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# PAARUNGSKONTROLLE UND SELEKTION BEI DER HONIGBIENE

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Controlled mating and selection
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# PART THREE
# SELECTION

## SEX ALLELES AND CONTROLLED MATING

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In order to obtain highly productive bees, stress should be laid on sex alleles. Maximum productivity is obtained only from the colonies with high survival rate of brood. The eggs of a queen with ab sex alleles mated with a drone (ab×c) are all heterozigous, with a 100% survival rate. The queen with ab sex alleles mated with an a drone will lay two kinds of fertilized eggs: aa and ab. From the heterozigous eggs worker bees will emerge. From the aa homozigous eggs diploid males will emerge which are eaten by worker bees, when newly hatched. Consequently, only 50% of the hatched eggs will develop into worker bees. The brood of such a queen will have gaps, the colony will be weak, and will never yield a high crop.

The naturally mated or instrumentally inseminated queen receives sperm from several drones.

When a virgin queen has the same sex alleles as the queen of the father colony, after mating she will lay ab×ab eggs, with the following combination of sex alleles: aa, ab, ba and bb. It results that workers will emerge from not more than 50% of eggs. When a virgin queen has only one sex allele similar to that of the mother queens of drones, for instance b, she will lay, after a bc×a, b mating, four kinds of eggs: ab, ac, bb, and bc. Worker bees will emerge only from 75% of the heterozigous eggs. Such mating is very frequent in mating stations where only one father colony exists, and the virgin queens are related to the queen which produces the males. The colonies including the descendants of the queens mated at the station will never have a strong population. When a virgin queen has both sex alleles, for instance de, different from those of the queen producing the drones, after a de×a, b, mating, she will lay ad, ae, bd, and be eggs, all of them having different sex alleles. All eggs laid by the young queen will have 100% survival rate.

We shall now consider a number of problems of controlled mating practice in a mating station or of instrumental insemination. First, the case when all males are produced by one queen alone, but two generations of young queens mate with them. The best mother queen is inseminated, according to ab×cd variant, with the sperm taken from an outbred queen. The queen of the father colony, which produces drones, has ef×? sex alleles which are different from those of the mother queen producing queens. The sex alleles of drones which had fertilized the queen of the father colony are of no concern to us, as the drones develop by parthenogenesis. The combination of sex alleles given in Table No. 1 will be achieved by reproduction. All

