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An Overview of Selection Concepts Applied to Honey Bees

Matthieu Guichard ⓘ, **Florence Phocas** ⓘ, **Markus Neuditschko** ⓘ, **Benjamin Basso** ⓘ **and Benjamin Dainat** ⓘ

Introduction

For beekeepers it is often difficult to empirically estimate the impact of genetics and selection on honey bee performance. This difficulty—encountered by all breeders of domesticated species—is even greater in the case of honey bees, due to their complex biology and reproduction. Thus, beekeepers can be divided into enthusiasts and sceptics: the former rely primarily on selective breeding as means of improving honey bee performance, while the latter prefer to use other levers for achieving their aims. To support beekeepers to distinguish between the improvements that can be achieved in honey bee performance through selection and those that can be achieved through animal husbandry approaches (e.g., colony management and treatments), a summary of useful concepts in honey bee genetics and their use in breeding is presented and illustrated by the example of two Swiss honey bee populations.

Genetic Concepts

Qualitative Traits

A single gene, or a small number of genes determine the expression of qualitative traits. The historic example is the inheritance of pea color genes, studied by Gregor Mendel in the nineteenth century. In his honor, genetic traits of simple inheritance are termed "Mendelian traits."

Crossing parental lines of peas (Figure 1) with different colors (green seeds x yellow seeds) results in an F1 hybrid generation (100% yellow). Additional crossings between individuals of the F1 generation generates an F2 generation with the proportion of three-fourth yellow to one-fourth green seeds. Thus, in F1 generation the "green" color was transmitted to the F2 generation, while it was simultaneously masked by "yellow"—"yellow" being the dominant trait, and green the recessive trait of the factor "color."

The subsequent development of the theory of genetics corroborated these initial findings on color inheritance. The trait "color" was attributed to a gene, namely, a protein-coding fragment located on a pea chromosome. This chromosome is composed of a deoxyribonucleic acid (DNA) molecule that stores genetic information. The gene coding for color exists in several "versions," the so-called "alleles" of the gene. Phenotype, i.e., the outward appearance of a trait, is directly associated with the alleles carried by the individual. In diploid species like peas, each cell normally contains pairs of chromosomes (one chromosome of maternal origin and one of paternal origin), which means that an individual may either carry two copies of the same allele, or two different alleles for the same gene. An individual carrying two recessive or two dominant alleles at one locus is termed to be homozygous at this locus and expresses the respective phenotype (yellow or green), while one dominant and one recessive allele at one locus is called heterozygous and only the dominant allele is expressed. This situation occurs in the F1 generation of our example: the pea has a yellow color but carries both a yellow and a green alleles, which can be transmitted to its offspring.

This simple inheritance pattern can also be applied on the combination of several traits (Figure 2). The F1 hybrid is 100% yellow and smooth (dominant alleles), while the recessive alleles (green and wrinkled) are only expressed in in few homozygous F2 individuals.

Qualitative traits with a simple inheritance pattern are easy to model as only a small number of genes are involved in their expression. Once the dominant and recessive alleles are identified and their frequency (ratio between G and Y allele) is known, it is possible to determine the occurrence of specific trait characteristics (e.g., color) within a population. More complex expression patterns can however also happen.

Another advantage of qualitative traits is that the environment has only little to no influence on the expression of the phenotype. Therefore, it is possible to associate the genotype information with the trait characteristics of a population. Through this direct link between genotype and phenotype the corresponding traits only show little variation within a population, e.g., if all individuals are homozygous it is not possible to observe a phenotypic variation within the population (e.g., color "yellow").

In the nature, especially monogenic disorders and coat colors follow the Mendelian inheritance. The most well-known example in honey bees is the sexual determinism, which is associated with the *csd* (complementary sex determination) gene (Beye et al., 2003). A honey bee carrying a heterozygous allele combination for this gene develops into a female (worker or future queen). In unfertilized eggs, the gene only carries the allele of the queen (haploid) and a viable drone arises from the larva, while at the homozygous state of the gene a diploid drone arises from the larva, which will be cannibalized by the workers. Thus, in order to minimize the probability of obtaining homozygous larvae from fertilized eggs, a wide variety of alleles for this gene will be necessary to obtain colonies with a high proportion of (female) workers: this small portion of the genome is extremely variable, and several dozen alleles have been described for this gene (Wang et al., 2012).

