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EFFECT OF POPULATION SIZE ON BROOD PRODUCTION, WORKER SURVIVAL AND HONEY GAIN IN COLONIES OF HONEYBEES

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Summary

The effect of population size on brood production, worker survival and gain or loss of honey was studied in colonies of honeybees (*Apis mellifera*) in Louisiana, USA. About 11 kg of bees were caged, stored for two days and subdivided into five populations numbering 2300, 4500, 9000, 17 000 and 35 000 bees. Each colony was started with a laying queen, no brood, and 230 bees per 1000 cm^3 of hive space. The test ended 19 days after queen release, just before adult bees began to emerge. The test was conducted 10 times (two replicates being used in each of February, April, June, August and October). The two largest populations produced more honey per bee and in dearth times and winter consumed less honey per bee. Colonies of 4500 bees produced the most brood per bee; as population increased above that number brood production per bee decreased. However, during summer dearth, the colonies of 9000 bees produced the most brood per bee. Overall, the optimal colony size was 9000 bees; the rate of weight gain in colonies of this size was nearer to that of the two largest populations and the rate of brood production was nearer to that of the two smaller colonies.

Introduction

In field evaluation of stock, characters commonly tested are honey production, brood production and length of life. All three characters are heritable and will respond to selection (Banby, 1967; Soller & Bar-Cohen, 1967; Rinderer et al., 1983), but they are also affected by the number of worker bees in a colony. The purpose of this study was to control the genetic variable and measure the effect of worker-bee population size.

Large populations are more efficient honey producers and smaller populations more efficient brood producers. Honey production per bee was found to increase as populations increased from 15 000 to 60 000 (Farrar, 1937), and broodless populations of ≥ 9000 bees consumed less honey per bee during winter than colonies with 4500 bees (Harbo, 1983). Larger populations of workers produce more brood than smaller populations, but smaller populations produce more brood per bee (Moeller, 1961; Free & Racey, 1968; Nelson & Jay, 1972).

Little is known about the effect of population size on worker survival. Harbo (1983) found that population size had no effect on worker survival during winter when broodless colonies contained 2000 cm^3 of hive space and one caged queen per 1000 bees. Neukirch (1982) found that flight activity during foraging is the major cause of worker mortality. Since larger colonies produce more honey per bee, large colonies probably have a higher foraging rate and perhaps a higher mortality rate.

Materials and Methods

Data were collected from colonies of 5 sizes (2300, 4500, 9000, 17 000 and 35 000 bees) at 5 times of the year (February, April, June, August and October) in Baton Rouge, Louisiana. Two trials were run each month; each trial contained 5 treatments (the 5 population sizes) and lasted for 22 days. To distribute the workload, the 2 trials within a month were begun 1 week apart.

Establishing populations

Control of one genetic variable, worker genotype, was largely achieved by collecting all the worker bees needed for a trial into one large, screened cage. This heterogeneous mixture of bees was then redistributed into 5 test populations, thus making the 5 populations genetically and environmentally equal at the beginning of the experiment. They differed only in size. The queens (naturally mated sisters) constituted the other genetic variable, and, to minimize their effect, the experiment was terminated just before any progeny emerged. If newly emerged workers had been allowed into the experiment, they would have confounded the calculations of adult survival and honey gain per bee.

Each trial was begun by collecting about 11 kg of bees into a large screened cage. Five queens were caged individually and placed in the larger cage with the workers, and the whole unit was fed 50% (wt/wt) sugar syrup. After 2 days the bees were subdivided into 5 unequal populations. These populations (the treatment) were collected into smaller cages until the bees weighed 0·3, 0·6, 1·2, 2·4 and 4·8 kg respectively. Three samples of 100–200 bees were taken from the original population as it was subdivided into the smaller cages, and by weighing and counting the bees in these samples, the number of bees in all 5 populations was estimated.

About 2 h after subdivision of the original population the 5 new populations were placed in hives spaced at least 20 m apart. Initially these experimental colonies contained no drones. (The procedure for hiving the bees and eliminating the drones has been described by Harbo, 1983). The hive sizes assigned to the experimental populations were as follows:

0·3-kg populations : 10-litre hives with 6 frames, each with comb 13 × 19 cm;
0·6-kg populations : 20-litre hives with 6 frames, each with comb 13 × 43 cm;
1·2-kg populations : 39-litre hives of 2 chambers, each with 6 frames;
2·4-kg populations : 64-litre hives of 2 chambers, each with 10 frames;
4·8-kg populations : 124-litre hives of 4 chambers, each with 10 frames.

