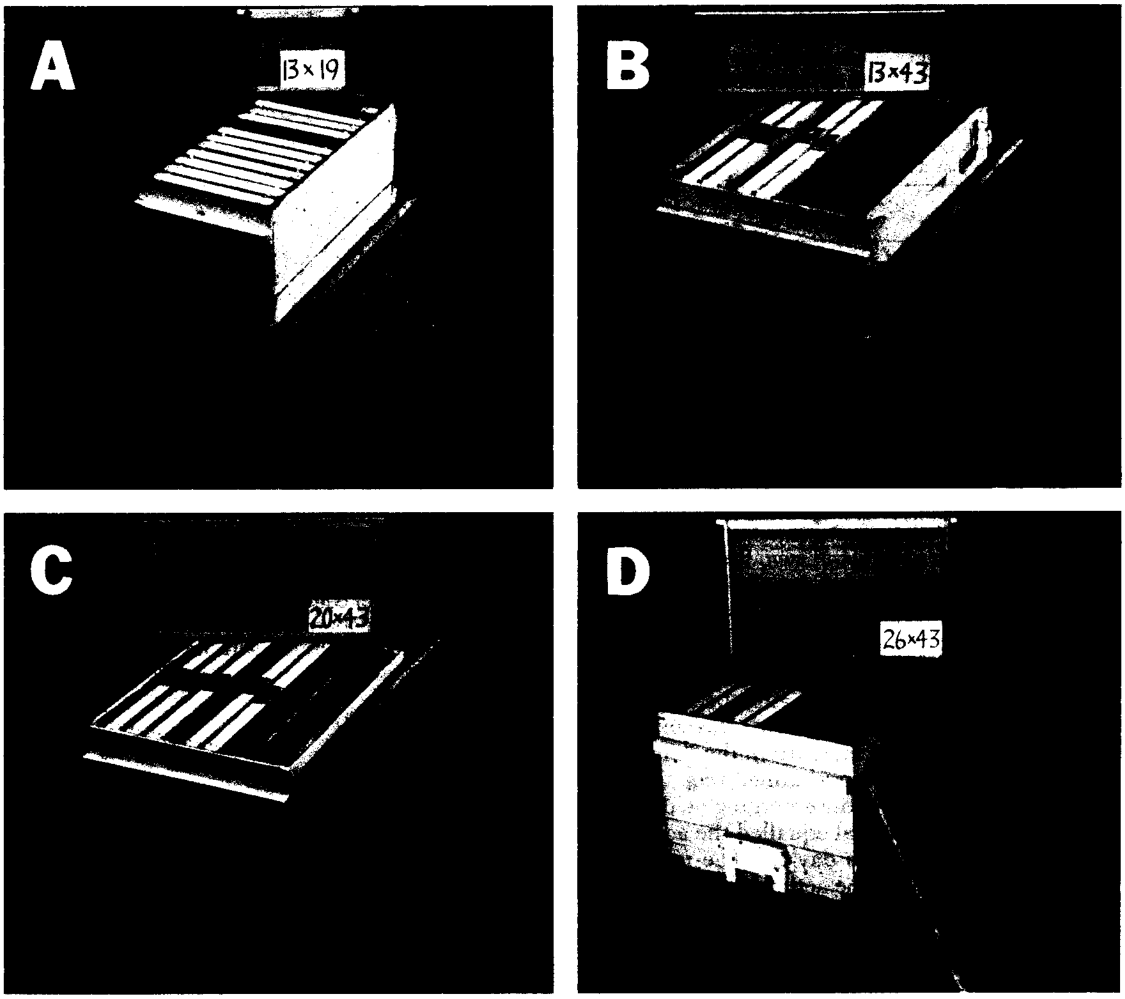

Fig. 1. Hives containing the four different sizes of comb foundation at the beginning of the experiment. Wooden partitions adjusted hive volumes to 40 liters, and all were expanded to 48 liters on 10 April. (A) Hive with 22 frames (13 by 19 cm of comb foundation in each frame). (B) Hive with 10 frames (13 by 43 cm). (C) Hive with six frames (20 by 43 cm). (D) Hive with five frames (26 by 43 cm).

of 60% sugar syrup (wt/wt) during the first 2 wk when nectar was not yet abundant in the field.

