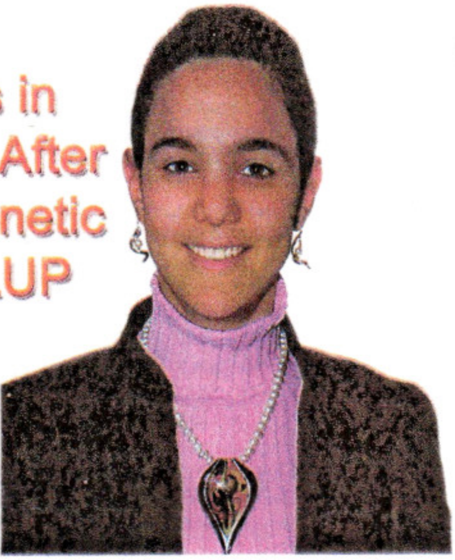
Bee Breeding Around the World

Noticeable Success in Honey Bee Selection After the Introduction of Genetic Evaluation Using BLUP



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The principle of breeding is very simple, yet the execution can be quite challenging.

The principle: In breeding one mates the best animals with one another to achieve good offspring.

The problem: The true quality of the animals is very difficult to determine, so that frequently the offspring leave much to be desired.

Only the hereditary disposition is significant in breeding, as only the hereditary disposition (genes) of the parents influence the quality of the offspring. The environmental conditions under which the parents live unfortunately mask these hereditary properties, but are not passed on to offspring. A decisive step forward in bee breeding was the formulation of uniform guidelines to test bee colonies (Ruttner 1972).

Breeding—The Difficulties

The standardization of the test is a necessary prerequisite for successful breeding, but alone it is insufficient. The nectar flow and the evaluation standards for behavior such as gentleness or steadfastness on the frame (which evaluates if the bees fly up at you when you lift out a frame) vary so much from apiary to apiary and beekeeper to beekeeper that such results only permit comparisons of colonies within a single bee yard. But still the significance of the comparisons made within a single apiary is minimal. Even under strict adherence to the evaluation guidelines, it is impossible to sufficiently take into account all the different influences (micro climates, disease, etc.) in a single apiary.

One can try to compensate for differences by testing multiple sister queens in the same apiary. One can safely assume that any systematic advantages or disadvantages caused by environmental factors are highly unlikely to influence all sister colonies identical.

This correction for differences in environment and evaluation standards (for behavior characteristics) has disadvantages that should not to be underestimated. We judge which colonies are exceptional by their deviation from the average. But these deviations are dependent on the genetic standard of the other colonies in the apiary.

An example from sports may help to clarify this concept. The deviation from the average of competitors in a 100 meter sprint will fall very differently, depending on whether it is an Olympics final or a regional competition. If one were to only judge the deviance from the average within a race, as one does with the selection of bee colonies, without taking note of the quality of the competitors, then a very good regional racer would often appear to be a superior runner. The regional winner would have outpaced the other runners by a greater difference. In the far higher standard of the Olympics, the ability of the racers is much closer and so the world record holder might only be slightly above the average. When compared to the regional runner, who shines out way above the average, the world record holder does not stand out much from the pack, even though he is in fact the superior runner. He just happens to have better competition.

Breeding Value Estimation—What is it?

The breeding value is the value of an animal for breeding. More precisely said, the breeding value states for a particular characteristic (i.e. for the honey bee, lbs of honey, less varroa, etc.) how much an animal is genetically better or worse than the average of the population. When one states that something is better or worse, it is only in relationship to the reference base. In breeding the reference base is the average of all breeding values, that is to say, the average genetic standard of the population. Because breeding values are always relative to the standard population, they are given as difference or percentage where the genetic average is represented as "0" or "100 %".

An example: A breeding value for honey of 120% means that the queen is 20% genetically above the standard level of the population. When this queen mates with average drones (whose breeding values are 100%), then one can expect offspring that are 10% ((120 +100) / 2) better than the average and would thus receive a value of 110%. Averaged out over all the different environments, such offspring will then produce 10% more honey than the average of the population.

How Does One Calculate Breeding Values in Honey Bees?