Combs for the four largest colonies all measured 13 × 43 cm.

The experimental period was measured from the time the bees were put into the hives. The 5 queens from the original cage were put into the hives (i.e. were caged) at the same time that the workers were added. The queens were released about 45 h later.

Sister queens were used throughout the experiment. Ten queens were used in the first two trials and the same 10 again in subsequent test periods, each with a colony of the same size, and any queen that died between trials was replaced with a sister queen.

Brood measurements

As much of the egg-laying was evaluated by measuring brood area, it was necessary to know the timing of egg-hatching, cell-capping and adult emergence of worker brood. Eggs hatch about 72 h after being laid, cells are capped about 5 days later (8 days after egg-laying, though capping of some cells was observed to begin at *c.* 7¾ days. Adult bees began to emerge 19 days after queen release. The tests were ended 19 days after queen release so that the adult population would not be increased by newly emerged adults.

Egg-laying rates of the queens were measured at 5 intervals: on the first day and on days 2–3, 4–5, 6–11 and 12–19. To estimate the numbers of eggs laid on the first day, larvae were counted 96 h after queen release. Since eggs require 72 h to develop before hatching, larvae for day 1 represented the eggs laid during the first 24 h that had hatched and survived. Eleven days after queen release, the area of capped brood was measured with a wire grid. Each square of the grid equalled 6·5 cm^2, and a value of 3·9 cells/cm^2 was used in calculations. Since brood is capped 8 days after egg-laying, the number of cells of capped brood 11 days later equalled the number of eggs laid during the first 3 days. The number of eggs laid during the first 24 h was subtracted to find the number of eggs laid on day 2–3. By measuring capped brood on days 14 and 19 and uncapped on day 19, the egg-laying rates for the other intervals were estimated. These estimates of capped brood were based on the assumption of no egg or larval mortality, so the estimates based on capped brood (days 2–3, 4–5 and 6–11) may be 5–20% too low.

Data collection

Honey gain or loss and total brood production were measured 19 days after queen release (21 days after the bees had been installed). At that time, all the combs were removed from the colonies, the queens were caged, bees were sampled to estimate the amount of honey in their foregut, and all colonies were reduced to 1 or 2 hive bodies containing unimportant combs that weighed very little (see below). In the laboratory, the combs from the experiment were weighed, areas of capped and uncapped brood measured, and the foreguts of 10 bees from each colony weighed. As in Harbo (1983), both foreguts and combs were considered honey reservoirs for a colony. The initial weight of honey included the initial weight of the combs plus the total weight of the foreguts of the original population. The final weight equalled the final weight of combs plus the total weight of the foreguts in the final population. The weight of the brood was then subtracted from the weight gain or loss to yield the net gain or loss of honey. A cell of brood (all stages) was given an average weight of 0·092 g (Nelson et al., 1924).

In addition to weight gain and honey gain, adjusted weight gain was calculated. Adjusted weight gain accounts for the pollen and honey that was used to produce brood; brood weight was converted back to pollen and honey weight. Thus the productivity of colonies with different amounts of brood could be compared more realistically.

The problem with adjusted weight gain is that there is no reliable measure of the amount of honey and pollen needed to produce a worker bee. Rosov (1944) estimated that 125 mg pollen and 142 mg honey are needed to produce one worker bee. Since a worker pupa weighs about one half as much as Rosov's combined honey and pollen weight, a 2:1 (wt/wt) conversion ratio of food to brood was used in the present calculations. For example, a colony that produced 2000 g of honey, pollen and brood (5000 cells of brood) was given an adjusted weight gain of 2460 g. The brood weight (5000 cells of all ages × 92 mg/cell) counted double.

Adult survivorship was measured the morning after the brood was measured. As the heavy combs and supers used for the larger colonies had been removed the day before, all hives were light enough to weigh in a van on a mechanical balance (22-kg capacity, with readings to the nearest gram). Hives were closed before dawn so that all the bees would be inside. Later in the morning, the entire hive was weighed, the bees were brushed into an empty box where the hive had stood, the population was sampled to obtain weight per bee, and combs and equipment were re-weighed. Thus the population of each colony was estimated 22 days after it had been established.

