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Effect of brood rearing on honey consumption and the survival of worker honey bees[1]

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SUMMARY

The cost of rearing a worker honey bee (*Apis mellifera*) was measured in terms of honey lost by the colony and the lifespan of the adult worker bees. Test colonies for each experiment were created by collecting bees from many different sources into a large cage and then subdividing those bees to make a group of uniform colonies. Colonies were evaluated outdoors in Baton Rouge, Louisiana, USA, during February when there was pollen but no nectar for bees to collect. Brood production did not have a significant effect on adult survival during the first cycle of brood rearing, but colonies that reared more brood during the first brood cycle had greater adult mortality during the next brood cycle. Bees used 121 g of honey to produce 1 000 cells of mixed-aged brood (eggs, larvae and pupae in a normal brood nest) and about 163 mg of honey to rear one worker bee to the pupal stage. In colonies containing brood of all stages, the weight of brood was nearly equal to (about 25% less than) the weight of honey that was used to produce it.

Keywords: worker honey bees, *Apis mellifera*, brood rearing, energy costs, food conversion, honey consumption, lifespan

[1]All editorial functions for this paper, including the selection of referees, have been undertaken by staff at IBRA headquarters

INTRODUCTION

The brood (eggs, larvae and pupae) of a honey bee colony can be valued in two ways. First, brood is part of the total bee population in a colony. The quantity of brood reflects the rate of population growth and can be used to predict the size of the future adult population. Secondly, brood is a product. Since a colony uses energy to produce brood, brood production ought to be included when measuring the total productivity of a colony.

This study attempts to measure the amount of energy that a colony uses to produce brood. Cost in energy was measured in grams of honey, and the total cost of brood rearing was measured as honey usage. This approach may seem incomplete because food for bee larvae clearly comprises water, pollen and honey. However, the cost of brood rearing is not simply food. Brood rearing includes the cost of warming brood, cleaning cells, tending brood cells, foraging for pollen, producing glandular food, and other activities. The cost of all activities associated with brood rearing (including the cost of collecting and using pollen and water) can be measured most simply by calculating energy (honey) loss.

A second cost of brood rearing may be its effect on the lifespan of nurse bees. Maurizio (1950) concluded that bees which receive an adequate protein diet will live longer if they do not rear brood. Delaplane and Harbo (1987) also found that worker bees lived longer in colonies with no brood than in normal colonies with brood. When varying the population of nurse bees, Eischen *et al.* (1984) reported that the intensity of nursing (number of cells nursed per bee) had little effect on the subsequent survival of nurse bees in incubator cages. This apparent discrepancy between Eischen's results and those of the two previous references may have been caused by confinement in an incubator, as Neukirch (1982) concluded that the lifespan of a worker bee was directly linked to flight activity.

MATERIALS AND METHODS

In this study, the cost of producing brood was measured in two different ways. Experiment 1 compared honey loss among uniform colonies which reared different numbers of worker bees. Each cell of brood was reared from oviposition to the capped cell stage. Experiment 2 estimated the amount of honey used to produce a normal brood nest containing brood at all stages of development. The results in experiment 1 are in weight of honey used to rear a worker bee from the egg to the pupal stage, whereas the results in experiment 2 are in grams of honey to produce 1 000 cells in a normal brood nest (containing all ages of eggs, larvae and pupae).

These experiments were conducted during winter months (January–February 1986) in Baton Rouge, Louisiana, USA, when there was pollen but no nectar in the field for the bees to collect. The design would be equally valid with or without a nectar flow, because differences in weight gain that are not associated with brood rearing should be random effects. I chose a period with no nectar flow to reduce the variance of weight gain, and thereby improve the ability to detect differences associated with brood production.

However, to include the cost of pollen in the analysis, it was necessary to conduct these experiments at a time when bees could forage for pollen in the field. Brood rearing stimulates bees to collect pollen (Todd & Reed, 1970; Free, 1967; Hellmich & Rothenbuhler, 1986), and the value of pollen in these experiments was equal to the weight of honey (energy) used to collect it. If factors other than brood rearing stimulate pollen collection, or if pollen collection exceeds pollen usage, the effects should be random and would be treated as such in the analysis.

