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BROOD SURVIVAL IN PRODUCTIVE BEE APIARIES IN AUSTRALIA AS A TEST FOR BREEDING HONEYBEES IN CLOSED POPULATIONS[1]

J. Woyke

Waite Agricultural Research Institute, University of Adelaide, South Australia

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Summary

Brood survival in 51 bee colonies was investigated. Of those, 15 were in an apiary where bee breeding was not practised and the queens mated at the apiary; 20 had queens mated in the mating stations of 4 professional queen breeders; 16 had queens that were each instrumentally inseminated with semen from 1 drone only. About 7% of larvae disappeared from the combs during the first developmental stages through factors other than ones related to sex alleles. The overall survival rate in colonies with queens mated naturally was about 85%, whether the queens were mated in the apiary or in mating stations. Thus the brood survival permitted by the sex alleles was 92%, which indicates the presence of about 12 sex alleles in the populations. Thus a bee breeding system that expects the sex alleles to allow 85% brood survival is acceptable, although in practice, it may not appear to be so because the overall survival is only 78%.

Introduction

The genetic mechanism of sex determination in honeybees imposes severe restrictions on bee breeding systems, because diploid drones develop from any fertilised eggs that are homozygous at the sex locus (Woyke, 1963*a*). These drone larvae are eaten by worker bees shortly after they hatch from their eggs (Woyke, 1963*b*). Different methods of natural or instrumental crossing, thus give 50–100% survival of diploid larvae (Woyke, 1963*c*, 1972). The number of sex alleles in a population and the number of matings the queens make determine the numbers of queens producing different populations of homozygotes (Shaskolskij, 1968), but the number of matings does not change the mean of homozygotes in the population. The population genetics of sex alleles in honeybees was first considered by Woyke (1976). He found only 6 sex alleles in the 100-year-old bee sanctuary on Kangaroo Island. This allowed only 75·6% brood survival, but despite this, the colonies were good honey producers. Woyke (1980, 1981) showed that colonies with 50% brood survival were much inferior to normal colonies but those with 75% survival did not differ very much from normal colonies. This was because when larvae were eaten, the queen laid new eggs in the empty cells instead of waiting until they would have become empty, had the larvae survived (Woyke, 1984).

Even in productive colonies, brood survival is normally below 100%, partly through the effects of sex alleles and partly as a result of other cases (Woyke, 1977). In the spring and autumn, when the queen is laying few eggs, she can increase her egg laying rate to compensate for brood that does not develop.

Queen breeders usually rear new queens from a few selected queens and put only a few colonies with drones in mating stations. This may restrict the number of sex alleles and so give low brood survival (Woyke, 1972). Instrumental insemination of queen bees gives complete control of parentage. By using it, inbred lines have been formed and then crossed to give hybrid interlines (Roberts & Mackensen, 1951; Cale & Gowen, 1958; Moeller, 1976). Another method has been to start by determining the sex alleles in breeding lines (Maul, 1972). With both methods, crossing compatible lines overcame production of diploid drones but both are difficult to perform and very laborious.

Lately, Page and Laidlaw (1982*a,b*), Page and Marks (1982) and Page et al. (1983, 1985) have proposed breeding honeybees in closed populations. They arbitrarily chose 85% as the minimum level acceptable for brood survival. The fact that brood dies in bee colonies for reasons other than sex-allele homozygosity must be taken into account in any consideration of the effect of sex alleles.

The purpose of this investigation was to determine brood survival rates in colonies in apiaries where bee breeding was not practised and in colonies with queens from professional

[1]Permanent address: Bee Division, Agricultural University, 02-766 Warszawa, Nowoursynowska 166, Poland.

breeders, and to use the results to assess the validity of the proposal to accept an 85% brood survival level in closed population breeding.

Materials and Methods

The investigations were made in South Australia in the months of February and March. Eucalyptus and alfalfa were flowering at the time. The brood survival rate was investigated in 51 colonies. Of those, 15 were in an apiary where queen breeding was not practised and the queens were mated at the apiary. Another 20 colonies were headed by queens from 4 professional breeders who had the queens mated at their own mating stations. Queens in a further 16 colonies were each instrumentally inseminated with semen from only 1 drone. In this last group, brood mortality due to sex alleles could be only 0% or 50%.

Altogether, the survival of 9138 brood individuals was investigated: about 250 from each colony with a naturally mated queen and 100 from each with an instrumentally inseminated queen. In each colony, the queen was placed under a queen excluder cap on 1 comb. Then, another comb containing eggs in the central area was selected and a plastic strip, 10 mm wide, was attached to the side of the frame with drawing pins put into the top bottom bars. Row numbers of cells were written on this strip and counting from it, the positions of individual cells containing eggs along the rows were recorded. The comb with the strip was returned to the colony, in the centre of the broodnest. It was removed after 3 days and the surviving larvae (1–3 days old) were counted.

Results

Survival of brood in colonies with queens inseminated instrumentally

Out of 16 queens, each instrumentally inseminated with semen from 1 drone, 2 produced brood of which about 50% survived and 14 produced brood with high survival rates: 87·8 – 99·2%, with an average of 93·5 ± SD 3·2% (Table 1). Since, in that group, the sex alleles would allow 100% survival, it seems reasonable to assume that about 6·5% of the brood was lost in the first 3 days of larval life for other reasons. Possible non-genetic causes of brood loss may be deficiency of protein in some nurse bees and cannibalism.

Survival of brood in colonies with queens mated naturally

Brood survival in the apiary, where bee breeding was not practised (CA), ranged from 73·2 to 97·1% (Table 2). The latter value is very high. The two next highest values were 94·4 and 93·1%. The mean brood survival was 85·5% ($n = 15$).

