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EFFECT OF SEX ALLELE HOMO-HETEROZYGOSITY ON HONEYBEE COLONY POPULATIONS AND ON THEIR HONEY PRODUCTION. 2. UNFAVOURABLE DEVELOPMENT CONDITIONS AND RESTRICTED QUEENS*

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Summary

Of 33 virgin queens mated to two of their brothers, 8, 16 and 9, respectively, produced brood of which 100%, 75% and 50% survived. Each queen was restricted to a single brood chamber by a queen excluder, and the 1979 season was unfavourable for colony development, so colonies did not reach their full summer potential. Similar brood areas were found in colonies of all groups in early spring and in autumn. In summer, colonies with brood of 50% and 75% survival respectively produced 67% and 81% of the brood area in the normal colonies, 63% and 85% of the worker population, and 75% and 87% of the surplus honey harvest, which was 13·3 kg in normal colonies. Of normal colonies, those headed by queens 2 years old produced 77·3% as much brood, 85·6% of the adult worker population, and 80·5% as much honey, as those with queens 1 year old. Differences between colonies with brood of 75% and 100% survival rates were, however, smaller for colonies with queens 2 years old than for those with queens 1 year old.

Introduction

In *Apis mellifera,* mating between related parents results in the production of diploid drone larvae from a proportion of the fertilized eggs (Woyke, 1963*a*), and these larvae are eaten by workers shortly after hatching (Woyke, 1963*b*). As a result, the brood pattern is scattered, because some of the cells in the brood area are empty. The proportion of larvae eaten may be up to 50%.

The question arises: how far does the diminished survival of brood affect colony population and honey production? The simplest expectation is that both the number of offspring and the honey production will be proportional to brood survival rate, but Woyke (1980) showed a distinct interaction between the rate of offspring production (by colonies with brood of different survival rates) and the season of the year. Compared with normal colonies (100% brood survival), groups of colonies with brood of 50% and 75% survival rates produced in summer, respectively: 68% and 82% of the brood area, 35% and 93% of the number of worker bees, and 50% and 103% of the honey harvested from the colonies.

The present work is a continuation of the previous investigation (Woyke, 1980), with the same kind of bees but with different weather and honey flow conditions, and a different method of apiary management.

Materials and Methods

The experimental apiary was divided into two parts. One consisted of 16 colonies headed by queens 2 years old, used in the previous experiment, the other of 33 colonies headed by queens 1 year old comparable with those in the previous experiment. To produce the latter, virgins were reared in 1978 from the original Caucasian queen

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inseminated instrumentally with a single Carniolan drone. Each of the hybrid Caucasian/Carniolan virgins was inseminated instrumentally with two of her Caucasian brothers. Brood survival of 33 queens was investigated, as previously (Woyke, 1980). From each queen, on average, 870 eggs were individually recorded (28·7 thousand in all), and the survival of the larvae hatching from them was investigated.

The brood area was measured during 9 periods at 21-day intervals between 2 April and 17 September 1979, by the method already described (Woyke, 1980). Altogether, 6008 measurements were made on 1502 combs; 4180 of the measurements were made in colonies with queens 1 year old and 1828 in colonies with queens 2 years old. For converting brood areas measured to numbers of cells, the factor 412 cells/dm^2 was used. The number of adult workers in the colonies in spring and autumn was calculated from measurements of the area of comb surface covered by the cluster of bees, assuming 170 bees per dm^2 (Woyke, 1980). In summer, all the bees were shaken into a box and weighed. The number was calculated on the assumption that 1000 bees weigh 114 g. No sugar syrup was fed to colonies at any time in the experiment.

The weight of honey extracted was calculated from the difference in weight of combs before and after extraction. Honey supers were given to colonies between 26 May and 12 June; they were separated from the brood chamber by a queen excluder, so that the queens could not lay eggs in them. During each brood measurement 2 brood combs were transferred to the super from the brood nest, where they were replaced by 2 frames with comb foundation. The brood chambers held 10 combs, each 26 × 36 cm.