Before starting the actual calculations, the original input data usually collected by beekeepers and breeders in their apiaries must first be corrected. First the inbreeding coefficients of all queens and all "average workers" of the colonies are calculated. Inbreeding of queens and workers clearly influences the performance and behavior of colonies (Bienefeld et al. 1989). As poor performances in honey yield and also

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behavior changes are due to inbreeding and not an expression of the quality of genes, all inbreed colonies are corrected for inbreeding effects of queens and workers on the corresponding trait. This mathematically equalizes the values in respect to performance and behavior as if all colonies had an inbreeding value of 0. In addition, another mathematical formula takes into account the wide ranging number of compared colonies per apiary. Once the data have been appropriately corrected, one can begin with the actual breeding value estimation.

From 1992 until 1994 the modern breeding evaluation system (BLUP Animal Model) was adjusted for the peculiarities of the honey bee at the Institute for Bee Research in Hohen Neuendorf, Germany. BLUP stands for "Best Linear Unbiased Prediction." This approach uses (the complicated) genetic relationships between all colonies, not just sister colonies. The performance of colonies are due not only to the genetics of the queen (i.e. egg-laying ability), but are also dependent on the genes of the worker bee (i.e. zeal for foraging) and so both generations must be factored in simultaneously.

For this estimation it is not necessary to measure or even know the individual influences of queens and workers on the colonies' characteristics. Instead one needs the degree of kinship between all queens, between the (average) workers and between the queens and the (average) workers of all colonies. The mathematical basis for these methods was developed by Wilham (1963) for motherly influence on the performance of mammals. The adaptation of this approach to the reproduction biology of the honey bee is the basis for the breeding value estimations for this species (Bienefeld et al. 2007). This approach has the following benefits:

1. By taking into account all degrees of kinship when evaluating breeding values, information from all related colonies influence the results of an individual colony. Test results of parents, grandparents, great grandparents, uncles, cousins, etc. are used proportionally to their degree of kinship in the calculation of the breeding value. Every colony is a source of information for related colonies. A colony thus profits from the evaluation of kindred colonies being incorporated into its own evaluation.

2. By separately taking into account the genealogy of the queen and workers of every colony, it is possible to individually calculate the genetic influence of the queen and workers for each colony attribute. This results in two breeding values per characteristic of each colony; one for the influence of the queen and one for the influence of the worker on each characteristic.

The separate calculation of breeding values for queen and worker influences has a very important advantage. It has been demonstrated that negative genetic relationships exist between queen and worker influences (Bienefeld & Pirchner 1990). This means that is it difficult to select queens that have good genetics for being a queen and also carry genes that make good workers. With many other animal species (i.e. in beef cattle breeding) it has been demonstrated that neglecting (negative) relationships between the traits of mother and offspring has led to significantly reduced success in selection.

A further important advantage of this method of evaluation: In addition to corrections for environmental and behavioral measuring standards (that can vary greatly from beekeeper to beekeeper), the different genetic levels of mating partners and comparison hives at each apiary are taken into account. Let me again compare it to the 100 m race: the superiority of a sprinter is measured differently, depending on whether he or she races against world class runners in an Olympics final or a regional competition. By simultaneously taking into account the genetic predisposition of all animals (using information from all related animals) and the environmental influences on colonies, the breeding value estimations calculated using this method are very exact.

How are the breeding values represented?

In the first few years the breeding values were given in their natural measurements (kilograms* of honey, actual points in the behavior tests). Interpretation of these numbers was often difficult for beekeepers. Is a negative value for swarm drive good or bad? Because of these difficulties in interpretation, the values were converted to percentages in 1997. The averages of breeding values from the last five years are used as a reference base in each category on a sliding scale. This means—given a selection response within the population—that the old breeding values are depreciated over time.

Since 1994 the Institute for Bee Research in Hohen Neuendorf has completed the breeding value calculations for the German Carniolans from the raw data, which is inputted by individual breeders and other institutes. As of 2002 they also have done the calculations for other European countries. At the moment the databank contains almost 100,000 records (Fig. 1).

The Results of the Breeding Value Estimations

Although breeding evaluations only started in 1994, previous data existed. These come from the stud book records that were archived by bee breeding organizations in Germany. Approximately 40,000 records with the bees' lineage and testing results were the basis for the evaluation system. This database is now enlarged by up to 6,000 records from Germany annually (Fig. 1).

