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CORRELATIONS AND INTERACTIONS BETWEEN POPULATION, LENGTH OF WORKER LIFE AND HONEY PRODUCTION BY HONEYBEES IN A TEMPERATE REGION

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Summary

An investigation of the factors influencing honey production was conducted using 12 colonies of honeybees (*Apis mellifera*), with 3 replications in time. Brood areas, colony populations and weights of honey produced were measured.

On the average, adult worker populations amounted to only 40–60% of the numbers that should have emerged, based on brood-cell estimates for the preceding 42–day period. Correlation coefficients (r) between numbers of brood and resulting numbers of adult bees varied from +0·20 to +0·86, and values of r for population and length of worker life from −0·39 to +0·92. Average length of productive life of workers varied from 21 to 25 days and average number of larvae reared per worker bee from 0·8 to 1·5. Workers rearing more brood were shorter-lived (r = −0·71 to −0·94).

Individual colonies produced between 4 and 26 kg honey. Production was related in varying degree to number of brood reared (r = +0·20 to +0·85) and to colony population (r = +0·38 to +0·70). Individual productivity of workers had a greater influence than colony population on the amount of honey produced, as evidenced by the high coefficients of non-determination obtained for regression of weight of honey on population and the large standard deviations of the regression coefficients, as well as the highly significant values of χ^2 for inter-colony comparisons of honey production per 1000 bees. Because of their higher brood production, colonies headed by queens 1 year old produced 19–27% more honey than those with queens 2 years old.

It is concluded that honey production is governed by the interaction of 3 primary factors: average daily brood production, length of worker life and individual productivity of workers. The relative contributions of these factors vary.

Introduction

It is commonly accepted by beekeepers that the egg-laying capacity of the queen directly affects the amount of brood produced in the colony, which in turn, through its influence on colony population, is a major factor in honey production. But, as any beekeeper should know, colonies with the most brood do not always become the most populous, nor do the most populous colonies always produce the most honey.

Nolan (1925) presented detailed studies of the brood-rearing cycle of honeybees during the season. Using Nolan's data, Bodenheimer (1937) presented a theoretical structure of a colony assuming 42 days as the average life-span of a worker bee. But Fukuda and Sakagami (1968), as well as Woyke (1976, 1977) showed that not all individuals in the brood develop into adult workers. Studies of relationships between amount of brood and colony population and between amount of brood and weight of honey produced have revealed that the coefficients of correlations are very variable, often being weak or even negative (Taranov, 1946; Moeller, 1958; Soller & Bar-Cohen, 1967; Villumstad, 1977; Ebbersten, 1978; McLellan, 1978). Moreover, the correlation between colony population and weight of honey produced has been found to vary, being sometimes weak or negative (Farrar, 1937; Lunder & Thyri, 1964; Ebbersten, 1978). Thus the relations are not as simple as commonly believed.

The length of life of the European honeybee has been investigated by several authors (Nickel & Armbruster, 1937; Maurizio, 1950; Free & Spencer-Booth, 1959; Sekiguchi & Sakagami, 1966; Sakagami & Fukuda, 1968; Taranov & Azimov, 1972; Villumstad, 1977) and that of the Africanized bee by Winston (1979, 1980). Maurizio (1950), Taranov and Azimov (1972), and Villumstad (1977) pointed out that life-span decreases when the bees feed more larvae. Doull (1974) and Wille and Gerig (1976) calculated the theoretical populations of colonies with honeybees with different life-spans.

Intuitively, the rules governing honey production may be presented in the form of 2 equations: (1) honey production = number of workers × individual productivity, and (2) number of workers = average number of brood produced daily × length of adult life.

Beekeepers make great efforts to increase brood production to achieve maximum populations while almost neglecting the other factors.

Until now the relative importance of numbers of bees and individual productivity in determining honey production has not been assessed. Correlations between length of life and many other factors (except brood production) have not been calculated. The purpose of the present investigation was to study the factors governing colony population and honey production in the temperate regions, and their variability and interactions. A paper on an investigation carried out in the tropics is in preparation.