Analysis of variance was applied to the results obtained, and a multiple-range test was used to find significant differences between particular means.

Results

Survival rates of brood produced by sibling-mated queens

Of 33 queens 1 year old, each mated to two of her brothers, 9, 16 and 8 produced brood of 50%, 75% and 100% survival, respectively. The proportions of queens producing brood at the three survival rates were close to 1 : 2 : 1, as expected.

Seasonal changes in brood area

The longest and most severe winter for a century occurred in 1978/79. As a result the colonies were very weak in early spring. On 2 April, during the first measurements, the average area of brood in normal colonies (100% survival) was only 6·4 dm^2 (Table 1). This is much less than in the previous year. Similar amounts of brood were found in colonies with brood of lower survival rates (Fig. 1), but a distinct improvement was apparent by the third measurements, on 14 May, when 19-29 dm^2 of brood was present. The differences between the 3 groups of colonies were, however, still not significant. The colonies were moved to a rape field on 19 May, but in contrast to the previous year, they were not yet ready for supers. A rapid increase of brood area (Fig. 1) occurred on the rape flow. At the maximum development on 4 June, 39, 46 and 58 dm^2 of brood, spread over 5, 6 and 8 combs, were found in colonies with brood survival rates 50%, 75% and 100%, respectively. For the first time statistically significant differences were found between the brood areas in colonies with different brood survival rates. Nevertheless, because of prolonged unfavourable weather the colonies did not become as strong as those in the previous year.

The colonies were then given supers, and were moved on 5 June to extensive raspberry crops. Hot dry weather prevailed for 1·5 months, but a good honey flow occurred, the results of which were very curious (Fig. 1). By 25 June, when the honey

TABLE 1. Mean amounts of brood observed in groups of colonies with 50%, 75% and 100% brood survival rates (1979).

Date	*No. combs with brood*			*Area of brood*		
				As % of 100% group		*Actual (dm^2)*
	50% group	*75% group*	*100% group*	*50% group*	*75% group*	*100% group*
2.4	2·3	2·2	2·1	108·6*a**	94·1*a*	6·4*a*
23·4	2·3	2·3	2·9	62·2*a*	70·8*a*	13·1*a*
14.5	3·1	3·5	4·1	64·5*a*	84·2*a*	28·8*a*
4.6	5·1	6·3	7·8	66·6*a*	79·5*ab*	58·3*b*
25.6	4·3	5·6	6·8	62·1*a*	87·2*b*	46·4*b*
16.7	4·7	5·1	6·4	60·9*b*	74·8*ab*	57·7*b*
6.8	3·5	4·1	5·0	63·9*a*	77·1*b*	40·0*c*
27.8	3·6	3·3	4·0	94·3*a*	86·8*a*	20·2*a*
17.9	2·0	1·3	1·5	287·5*a*	155·0*a*	0·8*a*

*different letters indicate statistically significant differences in brood area (dm^2) measured on the same day (multiple-range test, $P<0·05$)