Numbers of cells of brood produced during the brood cycle (cells per bee per day) and honey gain or loss (honey per bee per day) was calculated from a mean population at the midpoint between the initial and final populations. This assumed a linear decline in each population.

Statistical analyses

Analysis of variance was used to evaluate results. The sources of variation were month, trial within month, population size and interaction between month and population size. Since month was not replicated in other years, only population size was considered a valid variable, the other sources simply reducing variance. Population sizes varied only slightly from trial to trial, so were used as discrete classes. Honey loss or gain per bee, total weight gain or loss per bee, cells of brood produced per bee, total brood and percent survival were the variables tested. The least significant difference (LSD) test was used for separating means.

The results for each month of egg-laying were described by a regression formula that reflected total cells of brood produced in 19 days (Y-axis) by the different populations (X-axis).

Results and Discussion

Brood production

Colonies with initial populations of 4500 bees produced the most brood per bee in all periods except August (Table 1). The overall higher rate of brood-rearing by colonies of 4500 bees was significant at the 0·05 level (Table 2). The trend of smaller populations to produce more brood per bee as reported by Moeller (1961) and Free and Racey (1968) held true for the 4 largest initial populations. Logarithmic curves best fit these data. With Y = the total cells of brood produced in 19 days and X = the initial population, the regression equations were:

$Y = 5975 \ln X - 44379;\ r = 0{\cdot}96;\ n = 10$ (February)

$Y = 8235 \ln X - 59318;\ r = 0{\cdot}93;\ n = 10$ (April)

$Y = 6497 \ln X - 43166;\ r = 0{\cdot}93;\ n = 9$ (June)

$Y = 3530 \ln X - 26708;\ r = 0{\cdot}96;\ n = 10$ (August)

$Y = 4017 \ln X - 27600;\ r = 0{\cdot}95;\ n = 10$ (October)

Using these equations, one can plot cells per bee (Y-axis) by population (X-axis) to find the theoretical population that would have produced the most brood per bee. The most brood cells per bee were produced by initial populations of 4600 (February), 3700 (April), 2100 (June), 5300 (August) and 2600 (October). The actual numbers of brood cells per bee for the 5 population sizes are listed in Table 1.

The decline in rate of brood production by colonies with the smallest population (2300 bees) relative to populations of 4500 bees may not reflect a tendency to produce less brood, but rather a physical inability to produce more brood. Low temperatures may have forced the smallest colonies to restrict their brood-nest in February, for during warmer weather (June)

TABLE 1. The effect of honeybee colony size on brood rearing, worker survival and gain or loss of honey in 5 test periods in Baton Rouge, Louisiana.
Data are from 50 colonies and each value in the table is the mean of values for 2 colonies.
A mean population for each colony was used to calculate both number of brood cells per bee and honey gain or loss per bee per day.

Period	*Initial adult population*	*No. brood cells after 19 days*	*No. brood cells/ bee*	*Honey gain/ bee/day (mg)*	*% survival after 22 days*
February	2216	1806	0·90	−25·8	81
	4535	5996	1·44	−24·3	83
	8896	9512	1·20	−14·5	78
	17 670	14 422	0·88	−9·8	84
	35 598	18 070	0·56	−7·8	81
April	2316	4325	2·41	2·6	56
	4515	11 162	3·04	1·6	64
	9352	16 275	2·21	10·1	58
	17 099	22 875	1·67	11·9	63
	37 061	27 875	0·97	17·7	55
June	2252	5025*	2·78*	5·2	71
	4560	10 838	2·80	6·3	70
	9189	17 513	2·22	10·2	73
	17 862	22 950	1·56	16·6	66
	35 629	22 438	0·80	19·1	61
August	2321	1101	0·60	−6·4	62
	4441	2267	0·65	−8·1	58
	8962	5965	0·87	−5·1	53
	18 204	7191	0·54	−3·0	46
	36 337	10 763	0·42	−1·0	44
October	2265	3200	1·59	−7·4	73
	4284	6313	1·76	−7·6	62
	8594	8300	1·14	−0·7	65
	16 190	12 658	0·93	3·0	61
	31 937	13 038	0·53	7·3	60

*Value is based on only one trial, the queen in the other trial having been lost after 12 days.