I calculated the rate of brood production and the number of adult workers that emerged during the experimental period by measuring capped brood with a wire grid (Moeller 1961) and assuming 3.9 cells of brood per square centimeter. Brood in each colony was measured five times (26 and 28 March; 3, 16, and 29 April). For calculating populations and assigning an age to brood, I assumed a 20-d development period for worker bees (3 d for eggs, 5 d for uncapped larvae, and 12 d for capped larvae and pupae). The 20-d estimate was based on my observations in Louisiana and data from Sakagami & Fukuda (1968) and Bolten (1986).

Adult populations were measured on 13 May. Bees were confined to their hive by screening the entrances before dawn. The entire colony was weighed to the nearest gram on a triple-beam Ohaus balance (20 kg capacity) which was inside a van to prevent wind from affecting the weighing. The bees were then brushed from the combs into an empty hive body, and the equipment was weighed without bees. The weight of the bees was determined by subtraction. I sampled about 150 bees from the empty box to measure weight per bee for the colony. The number of bees was calculated by dividing weight per bee into total bee weight.

I estimated worker longevities that could explain the adult populations of each colony on 13 May. I simplified the model by designating that all worker bees in a colony have the same life span. From data in Table 1 (brood measurements and final populations), I calculated a life span for workers in each colony. Capped brood has a very low mortality rate, but based on data by Garofalo (1977),

Table 1. Experiment 1. Effect of comb size on the brood production of honey-bee colonies during a period of maximal colony growth in Louisiana (15 March–13 May 1985). Colonies began with no brood, 1,250 g of bees, equal comb area, and equal hive volumes

Test period (d)[a]	Mean no. cells of brood per d in colonies that differ in comb size[b]				Root MSE[c]	F^d	P
	13 × 19 cm	13 × 43 cm	20 × 43 cm	26 × 43 cm			
0–3	1,033a	1,057a	1,110a	1,072a	153	0.24	0.87
4–5	832a	1,049ab	1,112b	1,240b	171	5.91	0.006
6–11	556a	794b	889bc	1,045c	177	7.97	0.002
13–24	505a	582ab	676ab	749b	150	3.19	0.05
26–37	1,019a	1,109a	1,210ab	1,344b	180	3.82	0.03

Horizontal (row) comparisons only. Means followed by the same letter are not significantly different (α = 0.05, least significant difference mean separation [SAS Institute 1982]).

[a] Time period after queen release on 15 March (day 0) when the queens laid the eggs. Eggs that were laid during each period developed into the brood that was later measured as capped cells.

[b] Comb sizes are shown in Fig. 1. The means in the four columns represent 6, 4, 5, and 6 colonies, respectively.

[c] Square root of the mean square error, the pooled standard deviation of the samples.

[d] df = 3, 17 in all cases.

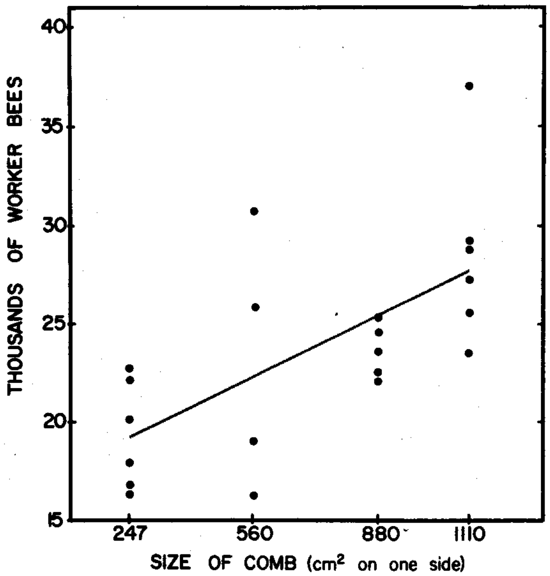

Fig. 2. Effect of comb size on the population of adult worker bees. Populations of 21 colonies were measured 59 d after being established with no brood, 1,250 g of bees, and a queen. The equation for the line is y = 16,794 + 9.68x (F = 14.65; df = 1, 19; P = 0.0011; r = 0.66).