Additional monogenic traits of honey bees, following Mendelian inheritance, are eye color (e.g., white-eyed honey bees), certain body colorations (e.g., Cordovan mutation, honey bees with very light-colored bodies), and certain wing malformations, as well as an absence of hairiness (Rothenbühler et al., 1968), which only occur in very rare cases.
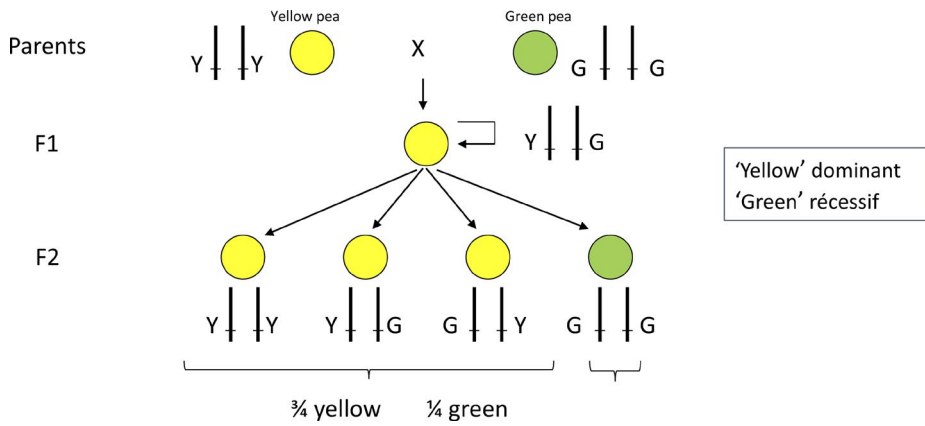
⬈ **Figure 1**. Crossing of two homozygous pea lines (yellow [dominant] and green [recessive]) generates a heterozygous F1 generation (100% yellow). The crossing between two F1 hybrids leads to an F2 generation with ¾ yellow and ¼ green peas. The F1 hybrid carries on the color locus the dominant "yellow" (Y) allele and the recessive "green" (G) allele, while only the dominant Y allele will be expressed ("yellow" color). At the F2 generation, the redistribution of the Y and G alleles present in F1 allows the reappearance of homozygous green (GG) and yellow (YY) peas.
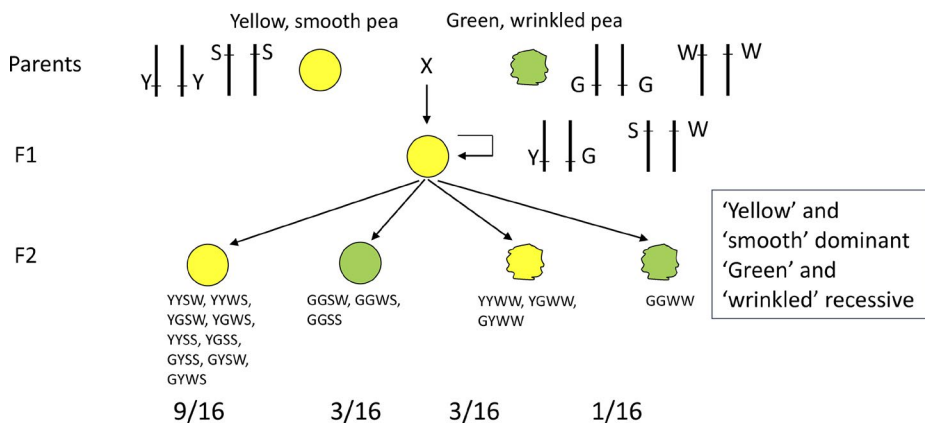

⬈ **Figure 2**. Crossing of two homozygous pea lines (yellow and smooth × green and wrinkled) generates a heterozygous F1 generation (100% yellow and smooth). The crossing between two F1 hybrids produces an F2 generation with a majority of peas being both yellow and smooth (phenotypes associated with the dominant alleles "Y" and "S," respectively) and a minority of green and wrinkled peas (phenotypes associated with the recessive alleles "G" and "W," respectively).