The described data records allow for the calculation of breeding values after the fact and so we can also determine genetic advances. If one looks at the five year average of breeding values since 1970 for honey production, a slow escalation until 1990 is evident. Between 1989 and 1994 (each year representing when the queen was born) a significant fall in the genetic standard is noticeable; only as of 1995 did the values begin to rise again. If one now calculates the genetic advances before and after the start of breeding value estimations in 1994, no significant genetic improvement in honey productivity (0.003%) exists before the

* **1 kilogram (kg) = approximately 2.2 lbs.**

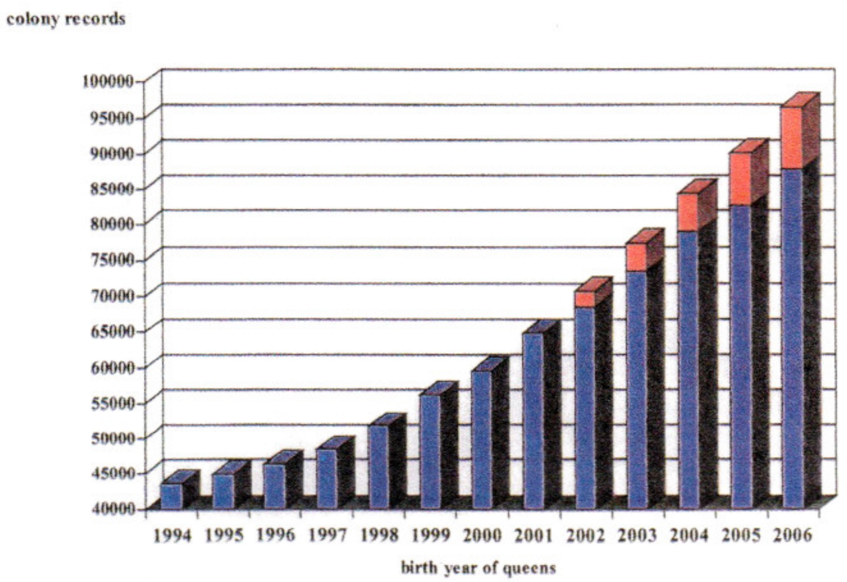

Fig 1: Development of the databank for the performance test data of Carniolans for breeding value estimations.

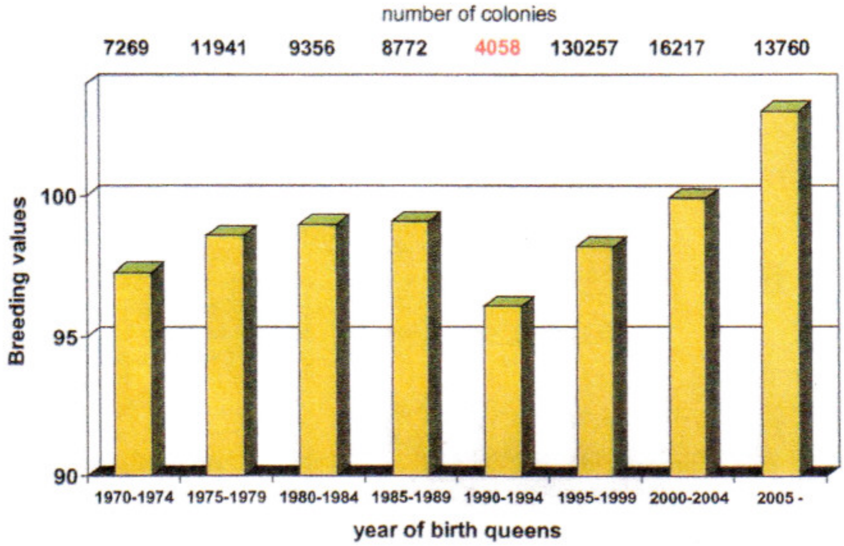

Fig. 2: Breeding values in 5-year averages for honey production. The values over the bars represent the number of colonies available for computing the averages.

implementation of the breeding value estimations, due to the negative developments between 1989 and 1994.

In Fig. 2 the number of data records used for these calculations is also noted next to the development of the breeding values. Clearly visible are the small number of records available between 1989 and 1994. During this time period East and West Germany were reunited. In the former GDR many breeders gave up breeding bees entirely or stopped their selection process; the consequences can be clearly seen. A further problem during the time period from 1989 until 1994 is that due to the end of a scientific research project, few data records from the western states are included in the data set. Taking the dates between **1989** and **1994** into account leads to an underestimation of the success of selection before the breeding value estimations began. For a fair comparison it is thus necessary to exclude this time period.