TABLE 1 — COMBINATION OF THE SEX ALLELES WHEN THE SAME QUEEN IS USED IN THE FATHER COLONY TWO YEARS RUNNING

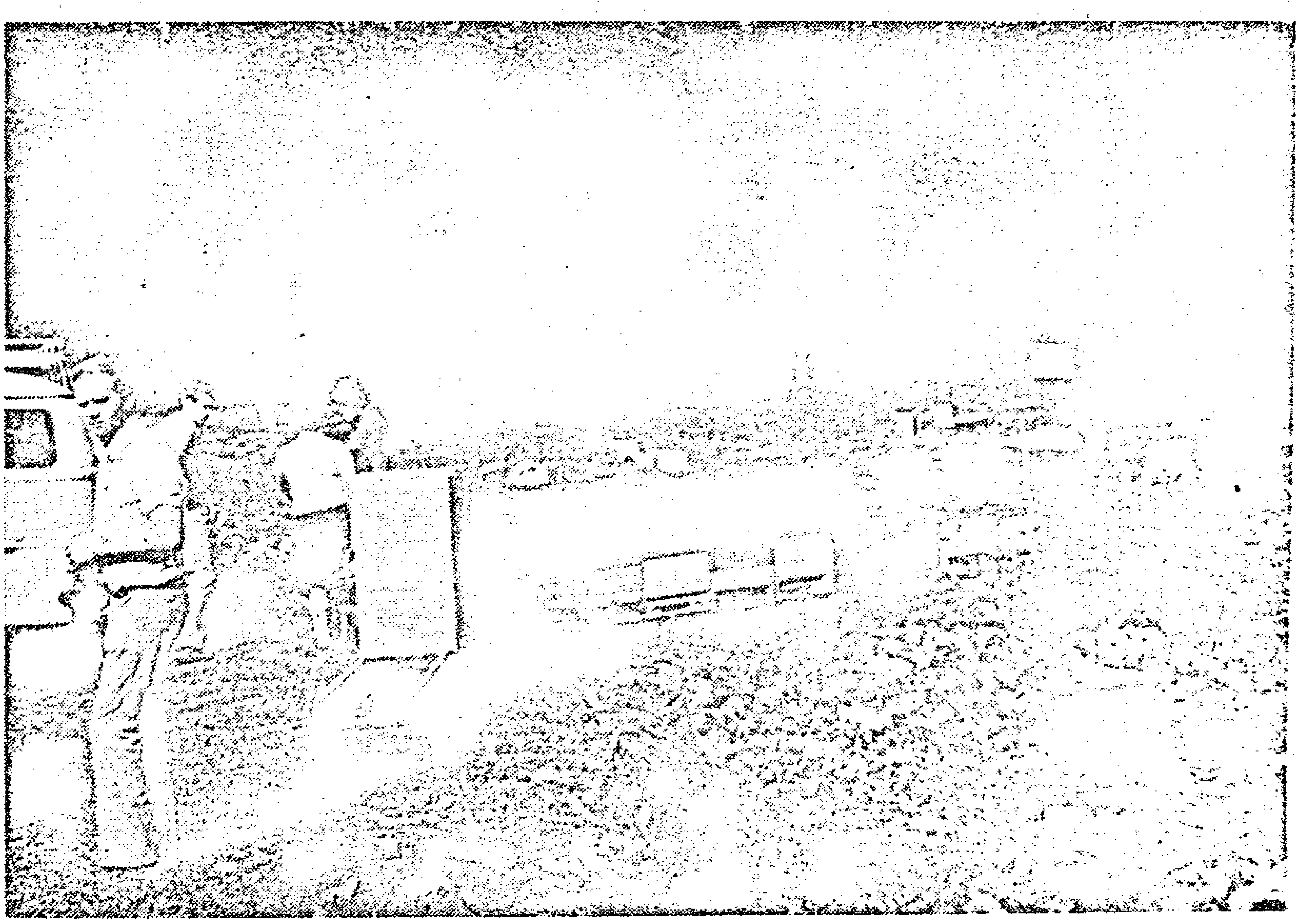
| Year | Queen of the mother colony | Queen of the father colony | Inseminated queens | | | | Survival rate of the brood |
|---|---|---|---|---|---|---|---|
| I | ab × c,d | ef × . . . | ac×e,f ; | ad×e,f ; | bc×e,f | bd×e,f | 100% |
| II | ac × e,f | ef × . . . | ae×ef ; | af×e,f | ce e,f | cf×ef | 75% |

TABLE 2 — COMBINATION OF THE SEX ALLELES WHEN THE QUEEN OF THE FATHER COLONY IS REPLACED WITH A DAUGHTER ONE

| Year | Combination | Queen of the mother colony | Queen of the father colony | Inseminated queens | The amount of queens with brood showing a certain survival rate | | |
|---|---|---|---|---|---|---|---|
| I | 1 | ab × c,d | ef × . . . , | ac × e,f ; ad × e,f ; bc × e,f ; bd × e,f | all — 100% | | |
| | 1 | ac × e,f | | ae × a,c ; af × a,c ; ce × a,c ; cf × a,c ; | all — 75% | | |
| | 2 | ad × e,f | | ae × a,c ; af × a,c ; de × a,c ; df × a,c | 1/2 — 75%<br>1/2 — 100% | 1/2 — 75% | |
| II | 3 | bc × e,f | ac × . . . | be × a,c ; bf × a,c ; ce × a,c ; cf × a,c ; | 1/2 — 100%<br>1/2 — 75% | 1/2 — 100% | |
| | 4 | bd × e,f | | be × a,c ; bf × a,c ; de × a,c ; df × a,c | | | |
| | 1 | be × a,c | | ba × b,e ; bc × b,e ; ca × b,e ; ec × b,e ; | all — 75% | 3/4 — 75%<br>1/4 — 100% | 1/2 — 75% |
| | 2 | bf × a,c | | ba × b,e ; bc × b,e ; fa × b,e ; fc × b,e | 1/2 — 75%<br>1/2 — 100% | | |
| III | 3 | | bc × . . | | | | |
| | 3 | de × a,c | | da × b,e ; dc × b,e ; ea × b,e ; ec × b,e ; | 1/2 — 100%<br>1/2 — 75% | 1/4 — 100%<br>3/4 — 100% | 1/2 — 100% |
| | 4 | df × a,c | | da × b,e ; dc × b,e ; fa × b,e ; fc × b,e | all — 100% | | |