Materials and Methods

This investigation was conducted in Poland using Carniolan-Caucasian hybrid honeybees. To reduce genetic variation as much as possible, the original Caucasian mother queen was inseminated instrumentally with the semen of a single Carniolan drone. The hybrid daughter queens were used for the study and inseminated instrumentally with semen collected from drones originating from one Caucasian queen. One-year old queens were investigated in 1978 and 1- and 2-year old queens in 1979. Brood survival rate was checked as described by Woyke (1976), and for further investigations only those queens were used which produced brood with nearly 100% survival. The area occupied by brood was measured twice, at 21-day intervals, and converted into number of cells, assuming that 412 cells occupy 1 dm^2 of comb surface (Woyke, 1980).

The number of workers in each colony was determined 42 days after the first measurements. At this time, all bees which had emerged from the brood area measured 42 days earlier would be expected to be field bees, while most of those emerged from the brood area measured 21 days earlier would be hive bees. All the bees present in the hive were shaken into a box and weighed. Number of bees was calculated by using 113·8 g as the weight of 1000 bees (Woyke, 1980). The procedure of measuring brood area and calculating weight of bees was carried out once in 1978 and twice in 1979.

The amount of honey extracted from each colony was calculated from the difference in comb weight before and after extraction. The weight of honey left in the hive was estimated on the basis of 0·33 kg honey per dm^2 sealed comb.

Average length of life of the workers present in the hive on the day worker number was determined was estimated by dividing total bee-days (number of bees multiplied by 42) by number of bees emerged in the previous 42 days (combined brood counts).

Statistical procedures

Correlation coefficients (r) were calculated for the various parameters measured. Coefficients of regression (b), coefficients of determination (r^2) and coefficients of non-determination ($k^2 = 1-r^2$) were calculated for the regression on population of weight of honey produced. Colonies were compared for unit productivity (weight of honey produced per 1000 workers) by the χ^2 test.

Results

Conditions of honey flow

Weather conditions were better for colony development in 1978 than in 1979. In 1978 the first extraction of honey, obtained from rape (*Brassica napus*), was on 8 June and the second, from black locust (*Robinia pseudoacacia*), on 29 June. The number of workers in each colony was determined on 22 June, and thus may be related to both honey harvests.

In 1979 the spring was cold and unfavourable for colony development. Very little nectar was collected from the rape. The main nectar flow was from raspberry (*Rubus idaeus*), and the combined honey harvest was extracted on 28 June. Numbers of bees were estimated on 2 July. Colony population was determined for the second time on 6 August. After that date, a weak nectar flow occurred in heather (*Calluna vulgaris*). The honey was extracted on 19 September, when the amounts of honey left in the hives for winter were also determined.

Brood production

In the spring of 1978 brood present in the colonies in the 42-day period before the date when worker population was estimated varied from 45 800 to 59 300 and averaged 50 500. The

TABLE 1. Factors influencing honey production by honeybee colonies whose population was determined 22 June 1978 (first test).

Worker population (WP, in thousands of bees) was determined from total weight of bees in the colony on 22 June 1978. Numbers of brood cells (BC, in thousands) were obtained from measurements of brood area 42 days (BC_1, 11 May) and 21 days (BC_2, 11 June) earlier.
Average worker life-span (AWL) was obtained as the quotient of total bee-days for the 42-day period preceding 22 June (WP × 42) divided by total brood cells from the two counts (TBC).
Average daily brood production (ADB) was calculated for the 42-day period 11 May–22 June; average brood per worker (B/W) is the ratio of the 2nd brood count, 21 days prior to population estimation, to the worker population on 22 June (= BC_2/WP).
The coefficient of regression b for total honey production (THP) on WP was 0·35 kg/1000 bees with SD = ±6·99 kg; the coefficient of determination r^2 for regression of THP on WP = 0·15 and the coefficient of non-determination k^2 (= $1-r^2$) was 0·85.
χ^2 for unit honey production (UHP = honey/1000 bees) = 584 (df = 6, P<0·005).

