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EFFECT OF SEX ALLELE HOMO-HETEROZYGOSITY ON HONEYBEE COLONY POPULATIONS AND ON THEIR HONEY PRODUCTION

I. FAVOURABLE DEVELOPMENT CONDITIONS AND UNRESTRICTED QUEENS*

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Summary

Virgin queens were each mated to two brothers, giving three groups of queens producing offspring with different combinations of sex alleles. In all, 26 500 brood cells were individually examined to determine brood survival rates; also 7720 measurements of brood areas were made in colonies, weekly in 1977 and at 3-weekly intervals in 1978. Of 32 queens, 8 produced brood of 50% survival rate, 14, of 75% and 10, of 100%.

Influence of the composition of sex alleles on the brood area was apparent 3 weeks after equalization of colony populations. Similar brood areas were found in all three groups of colonies during spring and autumn, but in summer colonies with brood of 50% and 75% survival rates produced 68% and 82%, respectively, of the brood area found in normal colonies. When queens in normal colonies laid fewer than 1000 eggs daily, those producing brood of lower survival rates were able to replace non-surviving larvae by new eggs, but this was not possible with higher laying rates. Colonies with brood of 50% and 75% survival rates had (in relation to normal colonies) 79% and 89% of the worker population in spring. In summer normal colonies had 30 000 workers, and those with brood of 50% and 75% survival rates only 35% and 93% as many, respectively. In autumn the values were 65% and 91%. Colonies with brood of 50% and 75% survival rate produced 50% and 102%, respectively, of the 12 kg of surplus honey harvested from normal colonies. Interaction occurred between the progress of the season and the amount of brood, worker population and honey produced by the three groups of colonies.

Introduction

Breeding pure lines of honeybees (*Apis mellifera*) increases the number of homozygous loci and thus affects the production of both brood and honey. Sex alleles as well as other loci influence the survival rate of the brood. Mackensen (1951), Laidlaw, Gomes and Kerr (1956) and Hachinohe and Jimbu (1958) found a series of lethal alleles. Woyke (1963*a*) showed that homozygotes at this locus resulted in viable diploid drone larvae which were eaten by the workers shortly after hatching (Woyke, 1963*b*). Consequently only brood heterozygous at the sex locus survived, developing into workers. The survival rate of brood may range from 50% to 100%.

The number of sex alleles in a honeybee population was estimated to be 11-12 by Mackensen (1955), Laidlaw, Gomes and Kerr (1956) and Kerr (1967), and 18·9 by Adams et al. (1978).

Woyke (1963*c*, 1972) studied the theoretical survival rate of brood produced by queens mated in a mating apiary (or instrumentally) to drones originating from a varying number of related queens. Shaskol'skii (1968) studied the theoretical distribution of queen honeybees producing brood of varying survival rates in relation to the number of matings in populations with different numbers of sex alleles. Woyke (1976) studied frequencies

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of sex alleles and survival rate of brood in subsequent generations of different honeybee populations. He found a brood survival rate of 82·1% resulting from the action of sex alleles in the bee sanctuary on Kangaroo Island, S. Australia, showing that only 6 sex alleles were present.

Woyke (1976) was also able to demonstrate that 6·5% of brood were lost during the 3 first days of larval life due to factors other than sex alleles, e.g. other lethal loci or environmental conditions. This is almost the same as the 6% mortality found by Fukuda and Sakagami (1968) as a result of all unknown factors together.

Loss of brood caused by sex alleles is much higher than that caused by other loci in the same environmental conditions. To prevent it, Maul (1972) started a programme to identify the sex alleles.

It is important to know whether production of brood and of honey is proportional to the survival rate of brood. Theoretically it might be, although it could be higher—if the queen lays new eggs into emptied cells—or lower—if she is unable to replace cannibalized larvae by new eggs.

More information on this subject would be useful when breeding pure lines of honeybees, and also when creating and maintaining reserves of pure ecotypes.

Materials and Methods

The mother of all queens investigated was a Caucasian queen inseminated instrumentally by one Carniolan drone. The hybrid Caucasian/Carniolan virgins were instrumentally inseminated by two of their Caucasian brothers. This resulted in the combinations of sex alleles show in Table 1, and in brood survival rates of 50%, 75% and 100% in particular colonies.

Brood survival rate of 32 queens was investigated. For this, 26 500 eggs were individually investigated in 48 tests, an average of 550 eggs per test. Two further replications were made.

TABLE 1. Composition of sex alleles and theoretical survival rate of brood produced by experimental queens (originating from one *ab* × *c* mother), each mated to two of their brothers.