young queens descending from the ab×c,d, first-rate queen, mated with e, f drones will have no similar allele and will produce brood with 100% survival rate. All young queens are thus likely to also become first-rate queens. But, when the subsequent generation of queens will become adult and will mate with drones produced by the same queen of the father colony, 25% of the eggs will be homozigous as illustrated in Table No. 1. Consequently, when the queens of the second generation mate with drones produced by the same drone laying queen as of the previous generation, the survival rate of the brood hatched by all queens will be 75%. This means that commercial beekeepers are not recommended to keep, in mating stations, the same queen in the father colony two years running, or to use their sons for the instrumental insemination of queens of the second generation either.

Now we shall consider the case when the father colony is requeened every year. The new drone-laying queen is a queen already fertilized by drones, sons of the former drone-laying queen. Table No. 1 shows that in the first year when the sex alleles of the mother queen differ from those of the drone-laying queen, the brood produced by all daughter queens has a 100% survival rate and all are likely to become first-rate queens. The following year, the result obtained may be altogether different, even if the father colonies are of the best ones. The result will substantially depend on the sex alleles of the queens of the mother and father colonies. Let us now consider the case when colonies are taken at random. The beekeeper is likely to find queens with the same sex alleles in one of four cases (Table 2, second year, case No. 1). Consequently, the brood of all young queens descending from the mother queen mated with the drones produced by a drone-laying queen having differing alleles will have a 75% survival rate. In two cases of four, the beekeeper is likely to find queens for the mother and father colonies having one similar allele (Second year, case Nos. 2 and 3). Consequently, half of the young queens will produce brood with 75% survival rate, and the other half — with



*The mating stations of the Institute of Lunz are provided with lots of drone nuclei*