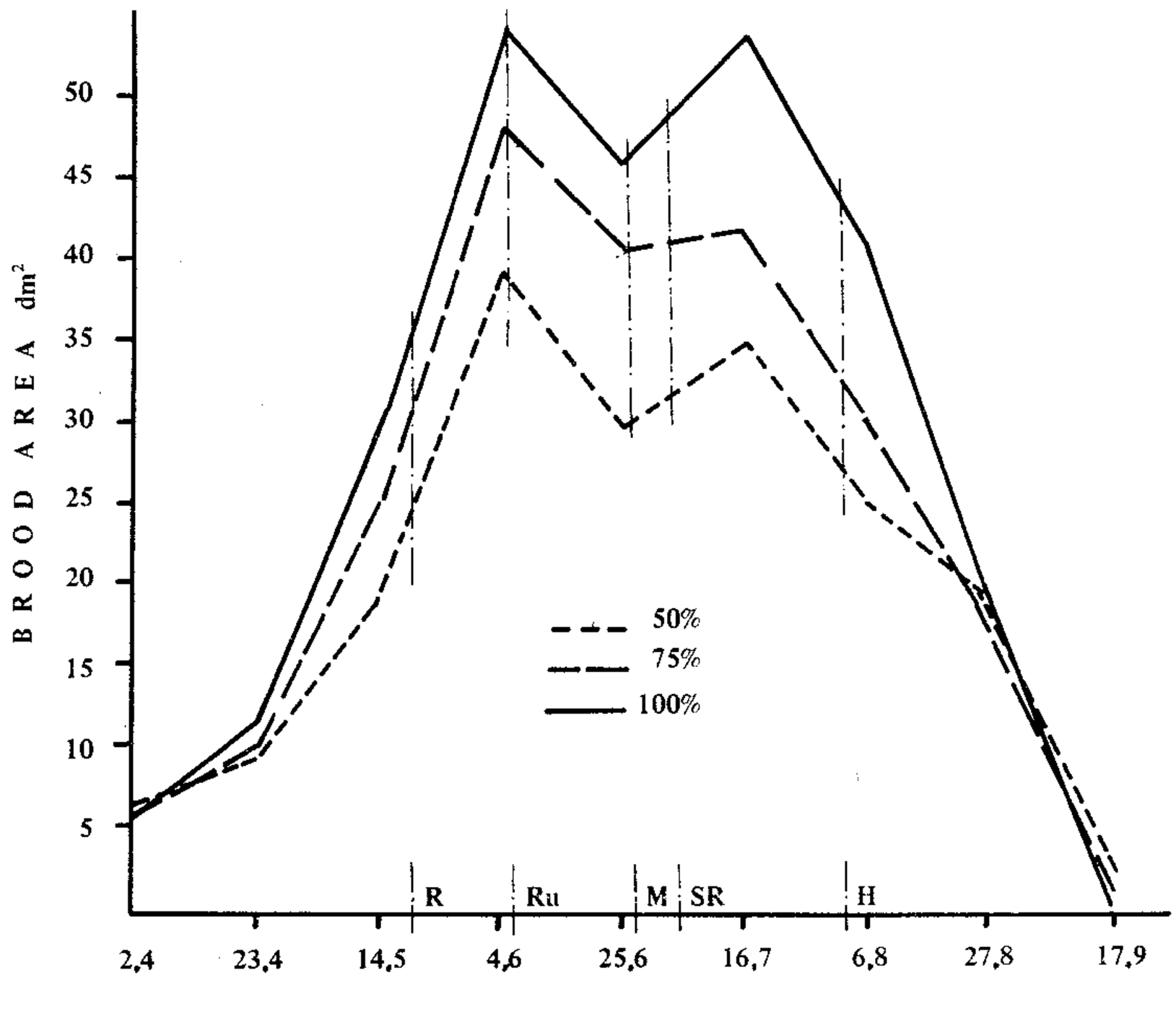

FIG. 1. Mean brood areas during 1979 in groups of colonies with 50%, 75% and 100% brood survival rates, headed by queens 1 year old.

Dates on which colonies were moved to nectar flowers: R = winter rape, Ru = raspberry, M = meadow, SR = summer rape, H = heather.

flow had diminished, the brood area in the three groups of colonies had dropped to 29, 40 and 46 dm^2 respectively. The relationship between the three groups is the reverse of what is usually found with other honeybee races, and is attributed to behaviour specific to Caucasian bees: they filled all empty cells round the brood with nectar, with

the result that egg laying was restricted. Cells from which adult bees emerged were also filled with nectar, and not re-used for brood rearing. The bees did this even though there was plenty of space for honey in the outer combs of the brood chamber, as well as in the super which was provided with 2 combs of brood to attract them into it. Without a queen excluder above the brood nest, however, the workers would probably have put more honey into the supers.