Sex alleles of queens and drones		*Sex alleles of progeny*	*% survival rate of brood*
ac × *a, a*	⟶	*aa ac*	50
ac × *a, b*	⟶	*aa ac ab bc*	75
ac × *b, b*	⟶	*ab bc*	100
bc × *a, a*	⟶	*ac ab*	100
bc × *a, b*	⟶	*ab ac bb bc*	75
bc × *b, b*	⟶	*bb bc*	50

Investigations on the amount of brood were commenced in 1977 using 28 colonies, and continued in 1978 using 25 colonies. Brood area was measured during 6 different periods in 1977, and 9 periods in 1978. A total of 7720 measurements were made on 1965 combs, in some of which brood was present on one side only.

All the drones emerged in queen-excluder isolators. Virgin queens treated with carbon dioxide were introduced into queenless colonies in queen-excluder isolators covering a whole comb. Queens inseminated instrumentally, with the semen from two of their brothers, were returned to the same isolators where they stayed until they started to lay eggs (Woyke, 1979).

To test the survival rate of brood, a comb with eggs was chosen. Eggs were located in the comb cells, and recorded using a plastic strip fastened to the sides of the bottom and top bar of the frame (Woyke, 1976). The comb was then placed in another colony between the brood combs but separated from the queen. The number of survivals was recorded after 3 days and again 6 days later. Survival rate of brood was calculated using data recorded 3 days after egg counts. If the difference between the numbers of survivals on the two last recording days was high, it indicated that conditions for brood rearing were not good in the colony, and the procedure was repeated in another colony.

The area of brood in a colony was obtained by measuring the long (D) and short (d) axes of the elipse occupied by brood on both sides of every comb (P) and applying the formula $P = 0{\cdot}785\ Dd$. Measurements were taken every week starting on 8 August 1977, and every 3 weeks from 30 March until 14 September 1978.

To convert the area of brood into number of brood cells, the length of 50 cells and the width of 30 cells were measured in 5 combs, giving the area occupied by 1500 cells. There were found to be 411·7 cells per dm^2.

The number of workers in the colonies in the autumn was investigated when the outside temperature dropped to 7-8°C and the bees formed a cluster. The surface covered by workers on both sides of every comb was measured in the same way as the brood area. Additionally for 5 colonies of the same race, all the bees were shaken and brushed into plastic bags and weighed. Workers covering 10 dm^2 of one of a comb in the cluster weighed 193·6 g. To calculate the number of bees in a cluster, 10 previously counted samples of bees (500-2500 per sample) were weighed from a total of 9500 workers. The weight of 1000 workers was found to be 113·8 g. This showed also that 170 workers were present on 1 dm^2 of the cluster.

The number of workers in a colony in the active season was investigated by another method. The hive, together with all the bees, was weighed early on a cloudy day, before the bees started to fly. The bees were then shaken and brushed off the combs into a new hive. The combs without bees were weighed with the empty hive; the difference gave the weight of all the bees, and hence the number of bees in the colony.

The weight of honey extracted was calculated from the difference in weight of combs before and after extraction.

The development of colonies was not stimulated in the spring by feeding of sugar syrup. The colonies were managed during the season so that the queen's laying was not restricted by a queen excluder. However, this method prevented the harvesting of all the honey produced, since only honey from brood-free combs was removed.

The data were treated statistically by Fisher's analysis of variance, and Duncan's new multiple-range test was used to identify significant differences between means.

Results

Survival rate of brood produced by 32 sibling-mated queens

After completion of the test for survival rate of brood produced by these queens, it was apparent that they could be grouped as follows:

No. queens	*Actual brood survival (%)*		*Theoretical survival (%)*
	Range	*Average*	*for group*
8	44-55	47	50
14	70-80	75	75
10	90-96	94	100

These three groups were designated as producing brood of which 50%, 75% and 100% survived, respectively. The actual percentage was in some cases slightly lower than that expected, as a result of cannibalism, which occurred to some extent in almost every colony. Results that were slightly higher than expected could have been caused by the pressence of diploid drone larvae less than 6 h old, which had not yet been eaten by the worker bees. The 75% survival group was also affected by unequal proportions of semen collected from the two drone brothers.

In 1977, 7, 12 and 9 queens with brood survival rates of 50%, 75% and 100% respectively were investigated, and in 1978, 6, 11 and 8 respectively. The proportions of queens producing brood at the three survival rates were close to the expected 1 : 2 : 1 ratio.

Brood of different survival rates in the combs

After some of the larvae surviving in the 50% and 75% groups were eaten, the queen did not wait for all the remaining brood to emerge before laying eggs in the combs. New eggs were laid in the empty cells shortly after the larvae were eaten. As a result the expected 50% and 25% of brood cells were not found empty, In the 50% and 75% groups, brood of similar age was scattered among brood of different age, whereas in the 100% group compact brood of the same age was found.

Seasonal changes of brood area in the first autumn

After the queens were introduced, the colony populations were equalized three times. Equal numbers of brood combs were present in every colony during the period when the survival rate of brood was tested. The first measurements of brood area were made one week after the last equalization.