Quantitative Traits

The vast majority of important traits for beekeepers (e.g., honey yield, hygienic behavior (Figure 3), etc.) can be measured quantitatively. Compared to qualitative traits, quantitative traits are characterized by a complex mode of inheritance, which usually causes a high phenotypic variation between the individuals within a population.

These individual trait variations within a population build the base for selection. In this context, it is important to determine the mean value and the distribution of a trait in order to investigate if this trait can be improved by human-mediated selection. Figure 4 shows the distribution of four currently applied selection traits in honey bee breeding programs, namely honey production, steadiness on comb, growth rate of mite infestation and

hygienic behavior. In such an analysis, the distribution often follows a normal distribution, also known as a "Gaussian bell curve," with a small number of extreme values at both ends of the distribution, while the majority of the data is accumulated close to the mean.

Compared to qualitative traits, the expression of quantitative traits is influenced by many genes (several hundreds to thousands). Therefore, the mode of inheritance of these traits is called polygenic (Figure 5), while the genes can have different effects on trait expression. Generally, the majority of genes only have very weak impacts on the expression of the trait. Nevertheless, it is also possible that a few genes significantly influence the expression of the trait. Such genes are called QTL (Quantitative Trait Locus). In rare cases it is feasible that a quantitative trait
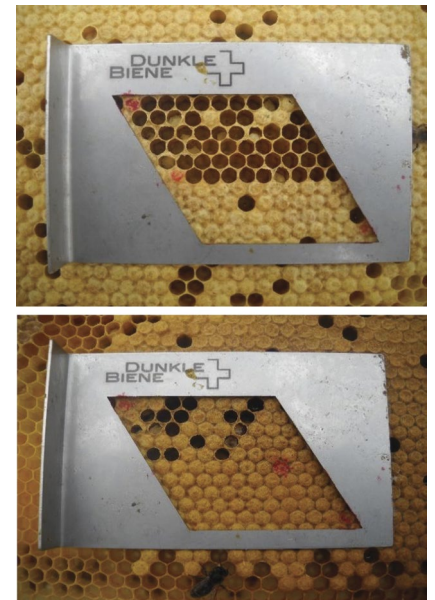

⬈ **Figure 3**. Hygienic behavior towards dead brood is an example of a quantitative trait measured in honey bee selection programs. The colony represented by the brood picture on top has evacuated more experimentally-killed brood than the colony represented below. For both colonies, the photos of the results were taken 12 hours after the pin test, in which 50 pupae were pierced with an entomological needle (Pictures: Matthieu Guichard, Agroscope).

is controlled by a single gene or a very few genes. Despite the successful identification of QTL, the reciprocal associations, the possible dominance effects and interactions between the genes (epistasis) remain unknown for most of the traits.

Honey production (quantitative trait) is a perfect example to illustrate the multitude of possible genes involved, as this trait depends on several factors including early detection of potential honey resources, good flying ability, low susceptibility to robbing, resistance to disease and laying performance of the queen. All these traits are influenced by several genes, which might have an indirect effect on the honey production of a colony. Thus, the honey production encompasses the additive effects and reciprocal relationships of numerous genes whose individual effects are difficult to identify. In addition, honey production is strongly influenced by the following environmental conditions:

- the weather (precipitation, temperature, etc.),
- the geographical location of the hive (orientation),
- the honey and pollen resources (presence of flowers, nectar production, aphids, etc.),
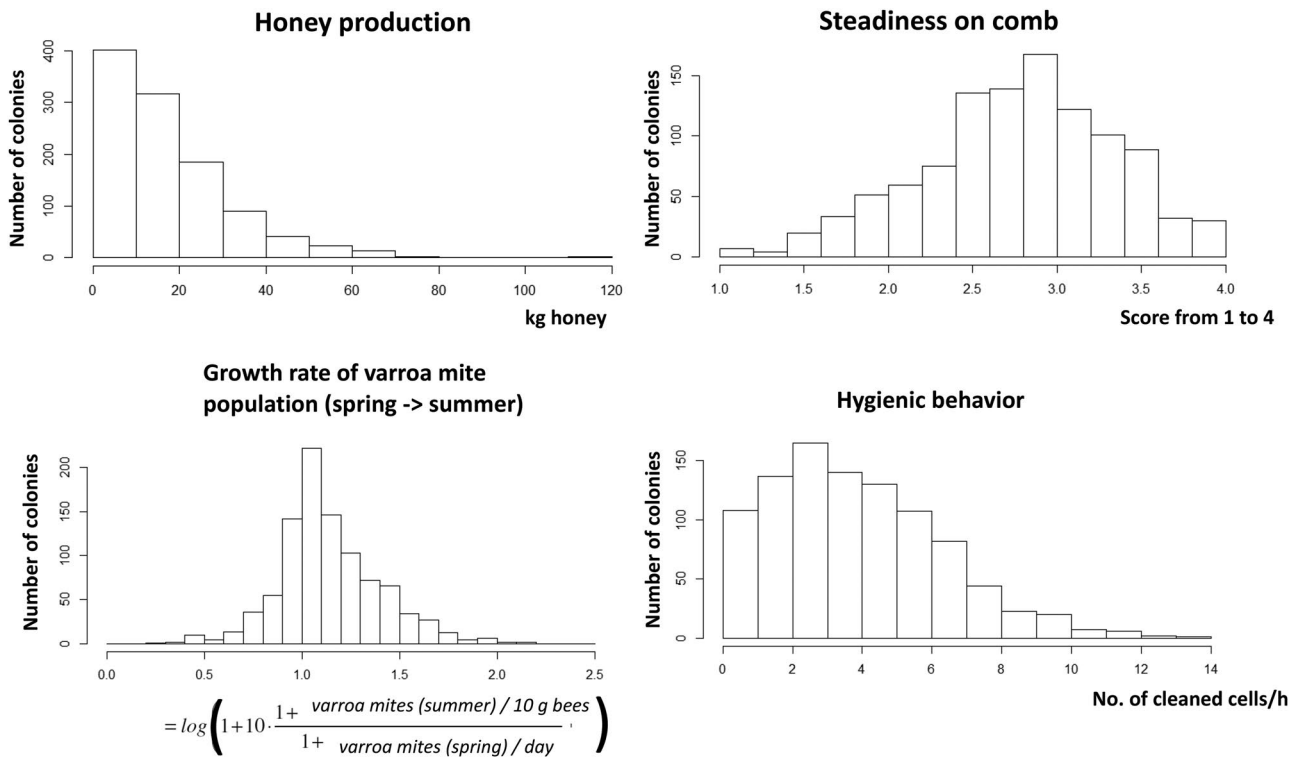
Figure 4. Distribution of four routinely recorded selection traits (honey yield, steadiness on comb, varroa infestation growth rate and hygienic behavior): The number of colonies and the corresponding performance/ratings are plotted on the y- and x-axis, respectively. For some traits (e.g., varroa infestation), it can be noticed, that the dataset is almost normally distributed (a few extreme values at both ends of the distribution, while the majority of the data is accumulated next to the mean.
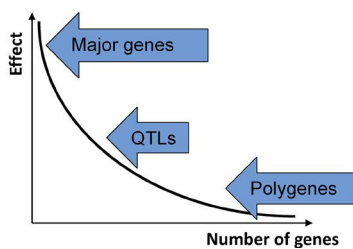
Figure 5. Number and effect of QTL on the expression of a trait. Several genes (polygenes) showing different gene effects (strong to weak) are usually involved in the expression of a quantitative trait.

$$P = G_A + E + \varepsilon$$

Phenotypic value ('Performance')   Additive genetic value   Environmental effects   Residual effect

Figure 6. The statistical model for the phenotype (a trait observed in the studied individuals). The observed phenotype is the sum of the additive genetic effects, the environmental effects and the residual effect.