Colony no.	*BC_1*	*BC_2*	*TBC*	*WP*	*WP/TBC (%)*	*AWL*	*ADB*	*B/W*	*THP (kg)*	*UHP (g)*
212	16·5	31·6	48·1	21·3	44·3	18·6	1145	1·49	4·2	197
234	19·3	30·2	49·5	34·3	69·3	29·1	1179	0·88	7·9	230
242	16·4	29·8	46·2	20·9	45·2	19·0	1100	1·43	8·3	413
241	15·0	30·8	45·8	41·0	89·5	37·6	1090	0·75	10·2	249
247	18·4	36·0	54·4	33·3	61·2	25·7	1295	1·08	12·9	387
220	19·1	31·0	50·1	26·9	53·7	22·6	1193	1·15	14·0	520
216	22·6	36·7	59·3	34·3	57·8	24·3	1412	1·07	25·7	749
Mean	18·2	32·3	50·5	30·2	60·1	25·3	1202	1·12	11·9	392
					Correlation coefficients					
WP	+0·16	+0·30	+0·26			+0·92*	+0·25		+0·39	+0·04
AWL	−0·20	+0·05	−0·13	+0·92*			−0·10	−0·94*	+0·07	+0·98*
THP	+0·80*	+0·74†	+0·85*	+0·39		+0·07	+0·86*		—	+0·93*

*Significant at P<0·05
†Significant at P=0·06

difference between the most populous and the least populous colony was only 13 500 (Table 1). In the second test, in July 1979, total numbers of brood were calculated for a 49-day period (Table 2). For each colony, one-third of the brood number determined at 42 days was added to the total obtained for the 21- and 42-day counts. Brood occupied totals of 26 900 to 62 900 comb cells in colonies headed by queens aged 1 year (Table 2). Thus the range (36 000) was much greater than in 1978. Average brood numbers were lower in the unfavourable spring of 1979.

Colony population

Colonies in the favourable season of 1978 reached a strength of 20 900–41 000 workers, with an average of 30 200. In July 1979 an average of 17 400 workers were found in colonies whose queens were 1 year old and 16 600 in colonies with queens of 2 years (Table 2). When the procedure was repeated in August 1979 colony populations averaged 22 200 and 14 900 workers for colonies with queens 1 and 2 years old respectively. In all cases numbers of worker bees were less than the numbers of brood cells from which new workers had emerged in the previous 42 (or 49) days; worker survival averaged 40–60% of total brood. The coefficient of correlation between brood production and colony population (r = +0·26) was low in the favourable season of 1978 when differences in brood production were relatively small (Table 1), but higher in 1979 (r = +0·83, Table 2, and r = +0·65, Table 3) when conditions for development were poorer and when differences in brood production were greater. Thus, colony population was more closely related to brood production when the weather was less favourable.

TABLE 2. Factors influencing honey production by honeybee colonies whose population was determined 22 July 1979 (second test).

See Table 1 for explanation of abbreviations.

Brood counts were made 14 May, 4 June and 25 June. Average daily brood production was based on a 49-day period, one-third of the brood number present on 25 June (after 42 days) being added to the combined counts for 14 May and 4 June.

Each correlation coefficient in the lower section of the table applies to data for both 1- and 2-year queens. The coefficient of regression b for THP on WP = 1·46 kg honey/1000 bees with SD = ±3·66 kg; the coefficient of determination r^2 = 0·49, and the coefficient of non-determination k^2 = 0·51.

χ^2 for UHP = 996 (df = 11, P<0·005).