I subtracted 1.5% when converting total capped brood to the number of young, adult bees produced in the next 12 d. Beginning with day 59 (when adult populations were measured), the daily number of emerging bees was summed (e.g., workers emerging on day 59 + those emerging on day 58 + day 57, etc.) until the total equalled the adult population of that colony on day 59. The number of days required to reach the actual adult population was my estimate of worker longevity. For example, 7,310 cells of capped brood on day 35 and 12,183 on day 47 would mean 600 bees emerging per day on days 36–47 and 1,000 per day on days 48–59.

Experiment 2. This experiment was a 2 × 2 factorial design having the variables comb size (only the smallest and largest sizes, Fig. 1A and D) and queen mating (instrumentally inseminated or naturally mated). Twenty-eight colonies were used, with seven per treatment.

Packages, each with 1,130 ± 30 ($\bar{x}$ ± SD) g of bees, were collected and put into hives on 15 April 1986. Each hive had a 40-liter volume and 1.2 m^2 of comb surface area. However, unlike experiment 1, this experiment began with drawn comb rather than foundation, and the colonies were not fed sugar syrup. Fourteen hives each received 24 small combs (13 by 19 cm) and 14 others each received five large combs (26 by 43 cm).

The queens used in experiment 2 were all sisters (unrelated to the queens in experiment 1) and emerged as adults on 4 March 1986. Fourteen were instrumentally inseminated (II) and 14 were naturally mated (NM). The II queens each received two inseminations of 2 μl of semen and 90 s of CO_2 narcosis on 17 and 20 March and 2–3 min of CO_2 narcosis on 26 March. The queens remained caged in a single storage colony until 26 March. The NM queens mated from small colonies (about 3,000 bees), and both II and NM queens began laying eggs in small colonies in late March.

Queens were taken from the small colonies, placed in individual cages, and put into the test hives on 15 April when the worker bees were put in. Queens were released 17 April. Capped brood was measured as in experiment 1 on 28 April, 1 May, and 6 May to evaluate the first 10 d of brood production.

Statistical Analyses. Analysis of variance was used to analyze both experiments. Experiment 1 was a completely randomized design with least significant difference (LSD) mean separation; experiment 2 was a 2 × 2 factorial. The relationship between comb size and final adult population in experiment 1 was analyzed with linear regression using the General Linear Model (SAS Institute 1982).

Results and Discussion

Colonies with larger combs contained more bees at the end of experiment 1 (59 d after queen release) than did colonies with smaller combs. Final populations were 19,300 ± 2,700 ($\bar{x}$ ± SD); 22,900 ± 6,600; 23,600 ± 1,300; and 28,400 ± 4,600 for the smallest to largest combs, respectively. Linear regression showed that comb size explained a significant amount of variation (F = 14.65; df = 1, 19; P = 0.0011) with the equation y = 16,794 +

Table 2. Experiment 2. Brood production in colonies that began with no brood and 1,130 g of bees (18–28 April 1986). The experiment was a 2 × 2 factorial design with comb size (small [13 by 19 cm], or large [26 by 43 cm], Fig. 1A or D, respectively) and insemination (naturally [NM] or instrumentally [II] inseminated queens) as factors

Test period (d)[a]	Cells of brood per colony per d[b]				Root MSE[c]	F and (P) values for factors in ANOVA[d]		
	Small combs		Large combs			Comb size	Insem	Comb × insem
	II	NM	II	NM				
0–2	566	643	593	666	161	0.2 (0.68)	1.5 (0.23)	0.0 (0.98)
3–5	706	684	750	838	147	3.2 (0.09)	0.4 (0.55)	1.0 (0.33)
6–10	572	535	721	871	172	13.8 (0.001)	0.8 (0.40)	2.1 (0.16)
0–10	611	601	704	820	139	8.8 (0.007)	1.0 (0.32)	1.4 (0.24)

[a] Time period after queen release (day 0) when the queens laid the eggs. Eggs that were laid during period developed into the brood that was later measured as capped cells.
[b] $n = 7$ for each of the four variables.
[c] Square root of the mean square error, the pooled standard deviation.
[d] df = 3, 24 in all cases.