General design

Artificial colonies were used to establish uniformity among the test populations. These populations were similar to commercial colonies that are started from package bees, except that the bees for the packages are derived from a single source. Both experiments used the same basic procedure for establishing test populations and evaluating results (Harbo, 1986). In each experiment, 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 one or two days before the experiment began. The bees in the big cage came from many different sources, so when the bees in this cage were subdivided into test populations, the test populations were uniform (one to another), but genetically diverse within each colony. To maintain this uniformity among populations, the experiments ended the day before any progeny emerged from the brood cells. The number of brood cells was counted at the end of an experiment by measuring brood area on the combs with a wire grid (6.5 cm^2/square) and using a conversion factor of 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 big cage. Subsamples of bees from the big cage were weighed and counted to calculate numbers of bees. Each package was then added to a hive that contained pre-weighed 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. Inter-colony movement of flying bees was minimized by confining bees (keeping entrances screened) until the next day. After the entrances were opened, the packages (which then contained dead workers and live drones) were removed from the colonies. These drones and dead workers were counted and subtracted from the estimate of the initial population. Each drone was counted as 1.6 workers.

Colonies for each experiment were located at least 0.5 km from the nearest apiary and at least 10 m apart. To prevent skunks and opossums from eating bees and disturbing colonies, a semicircular fence (75 cm high) was fastened to a stake set about 30 cm in front of the entrance and nailed to the front corners of each hive. Hive entrances were modified to prevent robbing (Harbo, 1988).

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 the colonies, and then reweighing the equipment without bees. A sample of bees was collected from each colony to calculate weight per bee, 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 experiment. 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 and final populations (respectively) to obtain a precise measure of honey consumed by each colony. Bee weights used to estimate populations were also used to calculate foregut weights with the equation, Y = 0.76X – 70.4, where Y is the weight of the foregut and X is the weight of the entire bee (in mg) (Harbo, 1993).

To estimate honey loss, the weight of the brood must be subtracted from total weight loss. Brood weight was estimated for each colony from a measure of the number of brood cells (measured at the end of the experiments). This requires an estimate of the average weight of a brood cell. The cells were all capped in experiment 1, so an average weight of 130 mg was used (bees lose weight during the capped period from a fully fed larva (*c.* 155 mg) to an emerging adult (*c.* 115 mg). In experiment 2, where brood cells ranged in age from 1 to 20 days, an average weight of 90 mg was used (Nelson *et al.*, 1924).

Experiment 1

The objectives of this experiment were to estimate the amount of honey used to rear one worker bee to the capped cell stage, and to measure the effects of this brood rearing on the subsequent survival of nurse bees.

On 6 February, 13 colonies were established, each with five combs (20 × 43 cm) in standard Langstroth hives that could hold ten. Initial populations were 7 940 ± 129 (mean ± s.d.).

The first portion of the experiment was conducted in winter (6–27 February 1986). Late winter was chosen so that the colonies would produce as much brood as possible, but not so late as to have nectar available in the field. To vary the amounts of brood produced in the colonies, the queens (naturally mated sisters) were released for different lengths of time (1–11 days) between days 2 and 13 of the experiment. The queens were recaged on or before the 13th day, so that all cells would be capped by day 21 (27 February) when the first part of the experiment ended. The mean temperature between 6 and 27 February was 13.2°C with 14 days having maximum temperatures of > 20°C.

The second part of the experiment began on 27 February after all the brood was removed. The same 13 colonies were evaluated for 19 more days to detect any delayed effect of brood rearing on adult survival and brood production. All queens were released on 28 February, and they remained free for the remainder of the experiment. Honey gain or loss was not measured during this second period.

Regression analyses were used for both segments of this experiment.

Experiment 2

This experiment was designed to estimate the cost (in honey and bee mortality) of producing a normal brood nest. Honey consumption in colonies with a laying queen and brood was compared with that of colonies having a caged queen and no brood.

Twelve uniform colonies were established on 8 January, each with 9 180 ± 140 (mean ± s.d.) bees and 12 combs (each 13 × 43 cm). Hives with a volume of 39 litres were arranged with six combs in a bottom chamber and six in the top. On 24 January, queens were released in eight of the colonies.

The experiment ended on 13 February, 36 days after the colonies were established and 20 days after queen release. During the 20 days of brood rearing, the mean temperature was 11.7°C, with nine days having maximum temperatures of > 20°C. Data on weight gain and adult survival were analysed with *t* tests.