Before and After the Breeding Value Estimations: A Comparison

When one removes the time period between 1989 and 1994 from the comparison, then before the breeding value estimations began there was also an average genetic advance for honey production of 0.11% per year. Since the beginning of the breeding value estimations this value has increased to 0.59% per year, significantly higher (Fig. 3). Honey production before the start of the breeding value estimations rose 0.51 kg (1.124 lbs) per colony per year and since then at around 0.72 kg (1.587 lbs).

For gentleness the comparison is even more impressive. Before the start of breeding value estimations, there was an insignificant genetic change for gentleness of 0.01% per year. Since breeding value estimations began, there has been a highly significant annual increase in gentleness of 0.41% (Fig. 4). This can be explained by the higher heritability of gentleness than honey production (Bienefeld & Pirchner 1990).

The breeding value estimation of the honey bee has proven to be an important component of selection decisions for breeders in Germany and other European countries. At the website www.beebreed.eu are not only all inbreeding coefficients (of workers and queens) and the breeding values for different characteristics listed and controllable via filters, but also a breeding planning program is also available. Using this program, simply enter the codes of both potential parents and in return receive an estimation of the inbreeding and breeding values of the expected offspring. This allows breeders to visualize what the potential results of a specific cross will produce, before actually making the cross.

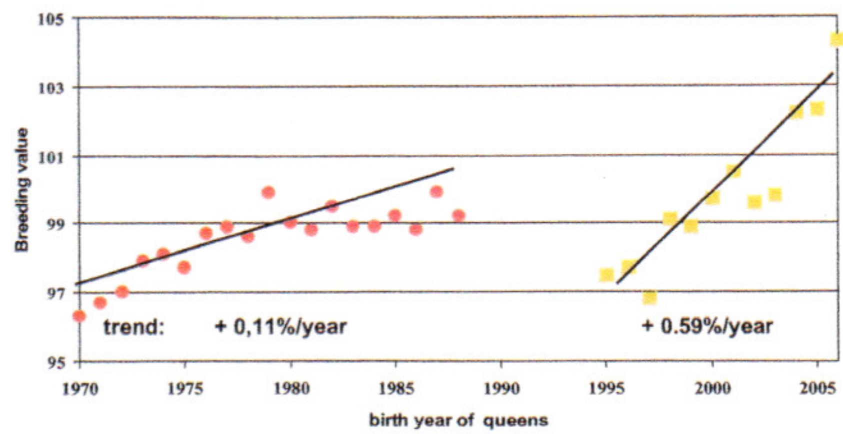

Fig. 3: Genetic improvement for the characteristic "honey production" before and since the start of the breeding value estimations. (100% is the average of the last 5 years for this characteristic).

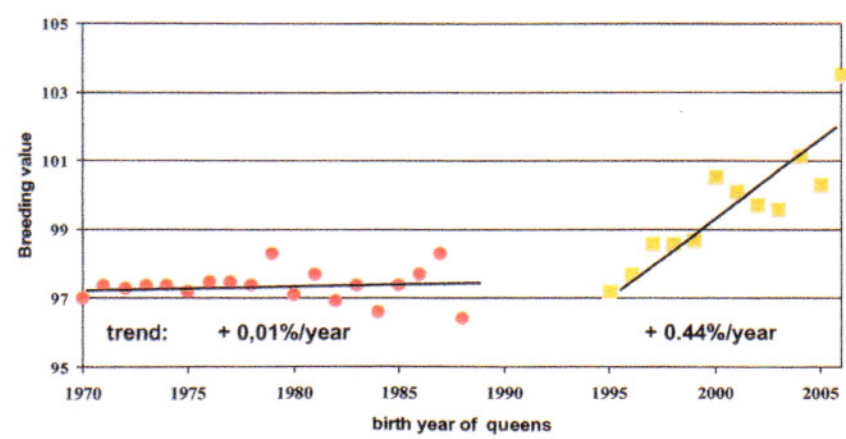

Fig. 4: Genetic improvement for the characteristic of "gentleness" before and since the start of the breeding value estimations. (100% is the average of the last 5 years for this characteristic).

Literature

Bienefeld, K.; Ehrhardt, K., Reinhardt, F. (2007) Genetic Evaluation in the Honey Bee considering Queen and