The brood survival of queens mated at mating stations differed according to the breeder who reared the queens. Queens supplied by one breeder (GY) produced brood with 70·9% to 95·7% survival. The mean survival was 85·8%, almost the same as that in the apiary where there was no breeding. The survival of brood produced by 1 queen originating from each of

TABLE 1. Brood survival of 14 Italian (*It*) queens, each inseminated instrumentally by sperm from one Italian (*It*) or one Carniolan (*Ca*) drone.

It × *It*		*It* × *Ca*	
Queen No.	*% Survival*	*Queen No.*	*% Survival*
2	92·0	1	90·4
3	89·0	17	92·9
6	97·4	19	94·7
12	99·2	20	94·2
13	92·3	21	92·3
15	96·8	24	96·1
16	87·8	27	94·2
$\bar{x}$ ± SD	93 ± 4·4		93·5 ± 1·9
Overall $\bar{x}$ ± SD		93·5 ± 3·2	

Table 2. Brood survival (%) in one apiary where bee breeding was not practised (CA) and in apiaries with queens from four queen breeders (GY, RI, GD, ST).

		Breeders			
CA		*GY*	*RI*	*GD*	*ST*
73·2	85·1	70·9	60·9	59·2	81·3
74·9	85·7	83·5	86·7	83·6	87·2
80·7	87·6	84·5	87·8	93·9	92·7
81·4	88·3	94·5	91·4	96·0	96·0
82·6	90·4	95·7	95·7	96·4	99·7
83·3	93·1				
84·8	94·4				
	97·1				
$\bar{x}$	85·5	85·8	84·5	85·8	91·4
SD	6·68	10·03	13·65	15·77	7·27
V%	7·81	11·69	16·15	18·38	7·95

two other breeders (RI, GD) was 60·9 and 59·2%, respectively. Queens producing such poor brood should not be used in colonies intended for honey production. However, the average brood survival was about 85% in these two breeding-controlled apiaries, again similar to that in the apiary with queens mated without breeding control. Queens of the fourth breeding line (ST) produced brood with a higher survival rate (Mean, 91·4%) than that from queens mated without breeding control.

When the value, 6·5%, of brood lost owing to factors other than sex-allele related ones, is added to the 85·5% general survival of brood produced by queens mated without breeding control, the value of 92% is obtained for the brood survival permitted by sex alleles. Applying the formula, N = 100/100−S (N, number of sex alleles; S, % brood survival; Woyke, 1976), 12·5 sex alleles is calculated for the population of that apiary. Similar numbers of sex alleles must have been present in the 3 breeding-controlled apiaries: GY, RI and GD. The brood survival permitted by sex alleles in the fourth controlled apiary (ST) was 91·4 + 6·5 = 97·9%. For this to have been caused by sex alleles distributed uniformly throughout that population, 47·6 of them would have had to have been present. The coefficient of variation (V%) was higher in the three breeding apiaries (GY, RI and GD) than in the two remaining ones.

Discussion

It seems doubtful that the high survival rate of brood produced by queens from one breeding apiary was caused by the presence of 47 alleles in that population. Probably, the queen breeder introduced queens from another population to his apiary and the virgins mostly mated with drones possessing sex alleles that were different from theirs. Also, it is possible that other factors were more favourable for brood rearing in his apiary than in the others.

The very low brood survival of some queens from 2, (RI, GD) of the 3 other breeding lines could indicate that the virgins were reared from few queens and mated with related drones. Beekeepers buying such queens would suffer losses. On the other hand, the fact that the average brood survival in breeding lines RI, GD and CA was about 85% and similar to that in the apiary where queen breeding was not practised, means that the queen breeders' mating stations were not sufficiently isolated and some virgins mated with drones other than those provided in the stations. Brood survival in these last 4 apiaries allowed by sex-allele factors was about 92% and the number of alleles was 12·5. This number is very similar to the 11 alleles presented by Mackensen (1955) and 12·5 shown by Laidlaw, Gomes and Kerr (1956), but lower than the 19 estimated by Adams et al. (1977). The proposal to breed bees in closed populations with the brood survival permitted by sex alleles falling to 85%, assumes populations with 7 sex alleles, which is only 1 more than was found in the Kangaroo Island bee sanctuary.

The fact that some loss of brood in early developmental stages is caused by factors other than sex alleles should always be remembered in breeding programmes. An overall brood viability of 85%, or less, can be expected even under conditions less restrictive than 40 generations of breeding in closed populations of 35–50 breeder queens. When these conditions do operate, an average brood viability of 85 − 6·5 = 78·5% is expected. Even this is only a few percent lower than is now encountered in many productive apiaries, where in unfavourable conditions, survival may be much lower (Woyke, 1977) without impairing the colonies' commercial performance (Woyke, 1980, 1981). Woyke (1976) calculated that for each increase of 1 in the number of alleles from 2 to 5, the survival improves in steps falling from 17% to 5%. From 5 to 8 alleles, each step gives less than 3·5% improvement and at still higher levels, the steps are less than 1·5%. An increase in sex alleles of up to 9 would be desirable in closed populations. This number would permit 88·5% brood survival, which would be practically the same as the 91·5% survival permitted by 12 sex alleles present in honeybee populations around many apiaries. The overall brood survival would be 88·5 − 6·5 = 82%; practically the same as the 85% survival found in commercial apiaries.

Altogether, a breeding programme that assumes 7 sex alleles and 85% brood survival is acceptable when no better, easily managed one is proposed. We now know that some brood disappears even from productive colonies, but an increase of sex alleles up to 9, permitting brood survival up to 89%, would probably be desirable.

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