Table 2 shows that the area of brood surviving in the 100% survival group decreased in the autumn: from 37·3 dm^2 on 8 August to 15·1 dm^2 on 12 September. The numbers of brood combs during the first measurement were almost identical in the colonies with the three different survival rates of brood; the area was probably not exactly equalized, because at this time 13·6% more brood was present in the 50% group. Fig. 1 shows that the area of brood surviving in the 50% and 75% groups decreased in a similar way to that in the 100% group.

TABLE 2. Amount of brood surviving in the 50%, 75% and 100% groups of colonies, in the autumn of the first season (1977).

Measurement no./ Date	*No. combs with brood survival:* 50%	75%	100%	*Amount of brood* *Area as % of 100% group* 50% *group*	75% *group*	*Area (dm²)* 100% *group*
1/ 8·8	5·9	5·8	5·9	113·6	94·7	37·3
2/15·8	6·0	6·0	5·9	95·8	98·9	35·4
3/22·8	5·6	5·9	6·2	88·6	88·7	36·6
4/29·8	5·4	5·8	5·8	88·8	86·6	31·2
5/ 5·9	4·5	4·5	5·2	88·6	83·3	19·7
6/12·9	3·8	4·1	4·9	94·7	84·3	15·1

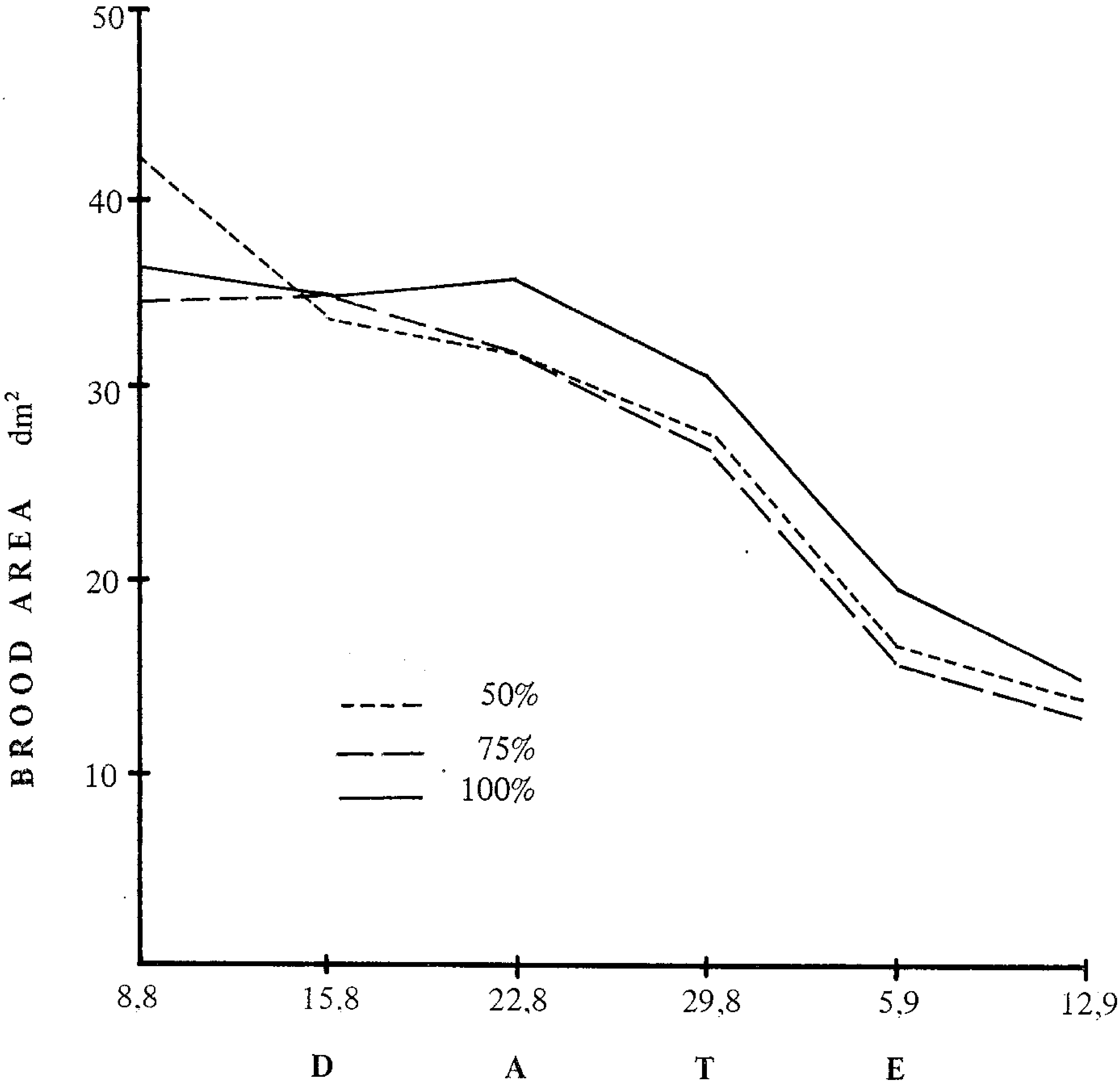

FIG. 1. Mean brood areas in the groups of colonies with 50%, 75% and 100% survival rates (autumn 1977).