TABLE 2. Means and statistical separation by least significant difference of combined data from 10 trials at Baton Rouge, Louisiana, for brood production, worker survival and honey gain by honeybee colonies of different sizes.
Means followed by different letters in the same column differ significantly at $\alpha = 0{\cdot}05$

Initial colony population	*No. brood cells/ bee*	*Gain of brood and honey (mg/bee/day)*	*Honey gain (mg/bee/day)*	*Adjusted* wt gain (mg/bee/day)*	*% survival after 22 days*
2300	1·65*b*	0·4*a*	−6·4*a*	7·2*a*	69*a*
4500	1·94*a*	1·7*a*	−6·4*a*	9·8*ab*	68*a*
9000	1·53*b*	6·5*b*	0·0*b*	13·1*b*	65*a*
17 000	1·11*c*	8·3*b*	3·7*c*	12·9*b*	64*ab*
35 000	0·65*d*	9·8*b*	7·1*c*	12·5*b*	60*b*

*Adjusted wt gain accounts for all honey and pollen used to rear brood, consumed by adults, or stored during the test.

the amount of brood produced per bee by 2300 bees nearly equalled that of the 4500-bee colonies. In addition, the smaller frames used with the 2300 bees may have been less space-efficient.

Data on total brood are listed in Table 1. The totals include all eggs, larvae and pupae present in a colony 19 days after queen release. The 5 population sizes differed significantly in amount of total brood. Note that these colonies were all newly established, so they had almost no accumulated pollen reserves, and they were not fed. Therefore, the amount of brood produced by them may differ from the amount produced in established colonies having equal populations.

Rates of egg-laying

Rates of egg-laying are reported in Fig. 1. In general, the rate increased rapidly for 2–5 days, declined rapidly, and then levelled off. Exceptions to this pattern were the 35 000-bee population in February and the populations of 17 000 and 35 000 bees in spring. Egg-laying in these colonies did not decline after reaching a 2–5 day peak, but continued to increase gradually (Fig. 1A, Fig. 1B). Of the other populations, the smaller ones tended to have earlier peaks, lower peaks and sharper declines.

The estimate of the number of eggs laid on the first day (Fig. 1) needs explanation. It was the number of eggs produced in the 24-h period following the release of a queen. So, unless a queen began to lay eggs immediately upon release, the actual rate of egg-laying would have been higher.

Even though the queens in the largest colonies laid as many as 1800 eggs per day in April (based on uncapped brood), none seemed to reach her maximum egg-laying rate during the test period. To study this, brood measurements in the February trial were continued until April. No brood was removed. Based on total brood in early April, the 2 queens in the populations that originally had 35 000 bees averaged 1990 and 1740 eggs per day during the last 20 days. On the basis of uncapped brood, 2500 and 1950 eggs were produced per day.

None of the queens stopped laying eggs. Even during summer dearth, queens in the smallest colonies continued to lay; the queens in the 4 smallest colonies in fact laid many more eggs than the workers would rear. This was not observed during other times of the year, and queens in colonies of 35 000 bees did not produce excessive eggs during summer dearth.

Thus, queens did not fill all the available space in a brood-nest and then stop laying. The strategy for a newly formed colony seemed to be for the queen to get into a rapid laying state as quickly as possible. This required about three days. In small populations, or under suboptimal seasonal conditions, this increase stopped early or the rate of increase slowed. At 5 days, the egg-laying of a queen levelled off to a fairly constant rate as if to fit the population size and season.

The result was that smaller populations ended a brood cycle with a higher proportion of older brood than did larger populations. When a colony is newly established, no young adults are added to the population for at least 20 days, so the population declines. A high proportion of old brood enables a colony to recover its losses more quickly and in some cases this might enable a small colony to recover from a perilously low population.

Honey gain or loss

When computing honey gain or loss, the colonies with more bees produced more honey per bee during times of production and lost less honey per bee during dearth periods (Table 1). Significant differences in honey gain were found between the middle group (9000-bee colonies) and the two larger and two smaller groups (Table 2). The two most populous groups were not different from each other, nor were the two smallest colonies.

On the basis of total weight gain (weight of brood plus weight of honey) per bee, those with ⩾9000 bees were not significantly different (Table 2). The respective weight gains of the two smallest populations were significantly lower than the others but not significantly different from each other.

Adjusted weight gain was not significantly different for populations ⩾4500 bees, and the adjusted weight gains of populations ⩾9000 bees were nearly identical.