– the chemical environment (pesticides used in agriculture, the quality of the
– wax foundations, anti-varroa treatments, etc.),
– the presence of pests and parasites (pathogens, etc.),
– the characteristics of the hive (size, material, etc.),
– the measures taken by the beekeeper (depending on training and technique)
– etc.

To sum up, the expression of quantitative traits (phenotype) is essentially influenced by two factors:

(1) Genotype, which is composed of a large number of genes;
(2) Environment, which summarizes all external factors (e.g., weather, location, etc.).

This combination was already described at the beginning of the 20th century (Fisher, 1919) using a statistical model to describe the phenotypes. It states that the sum of the additive genetic effects of the numerous genes and the corresponding environmental effects explain most of the observed phenotypic variation (Figure 6), while the residual effect refers to the variation that cannot be explained by the sum of the genotype and environmental effects.

Application to Selective Breeding

The Selection Strategy

The principal of selection is to choose, among several candidates for reproduction, the animals which improve the performance level of the next generation (Figure 7). To reach this aim, the performance of the selected animals must, in average, be above the mean of the whole population, i.e., to improve the level of a population, a selection rate is applied that leads to a difference, called selection differential (ΔP), between the population average and the average performance of the selected queens. The aim is to obtain a response to selection (R), i.e., an average performance of the offspring that is higher than the average performance of the parental cohort before selection.
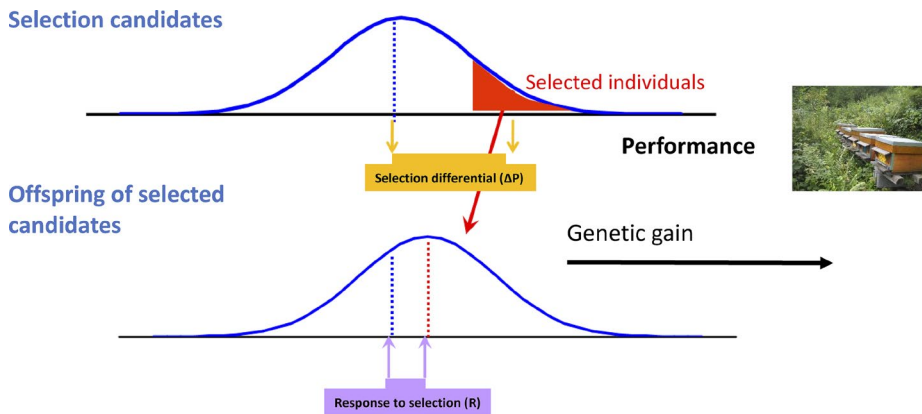
🔺 **Figure 7**. Graphical representation of a selection principal. The upper blue curve represents the distribution for a quantitative trait in a population: Here the curve resembles a so-called normal distribution, with few animals showing a high/good performance and many animals with an average performance (here equal to the median of the population, blue dashed lines). The best individuals of this population (red area) are selected as future breeding stock.

The lower curve represents the population distribution of the offspring of the selected individuals (red dashed line = average of the offspring). The goal of selection is to improve the performance level of a trait over generations (e.g., bees that are gentle, productive and resistant to pathogens): the selection is successful if a response to selection (R, difference between the average of the offspring and the average of the parents) is obtained. Adapted image courtesy of Florence Phocas (Phocas, 2011).

A successful selection and the associated genetic gain can only be achieved over time if the corresponding trait shows variation within the population and this variation is at least partly of additive genetic origin (the trait is heritable in the strict sense). Therefore, it is important to select breeding queens that are not exposed to different environmental influences (physical environment and beekeeping practices).