Age of queen	*Colony no.*	*BC_1*	*BC_2*	*TBC*	*WP*	*WP/TBC (%)*	*AWL*	*ADB*	*B/W*	*THP (kg)*	*UHP (g)*
1 year	203	6·9	16·2	28·2	15·1	53·5	26·2	576	1·07	4·7	311
	210	9·4	18·1	34·7	17·0	49·0	24·0	708	1·06	5·4	318
	258	6·2	16·4	26·9	17·8	66·2	32·4	549	0·92	6·2	348
	206	8·8	21·5	36·7	15·6	42·5	20·8	749	1·38	9·2	590
	228	12·3	18·9	36·1	14·3	39·6	19·4	737	1·32	9·7	678
	254	15·0	27·5	51·9	19·8	38·2	18·7	1059	1·39	13·1	662
	250	16·2	24·6	45·3	17·6	38·9	19·1	924	1·40	16·6	943
	219	20·2	33·5	62·9	22·0	35·0	17·2	1284	1·52	19·7	895
	Mean	11·9	22·1	40·3	17·4	45·4	22·2	823	1·26	10·6	593
2 years	212	6·1	13·2	24·0	13·9	57·9	28·4	490	0·95	4·7	338
	234	13·7	24·0	44·6	18·6	41·7	20·4	910	1·29	7·9	425
	220	15·2	20·4	42·2	16·0	37·9	18·6	861	1·28	8·8	550
	216	12·0	24·7	42·0	18·0	42·9	21·0	857	1·37	14·2	789
	Mean	11·8	20·6	38·2	16·6	45·1	22·1	780	1·22	8·9	526
	Correlation coefficients										
	WP	+0·69*	+0·86*	+0·83*			−0·39	+0·83*		+0·70*	+0·48
	AWL	−0·87*	−0·72*	−0·83*	−0·39		−0·83*	−0·89*		−0·71*	−0·74
	THP	+0·83*	+0·87*	+0·83*	+0·70*		−0·71*	+0·83*			+0·96

*Significant at P<0·05

Average length of productive life of worker bees

Since numbers of workers present in the colonies on the day that population was determined were less than the numbers which should have emerged during the previous 42 (or 49) days, average length of worker life obviously was less than 42 days. The ratio of number of days in average life-span to 42 must be the same as the ratio of number of adult bees to the number that emerged in the preceding 42 days. Thus in colony no. 212 (Table 1) the 21 300 workers present constituted 44·3% of the 48 100 workers which should have emerged. Average length of life calculated in this manner for bees in the various colonies was 18·6–37·6 days, and the average for the entire apiary was 25·3 days. The average for workers emerged in the 49-day period in 1979 (Table 2) was 22·2 days for colonies headed by queens aged 1 year and 22·1 days for those with queens aged 2 years. For the 42-day period in late summer of 1979 (Table 3) the averages were 22·3 and 18·3 days for colonies headed by queens aged 1 and 2 years respectively.

I propose to call the quantity calculated in this way the *average productive life* of workers. Its use permits the calculation of the expected colony worker population based on average daily brood production and number of cells occupied by brood. It must be pointed out that the brood area does not represent the exact number of adults emerging, and nor is the average *productive* life of workers equal to their true life-span. Productive life is a few days less because it is based on the entire area occupied by brood including those cells with occupants that fail to reach the imaginal stage.

TABLE 3. Factors influencing honey production by honeybee colonies whose population was determined 6 August 1979 (third test).

See Table 1 for explanation of abbreviations.
The coefficient of regression b for THP on WP = 0·52 kg honey/1000 bees with SD = ±5·94 kg; the coefficient of determination r^2 = 0·14, and the coefficient of non-determination k^2 = 0·86.
χ^2 for UHP = 1239 (df = 8, P<0·005).

Age of queen	*Colony no.*	BC_1	BC_2	*TBC*	*WP*	*WP/TBC* (%)	*AWL*	*ADB*	*B/W*	*THP* (*kg*)	*UHP* (*g*)
1 year	203	15·2	22·2	37·4	21·9	58·6	24·6	890	1·02	5·2	237
	210	21·7	24·0	45·7	19·9	43·5	18·3	1088	1·21	8·2	412
	206	19·2	30·0	49·2	22·1	44·9	18·9	1171	1·36	12·6	570
	250	13·5	19·6	33·1	23·8	71·9	30·2	788	0·82	18·4	773
	219	27·6	22·9	50·5	23·3	46·1	19·4	1202	0·98	22·1	948
	Mean	19·5	23·8	43·2	22·2	53·0	22·3	1028	1·08	13·3	588
2 years	212	14·0	9·1	23·1	11·5	49·8	20·9	550	0·79	4·7	409
	234	20·6	22·4	43·0	18·7	43·5	18·3	1024	1·20	8·4	449
	220	19·7	21·6	41·3	16·3	39·5	16·6	983	1·33	12·4	761
	216	15·7	16·0	31·7	13·2	41·6	17·5	755	1·21	16·4	1242
	Mean	17·5	17·3	34·8	14·9	43·6	18·3	828	1·13	10·5	715
						Correlation coefficients					
	WP	+0·36	+0·74*	+0·65†			+0·47	+0·65†		+0·38	−0·15
	AWL	−0·53	−0·14	−0·35	+0·47			−0·36	−0·71*	+0·10	−0·15
	THP	+0·42	+0·21	+0·20	+0·38		+0·10	+0·20			+0·83*