Worker survival

In the June, August and October trials bees in the more populous colonies had a lower survival rate (Table 1). Differences in survival seemed non-existent in February and April, but the June–October differences were strong enough to give an overall significant difference for the largest colony (Table 2).

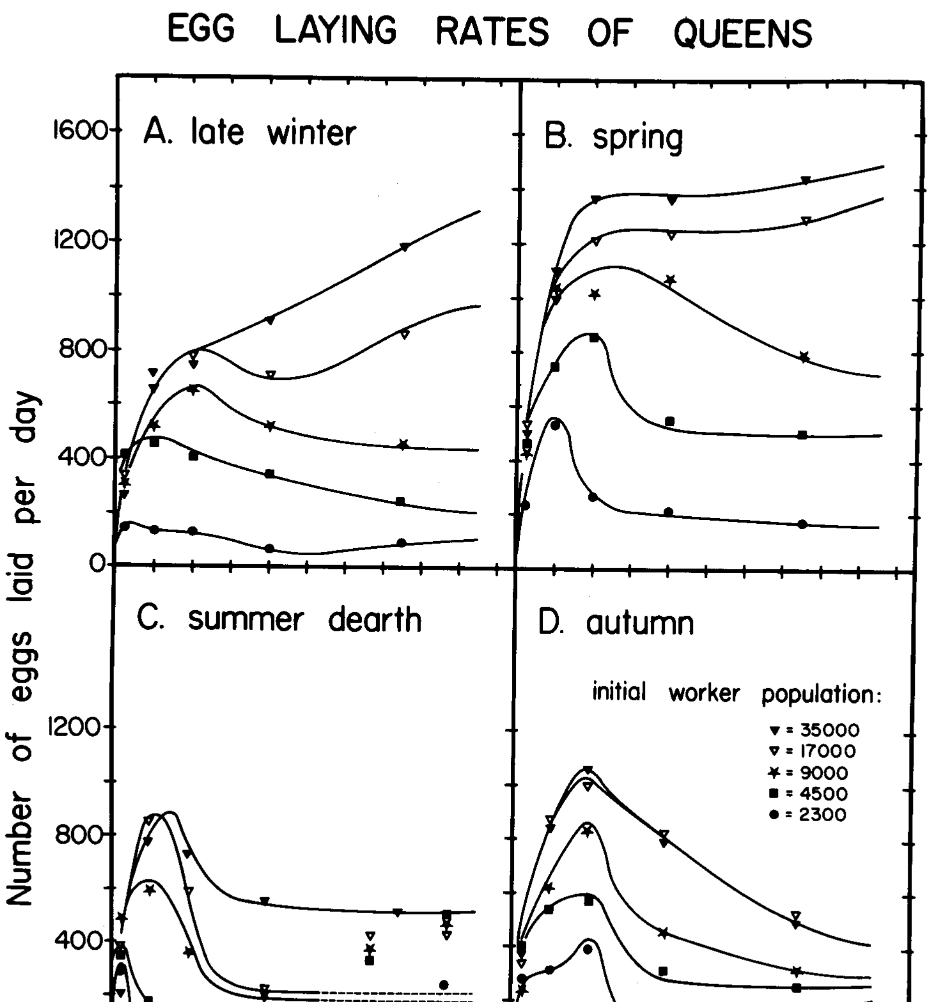

FIG. 1. Egg-laying rates of queens in southern Louisiana when given broodless combs and 2300, 4500, 9000, 17 000 or 35 000 worker bees.

Each symbol represents a mean of 2 colonies except in B where it is the mean of 4 colonies. Symbols are located at the midpoint of the days included in a data-collecting interval: day(s) 1, 2–3, 4–5, 6–11 and 12–19. Data were based on larvae (day 1), all stages of eggs and uncapped larvae (12–19), and capped brood (the other 3 intervals). When the number of eggs vastly exceeded the rate of brood rearing during the preceding 11 days (in summer dearth), eggs were reported separately from larvae and brood production was estimated (dotted line in C).

A. Late winter (3 February – 1 March 1984); mean temperature = 12°C, pollen available but not nectar.

B. Spring tests (27 May – 29 June 1983 and 11 April – 9 May 1984); mean temperatures = 25° and 19° respectively; both pollen and nectar available.