Heritability

Heritability (h^2) is an essential indicator to determine whether the observed phenotypic variation of a trait can be attributed to an additive genetic origin. Thus, heritability corresponds to the part of the phenotypic variability (observed variability corrected for identified environmental influences) that is of additive genetic origin. Heritability varies between 0 (no genetic influence on phenotypic variability) and 1 (the phenotypic variation of the trait is exclusively of genetic origin). The more heritable a trait is, the more likely it is that it can be successfully improved through selection over generations. However, a trait that shows little or no heritability does not rule out the possibility of breeding. Possible reasons for low heritability are mainly too low measurement accuracies and unidentified environmental effects that superimpose the genetic effects. Therefore, the objective recording of traits is of central importance to achieve better heritability (by objectively recording honey production in

kilograms, for example, genetic variability can be much better assessed than with a less precise estimate of production by the beekeeper like the number of combs of honey collected, or the number of harvested honey supers). In addition, the observed variability is less well explained if important environmental influences are not included in the analysis of the trait (e.g., heterogeneity of physical environmental conditions in an apiary not recorded by the beekeeper, fluctuating beekeeping practice). Heritability can also vary greatly from one generation to the next in small populations due to a decrease in genetic diversity as a result of selection.

The part of the phenotypic variance that is not of additive genetic origin can be attributed to unidentified environmental effects (e.g., causing epigenetic changes) or non-additive genetic effects (dominant effects, epistasis). As a result, heritability varies according to population, measurement conditions, environmental effects and statistical methods employed (i.e., model used for genetic evaluation). Indeed, environmental variability can be more or less strong depending on the region. Moreover, the same trait can have different biological causes depending on the population. If in one population honey production is particularly influenced by the ability to detect resources, in another it may depend more on flight capacity. This fact is very important because it

implies that the results obtained in a given population are not automatically transferable to another population. It is therefore necessary to perform population-specific heritability calculations in order to identify traits in the respective populations that can be improved by selection.

Genetic Evaluation of Individuals

In order to perform selection in a population, the candidates must be ranked according to a selection index that reflects the genetic potential of each individual. After that, it is possible to select the best individuals (e.g., the best 10 out of 100). This selection index, also called estimated breeding value, corresponds to the heritable genetic potential for the next generation, which is calculated based on the recorded performance and environmental effects (e.g., test environment). Moreover, the estimation of the breeding value of a queen or colony takes into account its own performance and the performance of the closest relatives (ancestors, siblings and offspring), whereby the relatedness between the different generations is determined on the basis of a pedigree (maternal and paternal origin). An animal whose close relatives (siblings, parents, offspring) show or have shown very high performance levels will potentially have a better estimated breeding value than an animal with the same own performance but whose relatives' performance is very poor.

The breeding value of an individual can be estimated even though it has no own performance, based on the recorded performance of the closest relatives and the relatedness. Following this principle, the breeding value of the offspring can be predicted based on the performance of the parents. The estimated breeding values of the parents can thus be used to rear and mate the following generations.

Different approaches can be applied to estimate breeding values in honey bees (Bienefeld et al., 2007; Brascamp & Bijma, 2014). In the statistical models, the effects of queens or workers on performance are investigated:

Model studying the observed performances as a function of queen identity:

Colony performance = average for the population
+ Genetic effect of queen of colony
+ Environmental effect
+ Residual effect

Model studying the observed performances as a function of the workers comprising the colony:

Colony performance = average for the population
　　　　　　　　　+ Average genetic effect of workers
　　　　　　　　　　 of colony
　　　　　　　　　+ Environmental effect
　　　　　　　　　+ Residual effect

Above a certain population size, it is also possible to jointly estimate queen and workers' effects in a single model.

The estimation of breeding values is routinely applied in livestock animals (cattle, sheep, goats, rabbits, pigs, fish and poultry) and named "genetic evaluation." Compared to aforementioned livestock animals, breeding value estimation is seldom applied in honey bees (e.g., Beebreed, www.beebreed.eu), as the honey bee has some peculiarities that complicate the calculation. Compared to other livestock animals, the performance of a colony is performed by thousands of individuals (i.e., the workers) that do not reproduce and are not individually identifiable either by their own performance or by their paternal origin. This circumstance is due to the complex mating biology of the queen, which can be mated by 10 to 20 drones. Only through targeted mating,

e.g., through special mating stations (Figure 8) or artificial insemination is it possible to record the paternal lineage.

Example of Application

Data and Model
The example below was adapted according to Guichard et al. (2020).