The smallest amount of brood was found in colonies of the 50% group at the second and third measurements, but in the 75% group at all other measurements. Statistical analysis did not show any significant difference in the area of brood in the three groups during the autumn. Three weeks after the last equalization, a new generation of brood (originating exclusively from the experimental queens) was already present in the colonies. Table 2 shows that, from 22 August, relation of the brood area was stabilized in all three experimental groups. Colonies with lower brood survival rates had 83% to 89% as much brood as that in normal colonies, much more than the theoretical rates (50% and 75%); at this time the queens replaced many cannibalized larvae by new eggs.

The higher relative amount of brood (113·6%) in the 50% group rate compared with that in the 75% group (94·7%) was probably caused by our placing more brood in colonies of the 50% group at the beginning of the experiment. The brood area expressed as a percentage of that found at the first measurement was highest in the colonies of the 100% group and lowest in those of the 50% group (Fig. 2). On 22 August, 3 weeks after equalization, the brood area in colonies of the 50%, 75% and 100% group respectively, was 75·8%, 82·9% and 99·8% of that at the first measurement. In the final measurements the values were 33·5%, 34·1% and 40·5%, respectively. Thus the differences between brood areas in the three groups were always smaller than the differences between brood survival rates.

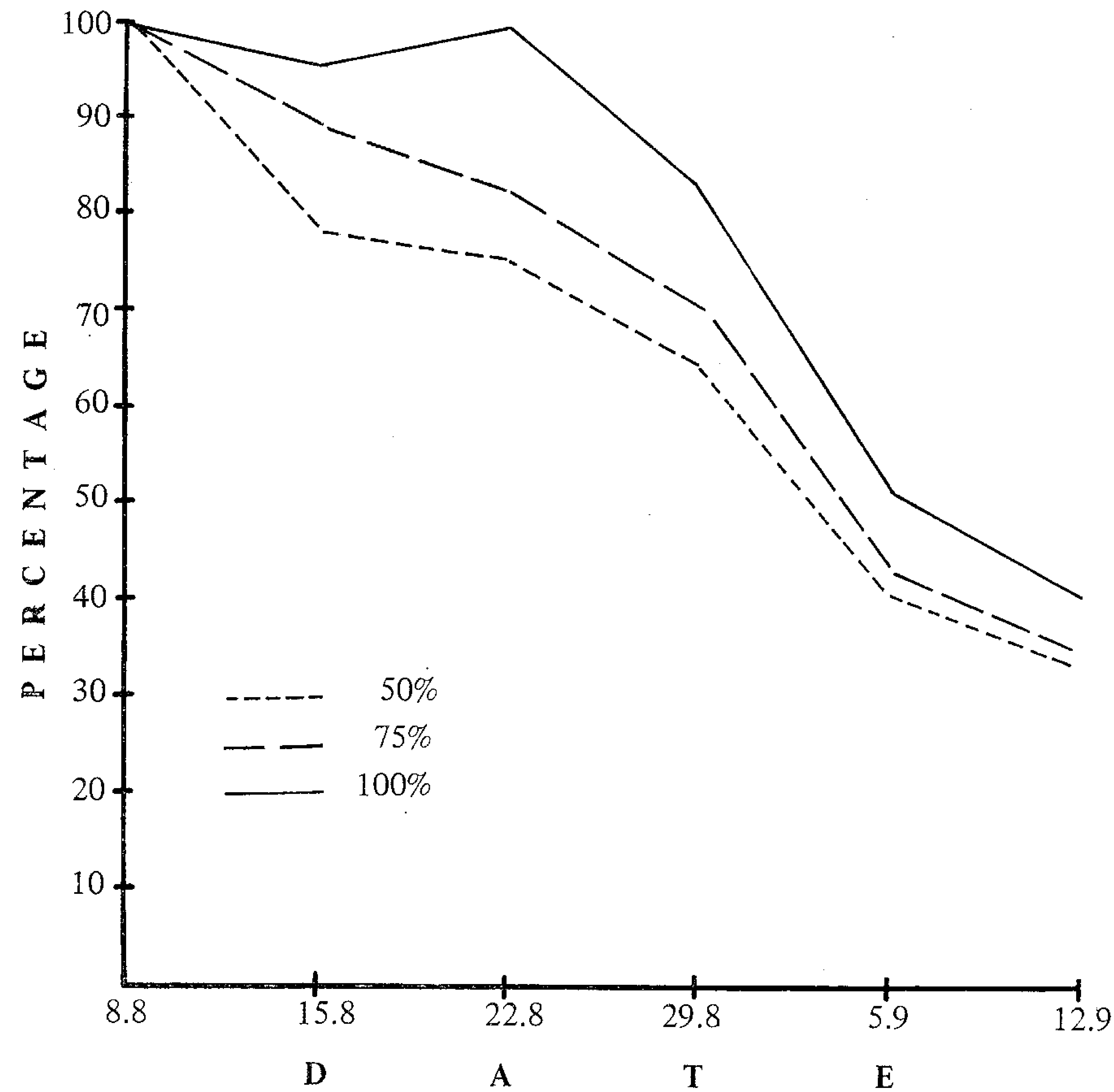

FIG. 2. Mean brood areas (as percentages of the area first measured) in groups of colonies with 50%, 75% and 100% survival rates (1977).