**TABLE 3 — COMBINATION OF THE SEX ALLELES IN YOUNG QUEENS MATED WITH DRONES FROM SEVERAL RELATED QUEENS**

| Queen of the mother colony | Queen of the father colony | Inseminated queens | | | | The amount of queens with brood showing a certain survival rate |
|---|---|---|---|---|---|---|
| | | **2 Drone Colonies. Variant 1** | | | | |
| be × a,c | be × . . . | ba × b, b, e, f ; | bc × b, b, e, f ; | ea × b, b, e, f ; | ec × b, b, e, f ; | 1/4 75 % |
| bf × a,c | bf × . . . | ba × b, b, e, f ; | bc × b, b, e, f ; | fa × b, n, e, f ; | fc × b, b, e, f ; | 1/2 87.5% |
| | = bbef | **da × b, b, e, f ;** | **dc × b, b, e, f ;** | ea × b, b, e, f ; | ec × b, b, e, f ; | 1/4 100 % |
| de × a,c | | **da × b, b, e, f ;** | **dc × b, b, e, f ;** | fa × b, b, e, f ; | fc × b, b, e, f ; | |
| df × a,c | | | | | | |
| | | **2 Drone Colonies. Variant 2** | | | | |
| be × a,c | be × . . . | ba × b, d, e, f ; | bc × b, d, e, f ; | ea × b, d, e, f ; | ec × b, d, e f ; | In all 87,5% |
| bf × a,c | df × . . . | ba × b, d, e, f ; | bc × b, d, e, f ; | fa × b, d, e, f ; | fc × b, d, e, f ; | |
| de × a,c | = bdef | da × b, d, e, f ; | dc × b, d, e, f ; | ea × b, d, e, f ; | ec × b, d, e f ; | |
| df × a,c | | da × b, d, e, f ; | dc × b, d, e, f ; | fa × b, d, e, f ; | fc × b, d, e, f ; | |
| | | **3 Drone Colonies** | | | | |
| be × a,c | | ba × b, b, d, e, e, f ; | bc × b, b, d, e, f ; | ea × b, b, d, e, e, f ; | ec × b, b, d, e, e, f ; | |
| bf × a,c | be × . . . bf × . . . | ba × b, b, d, e, e, f ; | bc × b, b, d, e, f ; | fa × b, b, d, e, e, f ; | fc × b, d, b, e, e, f ; | 1/2 83.3% |
| | | | | | | $\overline{x}$ = 87.5% |
| de × a,c | de × . . . = bbdeef | da × b, b, d, e, e, f ; | dc × b, b, d, e, e, f ; | ea × b, b, d, e, e, f ; | ec × b, b, d, e, e, f ; | 1/2 91.7% |
| df × a,c | | da × b, b, d, e, e, f ; | dc × b, b, d, e, e, f ; | fa × b, b, d, e, e, f ; | fc × b, b, b, e, e, f ; | |
| | | **4 Drone colonies** | | | | |
| be × a,c | be × . . . | ba × b, d, e, f ; | bc × b, d, e, f ; | ea × b, d, e, f ; | ec × b, d, e f ; | |
| bf × a,c | bf × . . . | ba × b, d, e, f ; | bc × b, d, e, f ; | fa × b, d, e, f ; | fc × b, d, e, f ; | In all 87,5% |
| | de × . . . | | | | | |
| de × a,c | df × . . . | da × b, d, e, f ; | dc × b, d, e, f ; | ea × b, d, e, f ; | ec × b, d, e f ; | |
| | = (bbddeeff) | | | | | |
| df × a,c | = bdef | da × b, d, e, f ; | dc × b, d, e, f ; | fa × b, d, e, f ; | fc × b, d, e, f ; | |

100% survival rate. At last, in one case of four, the beekeeper will find queens for the mother and father colonies with no similar allele. Consequently, all queens will produce brood with 100% survival rate, and each and every queen is likely to become a high-rate queen (Second year, case No. 4). It is obvious that there is a slight possibility to find a combination resulting in queens producing brood with 100% survival rate. Hence the most frequent combination will be that in which only half of the queens obtained produce brood with 75% survival rate. When the virgin queens descend from several queens, every combination is possible and consequently half of the queens will produce normal brood while the other half — brood with gaps.

The third year, the beekeeper will develop a third generation of virgin queens, only from first-rate queens producing normal brood. Whether no queen produces normal brood, it means that the combination No. 1 had taken place already in the previous year. Consequently, the former queen of the mother or father colony must be replaced and the breeding program taken from the beginning.

When two highly efficient queens had been selected for the mother and father queens, the brood prduced by their sisters must also be checked. Whether any of the sister queens produce brood with gaps this means that the combinations Nos. 2 and 3 took place in the previous year. In half of cases, the two queens — of the mother and father colonies — may have the same sex alleles (Table 2, third year, combination No. 1), while in the other half of cases the sex-alleles of the two queens are different (Third year, combination No. 2). In the first case, all new queens will produce brood with gaps with 75% survival rate, and in the second case, half of the queens will produce normal brood. As a result, when the queens for the mother and father colonies are taken from groups of sister queens some of which produce brood with gaps, there is no possibility for all queens to produce normal brood. At last, when the queens for the mother and father colonies are taken from groups in which all sister queens had produced only normal brood, this means that the combination No. 4 had taken place in the second year. This situation is similar to that occurred at the end of the first year. This means that the third generation of queens can produce four different groups (Table 2, third year, combinations 1, 2, 3, and 4) according to the sex alleles of the queens of the father and mother colonies. In 25% of cases, all queens obtained will produce normal brood (Table 2, third year, combination No. 4). It is obvious that the result depends on the group from which the queens for the father and mother colonies have been taken. When some of their sisters had produced brood with gaps it is practically impossible to obtain normal brood from all new queens. When all sister queens produce normal brood, there may happen that a few of them also produce in their turn queens which after mating will produce normal brood.