RESULTS

Experiment 1

The slope of the regression line is significantly different from zero ($F = 6.5$; d.f. = 1, 11; $P < 0.03$), so brood production had a significant effect on honey consumption (fig. 1, line a). The equation is Y = 0.099X + 1331. The Y intercept of 1 331 g (9 mg/bee/day) predicts the amount of honey consumed during this experimental period when no brood was produced. The slope of 0.099 indicates that each

FIG. 1. Relationship between number of worker bees reared and grams of honey lost in colonies containing 7 000 bees (experiment 1). The test ran for 21 days when there was pollen but no nectar forage available. The linear regression line a includes all 13 observations; line b excludes three outlying observations in the upper left.

colony consumed 99 mg of additional honey for each worker bee that it reared.

Based on data from experiment 2 and the distribution of data in fig. 1, regression line b is probably a more accurate measure of the slope of the regression. Slope b was created by removing the three observations in the upper left of fig. 1 that are outside the main trend of the other observations. Without these three observations, the equation becomes Y = 978 + 0.163X (fig. 1, line b). The zero intercept becomes 978 grams (6.7 mg/bee/day when no brood is produced), and the slope becomes 163 (163 ± 17 mg (s.e.) of honey used to produce each worker bee). Both slopes are significantly different from zero, so experimental significance is not affected by choosing one slope over another. Line a lies intermediate between two groups of data, whereas line b describes the larger group of data in experiment 1 and more closely agrees with the results of experiment 2.

Brood rearing had no effect on the survival of adult bees during the first 21 days of the experiment.

TABLE 1. Effect of brood production on honey consumption and worker lifespan in colonies with 9 000 bees. Colonies with a laying queen that were allowed to rear brood for 20 days were compared with identical colonies that remained broodless with a caged queen (experiment 2). Data are mean ± s.d.

Cells of brood	No. of colonies	Total weight loss (g)[1]	Honey loss (mg/bee/day)[1]	Adult survival (%)
0	4	1 653 ± 254	5.33 ± 0.85	87.5 ± 3.0
6 933 ± 742	8	1 842 ± 327	8.08 ± 1.1	82.0 ± 5.3
Probability[2] > *t*		0.34	0.002	0.09

[1] Total weight loss equals the initial minus the final comb and crop weights. The weights of bees are not included. Honey loss removes the weight of the brood from the total weight.

[2] Probabilities that the two numbers above are estimating the same population (based on *t*-tests with 10 d.f.).

could be expected to live two or three more weeks, thus producing a delayed mortality similar to what was observed.

The amount of honey used to produce brood in experiment 2 was very similar to regression line b from experiment 1 (fig. 1). I had used 130 mg as the average weight of a capped cell in experiment 1, so 163 mg per capped cell equals 163 mg per 130 mg of capped brood. To make the two experiments somewhat comparable, data from experiment 2 were converted to weight of honey to produce 130 mg of mixed brood. Bees in experiment 2 used 121 g of honey to produce 90 mg of mixed aged brood. Therefore, based on line a, line b, and experiment 2, 130 mg of brood required 99, 163, and 175 mg of honey, respectively.

The cost of producing a gram of mixed-aged brood (experiment 2) and the cost of producing one cell of capped brood (experiment 1) are difficult to compare because immature bees gain weight during the larval stage then lose weight during the prepupal and pupal stages. Therefore, one cannot extrapolate the result of experiment 2 (134 mg of honey to produce 100 mg of mixed-age brood) to conclude that bees would use 154 mg to produce one worker bee that weighed 115 mg at the moment of emergence. This would underestimate honey use. In experiment 1 (slope b) 163 mg of honey was used to rear a worker bee to the pupal stage. Those capped cells (1–11 days from emergence) should not require much more energy from the colony, but some would be required. Therefore, those colonies would probably spend more than 163 mg to produce one worker bee. By rounding the weight of honey up to the nearest tenth, the conversion ratio (honey weight : weight of an emerging adult) would be 1.5 : 1. The conversion ratio for mixed-aged brood (honey weight : weight of mixed-aged brood) was 1.3 : 1 (experiment 2).