Number of workers in colonies at the end of the first season

The number of workers in the clusters was investigated at the end of the season (19 October), 80 days after the last equalization of the colonies. Workers in the 50%, 75% and 100% colonies were clustered on an average of 8·0, 8·5 and 9·0 combs, respectively. In the three groups 10 900, 12 200 and 13 800 worker bees per colony were estimated, representing 79·9%, 88·4% and 100% respectively, of the number in colonies of the 100% group; 79·9% is notably higher than 50%, and 88·4% than 75%.

Seasonal changes in brood area during the second season

The brood area increased in normal colonies from 5·1 dm² on 30 March to a maximum of 78·4 dm² on 30 June, and then dropped to 54·2 dm² on 3 August and to 2·1 dm² at the end of season, 14 September (Table 3). Comparing the development of brood in the three groups of colonies, the brood areas were almost identical in all groups up to 11 May when 40-45 dm² of brood was present (Fig. 3). On 17 May the colonies were moved to a field of rape (*Brassica napus*), and on 24 May they received the supers; brood areas then rapidly increased, and the three groups showed distinct differences. At maximum development, 53, 64 and 78 dm² of brood (on 7, 9 and 10 combs) were found in colonies of the 50%, 75% and 100% groups respectively. The colonies were moved on 9 June to a forest of acacia (*Robinia pseudoacacia*). The weather was cold and rainy, and brood production decreased. Nevertheless, differences in the brood areas of the three groups were apparent.

TABLE 3. Amount of brood surviving in the 50%, 75% and 100% groups of colonies, during the whole second season (1978).

Measurement no./ Date	*No. combs with brood survival*			*Amount of brood*		
				Area as % of 100% group		*Area (dm²) 100% group*
	50%	74%	100%	50% *group*	75% *group*	
1/30·3	1·8	2·2	2·1	85·3a	101·2a	5·1a*
2/20·4	3·0	3·3	3·3	97·3a	103·4a	14·7a
3/11·5	5·2	5·8	5·9	93·4a	103·2a	44·1a
4/ 1·6	7·2	9·2	10·1	67·6a	81·6a	78·4b
5/22·6	6·6	9·6	11·1	61·4a	79·0ab	64·8b
6/13·7	7·0	6·4	8·7	76·3a	80·6ab	50·3b
7/ 3·8	5·8	7·4	8·9	65·8a	91·3b	54·2b
8/24·8	3·7	4·7	5·6	93·3a	110·6a	22·6a
9/14·9	1·7	1·6	1·4	170·0a	173·9a	2·1a

*Figures followed by different letters indicate statistically significant different brood areas calculated in dm² (new multiple—range test, $P<0\cdot05$).
(Only figures collected at the same measurement are compared statistically.)

The colonies were moved on 20 June to a *Phacelia* field, and the conditions improved until 10 August when they were moved to a field of red clover (*Trifolium pratense*). Statistical analysis showed significant differences in the brood areas only during the main season of brood production (1 June to 3 August). At maximum development (1 June) the excess of brood in colonies of the 100% group over that in the other two was statistically significant.

After brood production started to decrease, statistically significant differences were found only between the brood areas in colonies of the 50% and 100% groups; brood area in colonies of the 75% group mostly did not differ significantly from either of the other two. The differences might be found significant if more colonies were used. The difference between 50% and the 75% group was statistically significant only on 3 August, when brood production rose again (Fig. 3).

The production of brood fell after 3 August in all three groups, and no statistically significant differences were subsequently found between them. Brood production fell again after 28 August, when the colonies were moved on to heather (*Calluna vulgaris*). The last measurement (14 September) showed least brood in colonies of the 100% group. The average was 2·1 dm², but two colonies had stopped rearing brood, and none was found. Nevertheless the differences between the three groups were not significant.