*Significant at P<0·05
†Significant at P≃0·06

Length of worker life, brood production and colony population

The correlation between colony population and length of life in the favourable year 1978 was very high (r = +0·92); brood production differed relatively little among colonies (Table 1). The correlation between population and brood production (r = +0·26) was low and non-significant. Colony population depended mainly on length of worker life. In the next year when differences in brood production were large (Table 2 and Table 3) the correlations for brood with population were high (r = +0·83, r = +0·65) but the correlations for length of life with population were low or even negative (r = +0·47, r = −0·39). In this case colony population depended mainly upon the amount of brood produced.

Average daily brood production was obtained by dividing the total brood for the 42- or 49-day period by the appropriate number of days. In 1978 (Table 1) the daily average was 1202 with a range of 1090–1412, and in 1979 it was 823 and 780 for 1- and 2-year old queens respectively in the spring (Table 2), and 1028 and 828 in the summer (Table 3). Average colony population size (30 000 bees, in 1978) may be estimated as the produce of average daily brood production (1200) and length of average productive life (25 days). Thus, while colony population in one season depended chiefly on the quantity of brood produced, and in the other more upon length of life, it can always be estimated by the produce of numbers of brood produced daily and the average length of productive life of workers.

What determines length of life of worker bees?

It is seen from the tables that length of worker life varied with colony from 16·6 to 37·6 days. In Table 1 there is a weak negative correlation between length of life and the total numbers of brood or the number produced daily, but in Table 2 the correlation is highly negative (r = −0·83). Thus the workers' life tended to be shorter in those colonies which produced more brood.

Average number of larvae reared per bee was obtained by dividing colony worker population by number of brood 3 weeks prior to the date of population estimation. The average was 0·75–1·49 for the spring of 1978 (Table 1), 0·92–1·52 for the spring of 1979 (Table 2) and 0.79–1.36 for the summer of 1979 (Table 3). In all instances there was a high negative correlation between average brood production per worker and average length of worker life. Thus, length of life depended more upon larva-worker ratio than upon absolute numbers of brood.

Honey production

Colonies produced 4·2–25·7 kg honey in 1978. There was a high correlation between honey production and total brood present in the spring ($r = +0{\cdot}85$) but the correlation between honey production and colony population was not significant ($r = +0{\cdot}39$). Correlations between weight of honey and amount of brood and between weight of honey and colony population were high for the spring of 1979 ($r = +0{\cdot}83$, $r = +0{\cdot}70$, Table 2) but low for the summer (Table 3). It seems surprising that honey production depended more on the amount of brood than on population of adult workers. It is more surprising when length of worker life is taken into account. The correlation between honey production and length of life was very low in 1978 ($r = +0{\cdot}07$) and negative ($r = -0{\cdot}71$) in the spring of 1979. It would be unrealistic to conclude that more honey was produced by weaker colonies with shorter-lived workers. However, the relationships become clearer when the dates of nectar flow and estimation of colony populations are considered. Populations were not estimates until the end of the main flow; thus it was the number of workers surviving after the flow that was determined, not the number of workers at the beginning.

When the amount of honey produced is considered in relation to colony populations and length of life of bees working during the nectar flow, it is apparent that individual productivity was not the same for workers in all colonies. Over the 2 seasons, the average amount of honey produced per 1000 bees varied from 197 g to 1242 g.

Table 2 shows a negative correlation coefficient between weight of honey produced per 1000 bees and their mean life-span. This indicates a shorter average life for colonies in which unit productivity was higher. These colonies were weaker after the main nectar flow. The results indicate that life of workers is shortened not only by intensive brood rearing but also by intensive honey production. Brood rearing, however, shortened life more than honey production.