$9.68x$, where y is the final adult population on 13 May and x is the size of comb (cm^2 on one side) (Fig. 2).

Colonies with larger combs also produced more brood than colonies with smaller combs. The differences were significant in both experiments (Tables 1 and 2). Therefore, the hypothesis that colonies with larger combs produce more bees than colonies with smaller combs is supported by two different experiments and by two sets of data in experiment 1 (final adult population and brood production).

My estimates of worker longevity showed no difference among the four treatment groups of experiment 1. Means ± SD were 24.5 ± 2.75, 26.7 ± 1.5, 23.9 ± 2.4, and 26.7 ± 2.9 d for worker bees in colonies with the smallest to largest combs, respectively ($F = 1.73$; df = 3, 17; $P > 0.10$). The standard deviations represent the variation among colonies, not the variation among individual bees. Although there is evidence that brood rearing (or the pollen foraging that is stimulated by brood [Cale 1967, Free 1967]) does decrease worker longevity (Maurizio 1950, Woyke 1984, Delaplane & Harbo 1987), the data in this experiment indicate that the increased brood rearing in colonies with larger combs did not have a significant effect on worker longevity.

In experiment 2, comb size had a stronger effect on brood rearing than did insemination (natural versus instrumental) (Table 2). Neither the insemination effect nor the interaction (comb size by insemination) was great enough to be statistically significant. In both experiments, comb size had its greatest effect 6–11 and 6–10 d after queen release (Tables 1 and 2); neither experiment indicated any effect of comb size during the first 3 d of egg laying. In contrast, insemination has its greatest effect during the first days of egg laying (Harbo 1986b). This same trend, although not statistically significant, is evident in experiment 2, for the F value for insemination was greatest during the first 2 d. Therefore, comb size did not affect the initial egg laying of queens as did a physiological effect such as insemination treatment (Harbo 1986b).

Larger combs did not make the oviposition rate of instrumentally inseminated (II) queens more competitive with that of naturally mated (NM) queens. Larger combs did increase the oviposition rate of II queens, but NM queens also laid more eggs per day on larger combs. Moreover, the two groups appeared more equal on small combs than on large combs.

I concluded that the reduced brood production on small combs was not caused by excessive time needed for a queen to move among many combs. During the first 3 d, queens with the smallest combs laid eggs in 5–7 combs, while queens with the largest combs laid in 1–3. Even though the queens on small combs had laid eggs in more combs, there was no difference in egg laying rate among the groups during this time period (Table 1). If queen travel were causing reduced egg laying, I would have expected to see at least a slight effect of comb size during those first 3 d.

I think that the reduced egg laying on small combs was caused by the workers. Initially, there is probably a strong inclination by the workers in broodless colonies to rear brood and prepare cells for eggs, and the queens respond by laying eggs at a rapid rate regardless of comb size. However, as the broodnest grows, the workers become less inclined to expand the broodnest to yet another comb. In contrast, to expand the broodnest to a few more cells on the same comb is a relatively small step for a colony. Thus, broodnests continue to expand rapidly on larger combs and slowly on small combs.

In conclusion, comb size must be controlled when comparing brood production or characteristics of honey bee colonies that are affected by brood. Data in experiment 2 suggest that small combs tend to diminish differences in fecundity that might be expressed if colonies are allowed to rear brood in large combs. Unless one wants to retard population growth, I recommend using large combs (20 by 43 or 26 by 43 cm) as brood combs for research as well as for general beekeeping. The smaller size (13 by 43 cm) is useful in a honey chamber and, in my opinion, the very small size (13 by 19 cm) is practical only in colonies having fewer than 5,000 bees.

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