It may not seem reasonable that the weight of brood could be nearly equal to the weight of the honey that was used to produce it. However, previous studies have also shown bees to be very efficient at converting food to bees. In a greenhouse study, Rosov (1944) calculated that a colony uses 142 mg of honey and 125 mg of pollen to rear one worker larva to maturity. With solitary bees, Batra and Bohart (1970) reported that the weight of the mature larva of *Nomia melanderi* Cockerell was 59% more than the weight of its one-time provision of pollen and nectar (but not including food consumed by the adult bee that made the provision). It was possible for the weight of this larva to exceed the weight of its food because larvae of *N. melanderi* were 72% water, whereas their food was 40% water. Similarly, honey is about 20% water and adult worker bees are about 85% water (Grout, 1937; Eischen *et al.*, 1982).

In colony evaluation, assuming a 1 : 1 conversion ratio (honey weight : weight of mixed-age brood) is probably acceptable under most conditions. Although a 1.3 : 1 conversion ratio may be slightly more accurate, a 1 : 1 ratio is much simpler to use because it does not require measuring brood and estimating its weight. In support of this recommendation, the average weight loss of broodless colonies in experiment 2 was not significantly less than that of colonies that were rearing brood (table 1).

All data from these experiments (both slopes a and b in experiment 1 and data from experiment 2) show that bees use a significant amount of honey to rear brood, but that they are quite efficient in converting honey to bees. The cost of rearing brood is likely to be somewhat variable, but these estimates suggest that conversion ratios as high as 3 : 1 or even 2 : 1 (honey weight : brood weight) are probably unlikely to occur.

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REFERENCES

The numbers given at the end of references denote entries in *Apicultural Abstracts*.

BATRA, S W T; BOHART, G E (1970) Brood care in halictid bees. *Science* 168: 875. 59/72

DELAPLANE, K S; HARBO, J R (1987) Effect of queenlessness on worker survival, honey gain and defence behaviour in honeybees. *Journal of Apicultural Research* 26(1): 37–42. 151/88

EISCHEN, F A; ROTHENBUHLER; W C; KULINČEVIĆ, J M (1982) Length of life and dry weight of worker honeybees reared in colonies with different worker-larva ratios. *Journal of Apicultural Research* 21(1): 19–25. 1262/82

EISCHEN, F A; ROTHENBUHLER, W C; KULINČEVIĆ, J M (1984) Some effects of nursing on nurse bees. *Journal of Apicultural Research* 23(2): 90-93. 491/85

FARRAR, C L (1937) The influence of colony populations on honey production. *Journal of Agricultural Research* 54(12): 945–954.

FREE, J B (1967) Factors determining the collection of pollen by honeybee foragers. *Animal Behaviour* 15(1): 134-144 508/68

GROUT, R A (1937) The influence of size of brood cell upon the size and variability of the honeybee. *Iowa State College Research Bulletin* 218: 260–280.

HARBO, J R (1986) Effect of population size on brood production, worker survival and honey gain in colonies of honeybees. *Journal of Apicultural Research* 25(1): 22–29. 1191/86

HARBO, J R (1988) Effect of comb size on population growth of honey bee (Hymenoptera: Apidae) colonies. *Journal of Economic Entomology* 81(6): 1606–1610. 1205/89

HARBO, J R (1993) Effect of worker-bee crowding on brood production, honey production, and longevity of honey bees. *Journal of Economic Entomology* (in press).

HELLMICH, R L; ROTHENBUHLER, W C (1986) Relationship between different amounts of brood and the collection and use of pollen by the honey bee (*Apis mellifera*). *Apidologie* 17(1): 13–20. 135/87

MAURIZIO, A (1950) The influence of pollen feeding and brood rearing on the length of life and physiological condition of the honeybee. *Bee World* 31(2): 9–12. 137/51

NELSON, J A; STURTEVANT, A P; LINEBURG, B (1924) *Growth and feeding of honeybee larvae*. USDA Department Bulletin No. 1222; 38pp.

NEUKIRCH, A (1982) Dependence of the life span of the honeybee (*Apis mellifica*) upon flight performance and energy consumption. *Journal of Comparative Physiology B* 146(1): 35-40. 481/83

ROSOV, S A (1944) Food consumption by bees. *Bee World* 25(10): 94–95.

TODD, F E; REED, C B (1970) Brood measurement as a valid index to the value of honeybees as pollinators. *Journal of Economic Entomology* 63(1): 148–149. 623/71