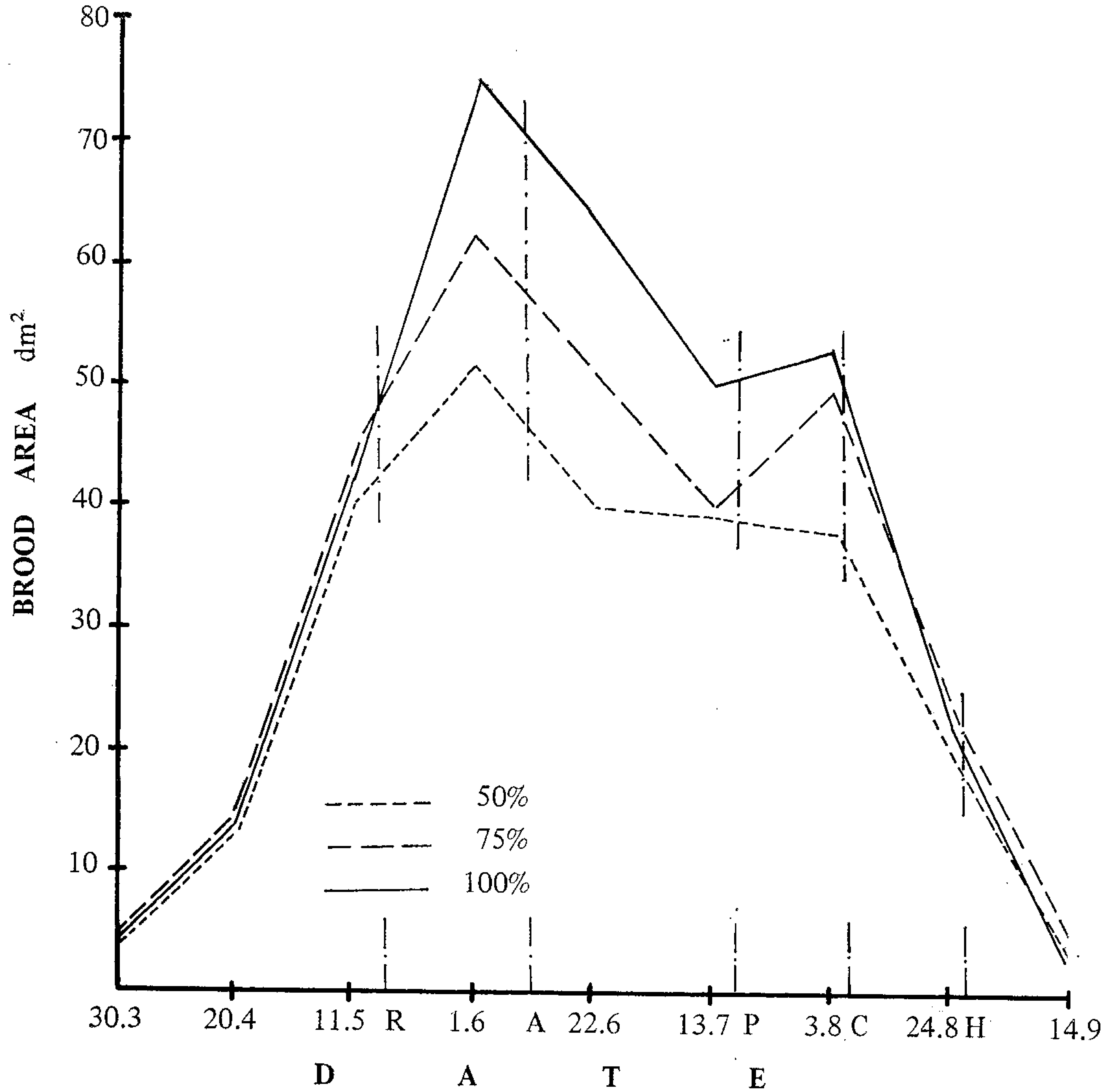

FIG. 3. Mean brood areas (as Fig. 1) throughout 1978.
Letters below show dates when bees were moved to new flows:
R rape, *A Robinia, P Phacelia, C* red clover, *H* heather.

Ratio of brood production in colonies with different brood survival rates

A better comparison between brood production and survival was obtained from the percentage of the amount of low-survival brood in relation to the amount of normal-survival brood Table 3.

In April and May about 5% less or 5% more brood was present in colonies of the 50% and 75% groups than in those of the 100% group. Maximum brood production on 11 May was approximately 45 dm^2. When brood production increased further, 65% and 80% as much brood was found (from 1 to 22 June) in colonies of the 50% and 75% groups as in those of the 100% group. The percentage of brood produced (compared with that in normal colonies) was thus now closer to the survival rate of the brood. Nevertheless it was 15% higher in colonies of the 50% group and 5% higher in those of the 75% group. When brood production fell again a similar amount of brood was present in all colonies, the percentage of brood present (in comparison with normal colonies) thus being much higher than the brood's survival rate. The same phenomenon had been found in the autumn of the previous season. It shows that an interaction occurs between the progress of the season and the amounts of brood production by colonies whose brood survival rates are different.

Relation between the number of eggs laid and the amount of brood reared

To examine the interaction between season and brood production in the three groups of colonies, the number of brood cells occupied (N = brood area in $dm^2 \times 411{\cdot}7$) was compared with the number of eggs laid daily by the queen (N/21).