In other cases, the queens for the mother and father colonies are not taken from a sister group but from two different groups. When the mother queen and the queen of the father colony are taken from two different groups in which some sister queens had produced brood with gaps, it is possible that the two groups have the same sex alleles (for instance, the two groups of the combination No. 3, second year). Consequently, only 1/4 of the new queens will produce normal brood. In half of cases, the group of queens of the second year will not be uniform ; for instance, the mother queen may come from the second group while the queen of the father colony — from the third group of queens of the second year. In the third year, combinations Nos. 3 and 4 will take place. Half of the virgin queens descending from certain queens will produce after mating brood with gaps, while the others, of other origin, will produce normal brood ; in all 3/4 of the new queens will produce normal brood. Finally the mother and father queens are taken from two groups — one in which half of the sister queens produce brood with gaps, and the other in which all queens produce only normal brood. Consequently, combinations similar to those mentioned above may occur (3/4 of the new queens produce normal brood), or similar to those occurring in the case when the queens come from a group of queens which all had produced normal brood (1/2 of the queens obtained produce normal brood).

Conclusions significant for practice follow from the above experiments. The queens for the mother and father colonies must not be taken from a group of sister queens part of which had produced brood with gaps, because only a quarter of them will produce normal brood. The two mother queens may be taken from a group of sister queens which produce only normal brood. In this case, the new queens originating from part of the mother queens will produce normal brood and for all combinations possible, half of the queens on an average will produce normal brood. When taking the two mother queens from two different groups of sister queens, for all combinations possible, 3/4 of the queens will produce normal brood.

The new queen may mate not only with several drones originating from one queen alone, but also with drones of different queens. When the sex alleles of the drones are different from those of the queens, all new queens will produce normal brood. But a queen mated with drones descending from a different queen, for instance ab×c,d, produces four kinds of queens. Hence it is possible that some queens mate with drones having the same sex alleles. 12 sex alleles were identified up to now. Consequently, 1/12 of the eggs laid by a queen mated with 12 drones with different sex alleles are homozygous, which means that the survival rate of the brood will be 91.7%. Hence, a queen mated with drones originating from one queen alone can produce brood with 50%, 75%, and 100% survival rate.

The poorly egg-laying queens can be easily identified and removed. The queens mated with drones originating from several queens will produce brood with a survival rate higher than 75% but often lower than 100%. It is difficult to identify the respective queens. In breeding work, the queens are quite often related to a certain extent to the drones they mate with.

We shall now consider the case when the queens of the father and mother colonies are taken from those mated in a mating station with only one drone colony. This is the case when all queens are instrumentally inseminated with the sperm of several drones originating from the same queen. The queens of the mother and father colonies are taken from the young queens of the second year (Table 2). The combinations of sex alleles obtained after the mating of the queens with drones originating from several queens are given in Table 3.

When two different queens are used for producing drones, two possibilities exist: the two queens either have one similar allele, or only one allele differing. In the first case, 1/4 of the young queens will produce brood with a 100% survival rate (Table, 3, 2 colonies, variant 1). In the second case, none of the queens will produce brood with 100% survival rate. The brood of each of them will have a survival rate of 87.5%. (Table 2, 2 coolnies, variant 2). When the drones originate from 3 different queens, half of the young queens mated with the respective drones will produce brood with a survival rate of 83.3%, while the other half — of 91.7%. The average survival rate will be of 87.5% (Table 3). When the drones originate from 4 queens, the young queens mated with them will produce brood with an 87.5 survival rate (Table 3).

Consequently, when the young queens are inseminated with sperm of drones originating from a related queen, their brood will have either 100% or 75% survival rate. The latter can be easily removed. When the queens are inseminated with sperm of drones originating from several related queens, the brood of most of them will have an 87.5% survival rate. When the queens are inseminated with sperm of drones descending from non-related queens, there is a much slighter possibility of finding the same allele than in the case of related populations. But the increase in the number of non-related queens producing drones leads to obtaining a population which has all sex alleles. It is perfectly possible that a virgin queen of this population mates with a drone having at least one allele similar to hers.

It results that in improving bees one must pay constant attention to sex alleles and the survival rate of the brood.