The honey was extracted on 28 June, and the colonies were moved to 18 ha of summer rape. By 16 July there was a considerable increase in brood area (Fig. 1). The greatest increase occurred in colonies with brood of 100% survival, and the least in those with brood of 50% survival. The differences between brood areas in the three groups were still significant.

The weather then became cold and wet and remained so until the end of the season. The colonies were moved to heather, but the brood area constantly decreased. At the two last measurements no significant differences were found between the brood areas in the three groups.

The above results can be seen more clearly by expressing the brood areas in the low-survival colonies as percentages of the areas in the normal survival colonies. On 2 April, 9% more and 6% less brood were found in colonies with brood of 50% and 75% survival, respectively. At maximum brood production, in June and July, 35-40% and 13-25% less brood were found in these colonies, respectively. The percentages of area occupied by brood were now closer to their survival rates. Nevertheless, the relative areas were up to 15% and 10% higher, respectively, than the survival rates of their brood. In the autumn, the brood areas were again similar or larger in colonies with brood of lower survival rate. Thus an interaction occurred between the season and the amount of brood in the groups of colonies.

Number of workers in the three groups of colonies

As a result of the severe winter only 9·1 thousand workers were found in normal colonies, and 76·9% and 72·5% of that number in colonies with brood survival rates 75% and 50%, respectively (Table 2).

TABLE 2. Mean adult worker populations in colonies with brood of 50%, 75% and 100% survival rate (1979)

Date	*Actual* ($\times 10^3$)			*As % of population for 100% group*	
	50% group	*75% group*	*100% group*	*50% group*	*75% group*
Spring					
26·3	6·6*a**	7·0*a*	9·1*a*	72·5	76·9
Summer					
2·7	10·9*a*	14·8*b*	17·4*b*	62·6	85·1
Late summer					
6·8	13·8*a*	17·9*ab*	20·3*b*	68·0	88·2
Autumn					
3·10	6·7*a*	7·3*a*	7·9*a*	84·8	92·4

*different letters indicate statistically significant differences between numbers observed on the same day (multiple-range test, $P<0·05$)

Even on 2 July only 17·4 thousand workers were found in normal colonies. The worker population in colonies with brood survival 50%. 75% and 100% increased 1·7,

2·1 and 1·9 times, respectively, by July, the highest population being found in normal colonies and only 85·1% and 62·5% of that population in the 75% and 50% groups. Thus the relative worker populations of these colonies were 10·1% and 12·5% higher than the survival rates of their brood, respectively. To some extent, therefore, the queens were able to replace the eaten larvae by new eggs.

The third estimation of the population, in late summer, showed 20·3 thousand workers in normal colonies and 88·2% and 68·0% of that number in the 75% and 50% groups.

In autumn the worker population in normal colonies dropped to 7·9 thousand, and 92·4% and 84·8% of this population were found in the 75% and 50% groups, respectively (Table 2). Thus in autumn the proportions of worker populations were close to each other, and in the low survival groups they were much higher than the survival rates of the brood. The queens producing brood of low survival rates replaced a greater proportion of cannibalized larvae by new eggs in the autumn than in the summer. Throughout the season the queens producing brood of low survival rate must have laid more eggs than those producing normal brood.

Honey production of colonies with brood of different survival rates

The very unfavourable weather conditions in the spring almost prevented the bees from collecting nectar from the rape, so the honey from rape and raspberry was removed together, on 28 June. Individual normal colonies yielded from 4·7 to 19·7 kg of honey. The average was 10·6 kg, and the yield from colonies of the 75% and 50% groups was 85·8% and 69·8% of that amount respectively (Table 3). The relative honey yields from the low brood survival groups were higher than their relative brood survival rates, but similar to the relative amounts of brood found 3 weeks earlier, 79·5% and 66·6% (Table 1), and to adult worker populations in these colonies in summer, 85·1% and 62·6% (Table 2).

TABLE 3. Mean honey production (kg/colony) by groups of colonies with brood of 50%. 75% and 100% survival rate (1979).