In this study, heritability estimates for the main traits of interest were calculated for two Swiss bee populations evaluated in the period 2010–2018. The populations were *Apis mellifera carnica* (Société Romande d'Apiculture, SAR, with a total of 1,009 tested colonies) and *Apis mellifera mellifera* (mellifera.ch), MEL, with a total of 1,071 tested colonies). The following traits were recorded in the two populations, namely honey production, gentleness, steadiness on comb, swarming tendency, hygienic behavior (pin test) and varroa infestation (infestation in spring and summer and growth rate between the two periods). In addition, the parental information of the queens/colonies was recorded in a pedigree file, tracing back up to 49 generations.

Based on this information, the heritability estimates (and the associated standard

errors) were calculated for the different traits, taking into account queen and worker effects, respectively. The corresponding heritability values and standard errors for all traits are summarized in Table 1.

Results and Discussion
The heritability estimates show that genetic improvement can be expected in the two populations only for a few traits (e.g., gentleness, steadiness on comb and hygienic behavior in the MEL population, and possibly honey production in the SAR population). For the majority of traits, the heritability estimates were very low or even zero (e.g., for varroa infestation growth rate). These low heritability estimates can have various causes, which are explained in more detail in the following section.

Important criteria for the heritability calculation are a complete pedigree over generations and a reliable recording of the performance data. The complete recording of the pedigree is often difficult in honey bee breeding, as there are always colony losses, which hamper relationship calculations between colonies and thus the breeding value estimation.

Most traits in honey bees are recorded by beekeepers as a note on a discrete scale.

◪ **Figure 8**. Controlled mating: Nucs containing initially virgin queens placed at a Swiss mating station with selected drones as part of a selection program (Photo: Matthieu Guichard, Agroscope).

The data distribution for gentleness and steadiness on comb in the SAR population, where half of the colonies were assessed with the top scores 3.5 and 4, shows that the current data collection is not optimal (hardly any variability between colonies can be detected): either the scoring system is not optimal, or the phenotypes have already reached their maximum with no possibility of further improvement. This current data collection is considered a possible cause for the low heritability estimates (Table 1).

The heritability estimates for honey yield are below average according to previously published data (mentioned in Guichard et al., 2020). A possible explanation for this result is the specific climate of Switzerland. Important for the honey production is the springtime harvest, which varies strongly in Switzerland every year. Furthermore, in summer, forest honey production is strongly influenced by temperature, humidity, and aphid populations and therefore varies sharply between the years. In addition, the high density of bees in some regions of Switzerland could promote competition between colonies located in the same apiary.

The importance of including the appropriate environmental effects in the model was demonstrated by the varroa infestation (spring, summer, and increase between the two periods), which is not heritable in the two populations. Currently, only the different location of colonies is included in the genetic analysis of varroa infestation, as it is assumed that colonies at the same apiary are subject to the same environmental conditions. However, this hypothesis does not consider possible transmission of varroa mite by robbing and drift between colonies at the same apiary or between colonies at different apiaries (DeGrandi-Hoffman et al., 2016; Frey & Rosenkranz, 2014; Frey et al., 2011; Peck & Seeley, 2019). The likelihood of robbing and drift increases with bee density, which, as mentioned above, is high in Switzerland. As these phenomena occur within a radius of several kilometers around the location of the test colonies, beekeepers are not able to consider these complex environmental effects in the recording/assessment of the trait. These unrecorded environmental effects may also be the reason why no heritability could be calculated for this trait in the two populations.

Levers for Genetic Improvement

Avenues of Genetic Gain and Limitations for Certain Traits

Honey bee breeding (or annual genetic gain) can be optimized through various measures (Figure 9). As already described in "Results and Discussion," successful selection is based on objective recording of breeding traits. In this context, it is necessary to optimize current test recording protocols and to develop new reliable methods (e.g., image-based analyses). Independent of these longer-term improvements, selection accuracy, (correlation between field measurement and breeding value) and selection intensity (smaller proportion of selected queens, i.e., proportion of red area under the curve in Figure 7) can be improved in the short- to mid-term. Artificial insemination, which is routinely used in many livestock animals, allows for a rapid increase in selection intensity, as this method enables the targeted selection of drones and their mating with the best queens. One of the main aims in animal breeding is to shorten the generation interval, which increases the genetic gain. Short generation intervals also limit the risk of losing the best queens before they are used for reproduction. Conversely, shorter generation intervals can decrease the amount of information recorded and taken into account for selection: for each trait, an optimum has to be found between the amount of information required and practical-breeding constraints. Traits with a good repeatability (high correlations between single observations) or being early predictors of others will favor shorter generation intervals, and will be preferred for selection.