Numbers of workers in the colonies were determined a third time on 6 August 1979. The correlation between honey production and colony population was slightly higher ($r = +0{\cdot}38$) than that for honey production and numbers of brood ($r = +0{\cdot}20$), which was the opposite of results obtained in the spring. Included in this calculation, however, was honey from a heather nectar flow, extracted on 19 September, as well as honey left for winter stores. As the colony population was determined before the nectar flow the correlation between honey production and colony population was elevated.

In the data of all 3 tables there is high correlation($r = +0{\cdot}83$–$+0{\cdot}96$)between unit productivity of a colony(honey/1000 workers)and total honey produced by the colony. To amplify the point that honey production may owe more to the inherent industriousness of the bees (reflected in unit productivity) than to their overall numbers, the regression of total honey production on colony population was calculated. Correlation coefficients between weight of honey and colony population for the 3 periods were +0·39 (Table 1), +0·70 (Table 2) and +0·38 (Table 3). Of these, only the second was high and statistically significant. The corresponding coefficients of determination (r^2), representing sums of squares for regression, were 0·15, 0·49 and 0·14, and the coefficients of non-determination ($k^2 = 1-r^2$), representing the squares of deviations from regression, were 0·85, 0·51 and 0·86. It may be inferred that population determined the weight of honey produced to the extent of 49%, in mid-season of 1979 (Table 2) and less in the other 2 tests. Coefficients of regression of weight of honey on colony population indicated that an increase of 1000 bees resulted in increases of 0·35 kg, 1·46 kg and 0·52 kg for spring 1978, early summer 1979 and late summer 1979, respectively; deviations from regression, attributable chiefly to differences in unit productivity among colonies, were high. Values of χ^2 for inter-colony comparisons of unit productivity showed highly significant deviations from equal distribution for all 3 periods.

Relationship of age of queens to honey production

Colonies headed by queens aged 1 year produced on average 19% (Table 2) and 27% (Table 3) more honey than colonies with queens aged 2 years. For the period up to 2 July (Table 2) both worker life-span and unit productivity were essentially the same for the groups of colonies, but the younger queens produced more brood and hence their colonies were stronger. In the period preceding 6 August workers in colonies with queens 1 year old were slightly longer lived, but unit productivity in colonies with queens 2 years old was on average somewhat higher. The resultant of these 2 factors was almost the same for the 2 groups. However, the younger queens produced more brood and their colonies were stronger. Their higher production of honey was due mainly to greater brood production and consequently a larger population.

Discussion and Conclusions

It is of interest to compare the values obtained in this study for colony parameters with those from other investigations.

As unfavourable weather conditions in 1979 prevented the colonies from reaching full strength by 1 June, only 1978 data will be used for comparisons. Daily brood produced at this date ranged from 1419 to 1748, averaging 1538, compared with 1000–1528 (for 1920) and 1000–1488 (for 1921) reported by Nolan (1925), and a maximum of 1831–2140 and average of 1046–1301 found by Moeller (1958).

The average number of 32 000 cells occupied by brood was somewhat higher than the maximum for 5 colonies found by Nolan (1925) or the 24 000 reported by McLellan (1978), and was close to Villumstad's (1977) figure of 30 000 and the 28 200 given by Bar-Cohen et al. (1978).

Average colony worker population of 30 200 on 22 June was less than the 35 000 listed by Farrar (1937), the 39 500 found by Moeller (1958), or the 37 000 found by McLellan (1978). Thus, despite similar brood production, populations in my experimental colonies did not reach the levels reported by other authors.

In the 3 trials I obtained an overall range for the correlation coefficients between brood cell numbers and worker populations of +0·26 – +0·83. This range contains the variations of +0·39 – +0·77 reported by Moeller (1958), and is similar to the range of +0·78 – +0·93 calculated by McLellan (1978) for the beginning of the season. However, a very high correlation (r = 0·92 – 0·95) was found by Taranov (1946) for the reverse relationship—size of population of worker bees and the number of brood produced by them.