	Date	*Actual*			*As % of yield for 100% group*	
		50% group	*75% group*	*100% group*	*50% group*	*75% group*
1st crop from rape and *Rubus*	28·6	7·4	9·1	10·6	69·8	85·8
2nd crop from heather	19·9	2·0	2·0	2·3	87·0	87·0
Honey left for winter	21·9	0·6	0·5	0·4	150·0	125·0
Total		10·0	11·6	13·3	75·2	87·2

Bad weather prevented nectar collection from summer rape and heather, and only 2·3 kg of honey was obtained from normal colonies at the second harvest; the other two groups both yielded 87·0% of this amount. Normal colonies produced an average of 13·3 kg of honey over the whole year, and those in the 75% and 50% groups 87·2% and 75·2% of this amount (Table 3).

Thus in unfavourable weather conditions, and with queens restricted by an excluder, colonies with brood of low survival rate produced less honey than normal colonies, but 13% and 25% more than would be expected from a direct relationship between brood survival and honey production.

Comparison between colonies headed by queens 1 and 2 years old

Out of 16 queens 2 years old that survived the winter, 2 produced brood with 50% survival, 7 with 75% and 7 with 100%. The 2 with brood of 50% survival became drone layers by the end of May. This may have been because the queens replaced the eaten larvae with new eggs, and so laid more eggs than the normal queens, and the spermatozoa in the spermatheca were depleted earlier. (All queens started with relatively few spermatozoa, because each received them from only two drones.) Brood areas in the 75% and 100% groups are compared in Fig. 2. The summarized results show some differences between queens 1 and 2 years old (Table 4). Normal queens 2 years old produced less brood than queens 1 year old (89% as great an area in spring and 77% in summer). However, the differences between the areas of brood surviving in the 75% and 100% groups in summer were smaller among the colonies with queens 2 years old (7·9%) than among those with queens 1 year old (19·3%).

When the brood area decreased in autumn, the queens 2 years old actually showed more brood surviving in the 75% group than in the 100% group.

Normal colonies headed by queens 2 years old had lower worker populations than similar colonies with queens 1 year old (91·2% in spring, 85·6% in summer). Differences between worker populations in the 75% and 100% groups in spring were lower in colonies headed by queens 2 years old (0·2%) than in those headed by queens 1 year old (23·1%). In summer, however, similar percentages of worker populations compared to their normal controls were found in both 75% groups (85·1% and 86·6%). The normal colonies with queens 2 years old did not continue to increase their populations into late summer, whereas those with 75% brood survival did so slightly. As a result, the latter became more populous than the normal colonies.

By autumn the normal colonies headed by queens 2 years old had only 82·3% of adult worker population in the colonies with queens 1 year old, but the relationship