Table 4 shows that queens producing brood of lower survival rates were able to replace the cannibalized larvae and to increase the brood area until there were 20 000 brood cells in a colony, i.e. until the queen in a normal colony was laying 1000 eggs daily. At the maximal development of the colonies, about 30 000 brood cells were present in normal colonies, the queen laying about 1500 eggs daily. Under these conditions queens producing brood of lower survival rates were not able to lay sufficient eggs to replace the cannibalized larvae and to increase the brood area.

On 3 August when the number of brood cells dropped to 22 000, and the queens again laid about 1000 eggs daily, the brood area matched that in normal colonies only in those colonies in the 75% group (Table 4). Queens in the 50% group could not yet (3 August) lay enough eggs to increase the brood area, probably because of an insufficiency of nurse bees, which had themselves emerged from a smaller brood area. After the rate of egg laying fell to 440 per day in normal colonies (24 August), queens in the 50% group were able to replace the cannibalized larvae, keeping the brood area as high as that in the 100% group.

Thus in spring, queens producing brood of lower survival rates were able to maintain a brood area similar to that of queens producing normal brood, providing that the latter did not lay more than 1000 eggs per day. At this time, therefore, queens producing brood of lower survival rates had to lay more eggs than queens producing normal brood.

TABLE 4. Amount of brood in the 50%, 75% and 100% survival groups of colonies in relation to the daily rate of egg laying.

Measurement no./ Date	*Brood production in normal colonies*			% *Brood area in colonies with low-survival brood*	
	No. eggs /day	*No. brood cells* (1000*s*)	*Brood area* (*dm*²)	50%	75%
1/30·3	100	2·1	5·1	85	101
2/20·4	290	6·0	14·7	97	104
3/11·5	870	18·2	44·1	93	103
4/ 1·6	1540	32·3	78·4	68	82
5/22·6	1270	26·7	64·8	61	79
6/13·7	990	20·7	50·3	76	80
7/ 3·8	1060	22·3	54·2	66	91
8/24·8	440	9·3	32·6	93	111
9/14·9	40	0·9	2·1	170	174

Number of workers in the colonies throughout the season

The areas of brood in the three groups did not characterize the colony populations accurately. Some cells were empty, and scattered brood of differing ages was present in the others.

The number of workers in the colonies was therefore investigated. In the previous autumn, colonies in the 50%, 75% and 100% groups contained respectively 10 900 12 200 and 13 800 workers (Table 5). Spring populations were not investigated, but since very few dead workers were found during the first spring inspection, it was believed that population changes were small in spring, and that the proportions of 79% and 88% in colonies of the 50% and 75% groups (in relation to the 100% group) did not change. If this is true, then the proportions of workers in colonies of the three groups were higher in the spring than the proportions of brood that survived.

The worker populations in summer were investigated 3 weeks after the brood area was greatest. The number of workers in a normal colony increased to 30 000 (Table 5), but only 10 700 were found in colonies of the 50% group: no increase above the spring population. In summer the colony worker populations were 35·3% and 92·7% of that in a normal colony for the 50% and 75% groups respectively (Table 5): lower for the 50% group and higher for the 75% group than the percentage brood survival. The ratio between the brood areas in the three groups 3 weeks earlier (1 June) was 68: 82: 100. Worker populations were therefore lower in colonies of the 50% group and higher in the 75% group, than would be expected from the area of brood present. This means that at maximal brood production, queens producing brood of 50% survival rate were not able to replace all the cannibalized larvae with new eggs, whereas queens producing brood of 75% survival rate were able to do so As a result the worker population in the latter colonies did not differ significantly from that in normal colonies, whereas it differed significantly from that in colonies with 50% survival rate.

In autumn, the worker population of normal colonies dropped to 12 000, and 65% and 92% of this population were found in colonies of the 50% and 75% groups, respectively. So the worker populations were then higher in proportion than the survival rates of the brood, and closer to each other. The queens producing brood of lower survival rates replaced a greater proportion of the cannibalized larvae by new eggs. Nevertheless, even during this period, colonies with queens producing brood of 50% survival rate were not able to produce as many workers as colonies with normal brood.

TABLE 5. Number of workers in colonies of the 50%, 75% and 100% groups of colonies.

Date	*Worker* (1000*s*) *for brood survival*:			*No. workers as % of that for* 100% *survival*	
	50%	75%	100%	50%	75%
Autumn 19.10.77	10·9	12·2	13·8	79·0	88·4
Summer 22.6.78	10·7	28·1	30·3	35·3	92·7
Autumn 20.9.78	7·7	10·8	11·8	65·3	91·5

Honey production of colonies with brood of different survival rates

Because the queens were not restricted by queen excluders, only combs without brood could be removed for honey extraction. During the first harvest in 8 June 1978, 0-10 kg honey were extracted from the colonies. The wide range was due in part to the presence of brood in many combs, and thus to much honey being left in some hives. At this extraction an average of 2·5 kg honey was harvested from normal colonies and 80% and 144% of this amount from colonies of the 50% and 75% groups, respectively (Table 6). From the early flow, therefore, percentages of honey harvested (compared with normal colonies) were higher than brood survival. Colonies in the 75% group stored even more honey than normal colonies. This was probably due to the favourable ratio between worker and brood populations. A little more brood was present in early spring in colonies of the 75% group, giving slightly more workers during the early nectar flow. At this time (1 June) these colonies had only 82% of the brood area of normal colonies, so more workers were available for foraging.