I obtained highly positive correlation coefficients between amount of brood and honey production in spring 1978 (+0·85) and early summer 1979 (+0·83) but a coefficient of only +0·20 in late summer 1979. This range spanned the ranges for r values reported by several authors: +0·43 – +0·50 (Moeller, 1958); +0·45 – +0·51 (Soller, 1967); +0·40 – +0·70 (Ebberston, 1978) and +0·37 – +0·80 (Taranov, 1946). McLellan, however, found only a single significant positive correlation for the 2 variables over the whole season. Over a 13-year period Bar-Cohen et al. (1978) found only a moderate correlation between queens' fertility and colony yields and doubted the value of selection for higher fertility to increase honey production. Taranov (1946) reported a negative correlation (−0·80) between honey production and amount of brood present during the main nectar flow.

My correlation coefficients for worker population and weight of honey produced in the 3 tests varied from +0·39 to +0·70; this range was slightly less than Farrar's (1937) range of +0·44 – +0·99 or Lunder and Thyri's (1964) range of +0·48 – +0·89, and McLellan's (1978) ranges of +0·78 – +0·93 for the first half and higher than −0·13 – +0·32 for the second half of the season.

My correlation coefficients for population and unit productivity were low or even negative. Farrar (1937) reported relative production per 1000 workers in colonies of 15 000, 30 000, 45 000 and 60 000 bees to be in the ratio of 1·00:1·36:1·48:1·54 but stated that these were not by any means invariant. Taranov (1952) found that in colonies of 1, 2 and 4 kg of bees, relative amounts of honey produced were in the ratio of 1·00:1·42:1·70 per kg of bees, but in somewhat stronger colonies there was a much lower rate of increase with increasing population. According to Lunder and Thyri (1964) colonies of medium strength produced the greatest yields per unit weight of bees. Weaker and, to a greater degree, stronger colonies had lower unit production.

In other studies length of worker life has been calculated directly by introducing marked workers into colonies. Nickel and Armbruster (1937) obtained average values of 15–24 days. Free and Spencer-Booth (1959) reported a decrease over the season from 33 days in April to 29 in June, while Taranov and Azimov (1972) found an increase from 24 days in April to 33 in July. Sakagami and Fukuda (1968) reported averages of 28 and 32 days and Sekiguchi and Sakagami (1966) reported 31 days. Winston (1979, 1980) reported that African bees lived a shorter time than European, averaging 12–24 days. The values calculated in the present study for length of productive life based on brood counts were somewhat smaller than many of those cited above, because not all cells produced adult workers. It would be difficult to correct for these non-effective cells using Wille and Gerigs (1976) method because the proportion of adults produced is not equal to the survival rate of brood (Woyke, 1980, 1981). The use of length of *productive* life would seem to have an advantage: it permits ready calculation of colony population, without overestimating it (Bodenheimer, 1937; Gromisz, 1962).

Maurizio (1950) found that workers which fed more brood lived a shorter time. The negative coefficients between larva-worker ratios and worker life span (+0.71 to −0.94) support her results and agree well with the value of −0·71 calculated by Villumstad (1977).

On the whole, the values for correlations reported herein agree well with those of other authors.

The present data provide some insight into the reasons for differences in honey production between colonies or groups of colonies. Although the factors that I have assumed on *a priori* grounds to govern honey production would seem in the light of experience and intuition to be truistic, they are formulated here for the first time as equations (1) honey production = worker honeybee population × unit productivity; (2) worker population = average daily brood production × length of adult worker life. As colony population is not a primary but rather a secondary factor whose magnitude is determined by 2 primary factors, equations (1) and (2) can be combined in a single equation (3): honey production = average amount of brood produced daily × average length of worker life × unit productivity. The values of the components of the equations are quite variable. In the present investigation the relative contributions to honey production of colony population and unit productivity varied among the 3 trials, but unit productivity generally appeared to be the more important. Colony population was in one instance influenced chiefly by length of worker life and in another by amount of brood. Correlations between length of life and unit productivity were either positive or negative.

One may regard the amount of honey produced as being the resultant of the interaction of 3 primary factors.

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