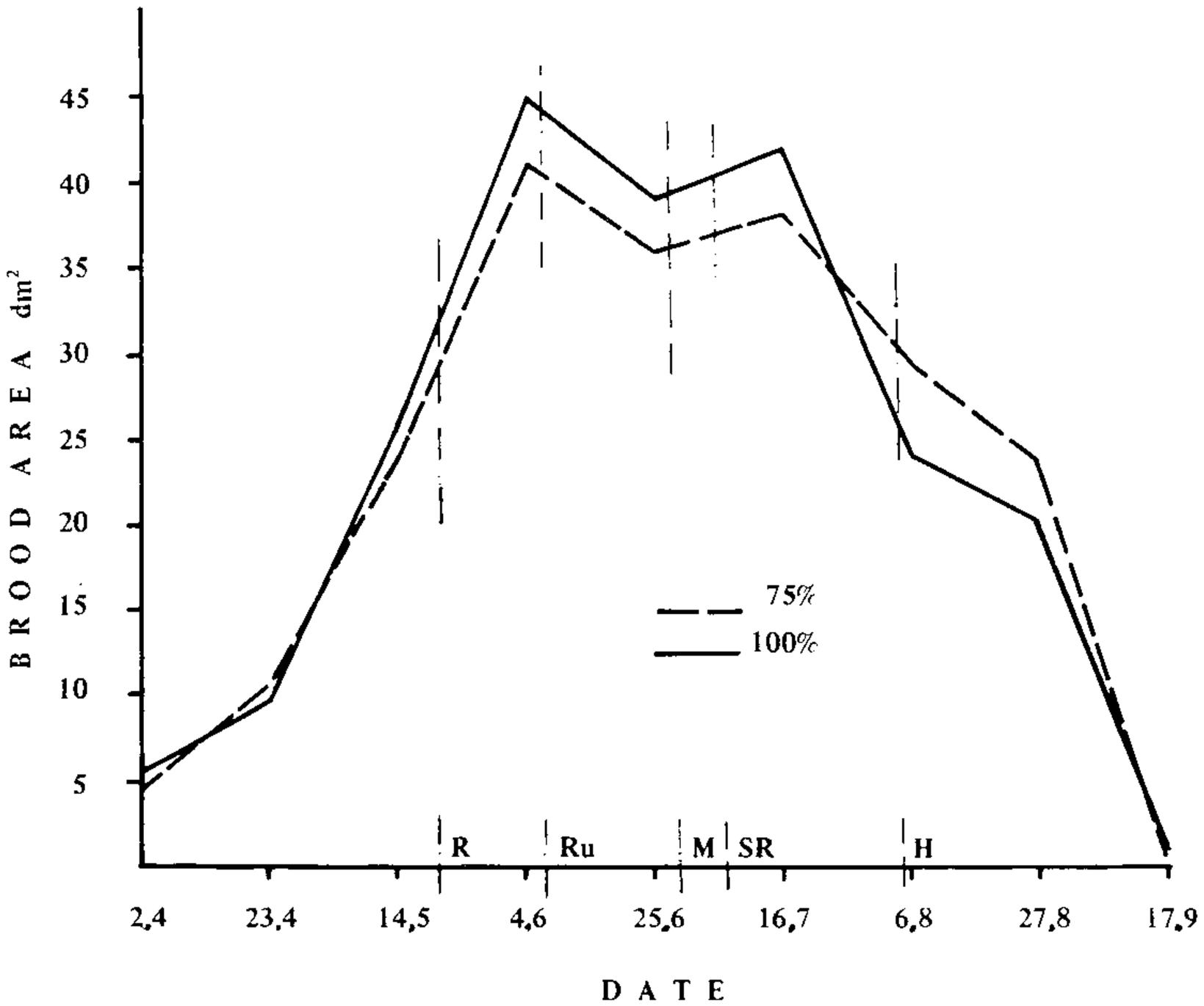

FIG. 2. Mean brood areas during 1979 in groups of colonies with 75% and 100% brood survival rates, headed by queens 2 years old. See Fig. 1 for key to dates.

TABLE 4. Summary of mean numbers of progeny and weights of honey produced by colonies with brood of 50%, 75% and 100% survival rates (1979).

Date	*Queens 1 year old*			*Queens 2 years old*		
	50% group (% of 100% group)	*75% group (% of 100% group)*	*100% group (actual)*	*50% group (% of 100% group)*	*75% group (% of 100% group)*	*100% group (actual)*
Brood area:						
spring 2.4	108·4	94·1	6·4 dm^2	37·6	85·5	5·7 dm^2
summer 4.6	66·6	80·7	58·3 dm^2	8·7	92·1	44·9 dm^2
autumn 27.8	94·3	86·8	20·2 dm^2	—	121·0	20·1 dm^2
Worker population:						
spring 26·3	72·5	76·9	$9{\cdot}1 \times 10^3$	59·7	99·8	$8{\cdot}3 \times 10^3$
summer 2·7	62·6	85·1	$17{\cdot}4 \times 10^3$	—	86·6	$14{\cdot}9 \times 10^3$
late summer 6.8	67·9	88·2	$20{\cdot}3 \times 10^3$	—	104·1	$14{\cdot}9 \times 10^3$
autumn 30.10	84·8	92·4	$7{\cdot}9 \times 10^3$	—	87·0	$6{\cdot}5 \times 10^3$
Honey harvested:						
summer 28.6	69·8	85·8	10·6 kg	—	97·5	7·9 kg
Total 21.9	75·2	87·2	13·3 kg	—	99·0	10·7 kg

between the populations of colonies with brood survival 75% and 100% were fairly similar for the groups of colonies headed by queens 1 and 2 years old.