C. Summer dearth was the period between blossoming of spring and autumn plants. Tests (5–31 August 1983); mean temperature = 28°; pollen available from grasses, very little nectar available.

D. Autumn tests (30 September – 27 October 1983); mean temperature = 20°; abundant pollen and some nectar available.

A higher rate of brood rearing did not shorten the life-span of workers, or at least did not have a major effect on it, for colonies that produced the most brood per bee had the highest survival and those that produced the least brood per bee had the lowest. However, it is still possible that brood rearing may shorten adult longevity if the younger bees in the mixed population were the ones that served as nurses and if the 22-day test period was too short to detect a shortened life-span of those young bees.

Length of life is certainly a factor in population growth, but its effect seems to be small when compared with the vast differences in rates of brood production. Laboratory studies have indicated that colony size may affect the length of life of the bees that they rear (Eischen et al. 1982). The bees in the present study were not reared in the colonies in which they were tested, so the rearing environment was a controlled factor. But by continuing to measure brood production and population growth from February until April in the February trials, it was calculated that the adult life-span of bees reared in larger colonies might have been slightly longer, as work by Eischen et al. (1982) would predict. However, any increase in life-span did not begin to balance the brood-rearing deficit in the larger colonies, for from late February (when brood began to emerge) until April the adult populations increased by factors of 2·4, 3·0, 2·5, 1·6 and 1·3 in the smallest to largest colonies respectively, a very close reflection of the different rates of brood-rearing (Table 1).

An optimal population

Of the population sizes tested, none was optimal for all 3 characters tested. The larger populations produced the most honey per bee when nectar was available and consumed the least per bee when it was not. Population growth, as expressed in length of adult life and brood production, was greater in smaller populations.

Consequently there is an optimal size for producing honey (the largest population) and a different optimal size for population growth (not the largest). A beekeeper must choose between producing bees or honey. Since bees produce honey only when there is a nectar flow, the logical decision is to have maximal populations during the nectar flow and perhaps smaller populations when there is no flow.

During the tests, a population of 9000 bees was optimal in many ways. This population combined the advantages of high weight gain found in larger colonies with high brood production found in smaller colonies (Table 2). Moreover, a 9000-bee population (without brood) consumed significantly less honey per bee during winter than a smaller population (4500 bees), but not significantly more than a larger population of 32 000 bees (Harbo, 1983).

An optimal population for autumn colonies was reported by Jeffree and Allen (1956) to be 11 000 bees. A colony with 11 000 bees in November had only 18% fewer bees the following March, whereas colonies with November populations of 7000 and 35 000 bees lost 36% and 44% respectively. They were puzzled by their results, but I believe that my February data (Table 1) help to explain why their highest winter growth-rate was in colonies that had 11 000 bees in the autumn. My data indicated that the survival rates of adult bees in winter did not differ with different population sizes (Harbo, 1983; February data in Table 1); without brood rearing, therefore, one would expect populations in all colonies to decline at an equal rate. Accordingly, colonies producing more cells of brood per bee in February and March would recover a higher proportion of their losses. Low temperatures probably restricted brood rearing in the smallest colonies (as in the February trial), but with larger populations the trend returned to normal, that is, more bees reared fewer cells per bee. Thus, the smallest population that was able to withstand the effects of stress (in this case cold) produced the most brood per bee and was best able to recover its winter losses.

Summer dearth was similar to a winter period in that population growth was most rapid for a population of intermediate size (see August, Table 1). This is comparable to the February data and to the winter results of Jeffree and Allen (1956); the colonies with 9000 bees produced the most brood per bee in August.

A population for evaluation of stock

This study has shown that in stock testing the variable of population size must be controlled. I do not recommend large populations (>30 000 bees) because they are costly to create and manage. Moreover, they do not test well for population growth because they are already near maximum size. Very small populations (2000–4000 bees) may be satisfactory in prime season, but succumb to winter and summer stress, even in the relatively mild Louisiana climate (Table 1).

The optimal size for stock testing will vary with climate as well as season. A population should be large enough to withstand the most severe stress that occurs during the test period (i.e., a population is too small if larger populations produce more brood per bee). In 1983–84, a population of 9000 bees was suitable in Louisiana (Table 1). During winter in Scotland (probably the period of greatest stress on honeybees), a population of *c.* 11 000 bees was suitable (Jeffree & Allen, 1956).

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