After the second flow, from acacia (29 June), colonies yielded 0-10·6 kg honey. An average of 4·6 kg of honey was extracted from the normal colonies (Table 6), and 26·1% and 110·4% of that amount, respectively, from colonies in the 50% and 75% groups. The low honey production of colonies in the 50% group was due to the small worker populations at this time (10 700 on 22 June, Table 5), as well as to the unfavourable ratio between worker and brood populations in relation to that in normal colonies—35%, 61% (Table 3, 22 June).

Colonies with brood of 75% survival rate produced 11% more honey than did normal colonies. Here again, the percentages of populations in relation to normal colonies (91% for workers, 71% for brood) favoured nectar collection.

Cold and rainy weather occurred subsequently. The colonies moved to *Phacelia*, red clover and heather collected little nectar, and consumed the honey stored earlier. Honey extracted from different colonies at the third harvest (18 September) was 0-4·5 kg. On average normal colonies yielded 2·4 kg, and those in the 50% and 75% groups 8% and 50% of that amount, respectively. The proportions of honey extracted from the two low survival groups were now much lower than their percentages of brood survival. This was due to the small number of workers emerging from the (smaller) areas of brood in these colonies in the summer, as well as to the unfavourable ratio between worker and brood populations. The amounts of brood were similar in August in all three groups of colonies, but fewer workers were present by 18 September. So honey consumption in relation to nectar income rose relatively faster in colonies with brood of lower survival rate than in normal colonies

TABLE 6. Honey production by the 50%, 75% and 100% groups of colonies (1978).

Crop	Date	*Honey yield (kg)* *Brood survival* 50%	75%	100%	*Honey yield as % of that for 100% survival* 50%	75%
Rape	8·6	2·0	3·6	2·5	80·0	144·0
Robinia	29·6	1·2	5·1	4·6	26·1	110·9
Phacelia, clover, heather	18·9	0·2	1·2	2·4	8·3	50·0
Honey left for winter		2·6	2·3	2·4	108·3	95·8
Total		6·0	12·3	11·9	50·4	102·5

About the same amount of honey was left for winter in all three groups of colonies (Table 6). During the whole season, normal colonies collected 12 kg honey, and those in the 50% and 75% groups, 50% and 102% of this amount, respectively. Thus the honey harvests in the three groups were not proportional to the brood survival rates.

Discussion and Conclusions

The most important results are summarized in Table 7. Brood production in spring and autumn, and worker production in spring, were similar in all three groups of colonies. The worker populations in summer (in relation to normal colonies) dropped to 35% in colonies with brood of 50% survival rate but were 93% in colonies with brood of 75% survival rate.

Most of the honey harvested originated from the early flow from rape and acacia (Table 7). Normal colonies produced 7·1 kg per colony from the two flows, whereas those with brood of 50% and 75% survival rates produced 45·1% and 122·5% of this amount, respectively.

If the weather conditions in the second half of the season were better, then the relation of the autumn harvest of 8%: 50%: 100% would have a greater influence on the total amount of honey produced. The total amounts of honey harvested would probably be the average of the two ratios, (about 27%, 86%, 100%) for colonies in the 50%, 75% and 100% groups, respectively. Thus the 50% group of colonies would produce relatively less honey than the percentage brood survival rate, and the 75% group relatively more, but still less than normal colonies.

Nevertheless colonies with brood of 75% and 100% survival rates produced similar amounts of honey during the early nectar flow, and those with brood of 50% survival rate only half as much. Thus colonies with brood of 75% survival rate could be normal honey producers in early nectar flow conditions.

TABLE 7. Summary of average number of progeny, and honey production, of colonies with brood of different brood survival rates.

	Survival rate of brood		
Contents/Date	50% (% *to* 100% *survival*)	75% (% *to* 100% *survival*)	100% (*absolute data*)
Brood in spring 20·4	97	103	14·7 dm²
Brood in summer 1·6	68	82	78·4 dm²
Brood in autumn 24·8	93	111	22·6 dm²
Workers in spring 15·3	79	88	13 800
Workers in summer 22·6	35	93	30 300
Workers in autumn 20·9	65	92	11 800
Honey in spring 8·6	80	144	2·5 kg
Honey in summer 29·6	26	111	4·6 kg
Honey in autumn 18·9	8	50	2·4 kg
Total honey collected	50	103	11·9 kg

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