In the summer, with queens 2 years old, normal colonies produced only 74·5% as much honey as similar colonies with queens 1 year old, but the honey yield of colonies in the 75% group was almost identical (97·5%) to that of the normal colonies; it was 85·8% in the group headed by 1 year old queens. The results for total honey production were similar. Normal colonies headed by queens 2 years old produced 80·5% as much honey as those with queens 1 year old; colonies in the 75% group produced 99·0% as much honey as the normal ones among the colonies with queens 2 years old, but only 87·2% among those with queens 1 year old.

Thus the colonies headed by queens 2 years old mostly produced less brood, lower adult worker populations, and less honey, than colonies with queens 1 year old, but the differences in brood area, adult worker population and honey production between colonies in 75% and 100% groups were lower with queens 2 years old than with queens 1 year old. The lower differences were probably due to lower egg-laying rates by normal queens 2 years old.

Discussion

In comparing the results of this 1979 investigation with those of 1978 (Woyke, 1980), the differences in the experimental conditions are important. The 1978/79 winter was extremely severe and long, the spring of 1979 was unfavourable for colony development, and in 1979 the queens were confined to the brood chambers by queen excluders.

In 1979 colonies were much smaller in spring (normal colonies having 6·4 dm^2 of brood and 9·1 thousand workers) than in 1978 (14·7 dm^2 of brood and 13·8 thousand workers), and because of the adverse factors they did not reach their full potential. Only 58·3 dm^2 of brood was found in normal colonies, compared with 78·4 dm^2 in 1978. On the other hand the relative amounts of brood surviving in the 75% and 50% groups in 1979 (80% and 67% respectively) were similar to those in 1978 (82% and 68%).

The number of adult workers in normal colonies in 1979 reached only 17·4 thousand, compared with 30·3 thousand in 1978. The relative numbers of workers found in colonies with brood of low survival rate differed distinctly between the two years. The numbers of workers in colonies of the 75% and 50% groups were 85% and 63%, respectively, of the population in normal colonies in 1979 (93% and 35%, respectively, in 1978). The colony populations of the three groups of colonies differed less in the unfavourable year, when queens producing brood of low survival rate were able to replace relatively more of the eaten larvae by new eggs, than in the favourable year when normal queens produced more eggs.

Lower differences in the populations of the groups of colonies in 1979 resulted in lower differences in honey production. In 1979 colonies in the 75% and 50% groups produced 87% and 75%, respectively, of the honey produced by normal colonies, whereas in 1978 they produced 103% and 50% respectively.

Conclusions

In unfavourable weather, and with restricted brood production, the differences in populations of three groups of colonies with brood of 50%, 75% and 100% survival rate were lower than in the more favourable conditions. As a result, in unfavourable conditions colonies with brood of 50% survival rate produced relatively more honey (75% of normal) than in favourable conditions (50% of normal). In such conditions colonies with brood of 50% and 75% survival rate produced less honey than normal colonies, but more (75% and 87%) than would be expected from the proportions of brood surviving.

Colonies headed by queens 2 years old produced less brood, and less honey, than those with queens 1 year old, but the differences between colonies with brood of 75% and 100% survival rate were lower in colonies headed by queens 2 years old than in those headed by queens 1 year old.

Thus it may be expected that, in favourable weather and nectar conditions, and with strains of bees producing much brood, there will be quite large differences in the number of offspring and in honey production between colonies producing brood of different survival rates.

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