Application at Beekeeper's Scale

Successful selection of honey bees is a complex process, where traits must be objectively recorded and the corresponding breeding values estimated for the queens. Based on this information, the best queens can be subsequently determined and selected for mating (Figure 10).

The first task of a breeding program is to define a breeding goal for the population

Table 1. Heritability estimates (h^2) and corresponding standard errors for the traits recorded in two Swiss honey bee populations (MEL and SAR).

Trait	MEL (*A. m. mellifera*)	SAR (*A. m. carnica*)
Honey production	WM: $h^2_W = 0.02 \pm 0.04$ QM: $h^2_Q = 0.10 \pm 0.06$	WM: $h^2_W = 0.11 \pm 0.06$ QM: $h^2_Q = 0.11 \pm 0.06$
Gentleness	WM: $h^2_W = 0.34 \pm 0.09$ QM: $h^2_Q = 0.32 \pm 0.08$	WM: $h^2_W = 0.02 \pm 0.03$ QM: $h^2_Q = 0.02 \pm 0.04$
Steadiness on comb	WM: $h^2_W = 0.16 \pm 0.07$ QM: $h^2_Q = 0.12 \pm 0.06$	WM: $h^2_W = 0.03 \pm 0.04$ QM: $h^2_Q = 0.09 \pm 0.05$
Swarming	WM: $h^2_W = 0.06 \pm 0.05$ QM: $h^2_Q = 0.07 \pm 0.05$	WM: h^2_W = not detected QM: $h^2_Q = 0.01 \pm 0.04$
Hygienic behavior	WM: $h^2_W = 0.19 \pm 0.08$ QM: $h^2_Q = 0.18 \pm 0.08$	WM: $h^2_W = 0.06 \pm 0.05$ QM: $h^2_Q = 0.09 \pm 0.06$
Growth of varroa population (*)	WM: h^2_W = not detected QM: h^2_Q = not detected	WM: h^2_W = not detected QM: h^2_Q = not detected
*Varroa in spring and summer: idem.		

The paternal and maternal ancestry was considered with the corresponding worker (WM) and queen (QM) model.

Annual genetic gain (in % of phenotypic standard deviation)

$$E(\Delta G) = (i * \rho * h)/T$$

with

i selection *intensity*
ρ selection *precision*
h root of *heritability*
T *generation interval*

Figure 9. Factors influencing annual genetic gain. The annual genetic gain increases with selection intensity (i), selection accuracy (ρ), heritability of the trait (h^2) and a short generation interval (T).

Figure 10. Production of mated queens via mating nucs as part of a selective breeding program (Picture: Matthieu Guichard, Agroscope).

or breed (for example, a significant improvement of gentleness in the next three generations). According to this aim, objective selection criteria must be established to ensure that variation exists between the individual colonies. Before recording a selection trait, the queens must be clearly identified to avoid that the queen is replaced by the colony before or during the test period (re-queening). In order to compare the performance of the colonies from different apiaries, closely related colonies (e.g., sister colonies) must be distributed among all test apiaries. Through this procedure it becomes feasible to assess the environmental effects of the location (geographical position, beekeeper, temperature, etc.) on the performance and to include these effects in the genetic evaluation model. The estimated breeding values can be used to compare the genetic potentials of the queens and to select the best ones for mating. Given the involved costs to host and evaluate population of sufficient size, collective programs clearly provide benefits in honey bee selection.

Conclusions

The studies of Mendel mentioned at the beginning of this review article still form the foundation of the theory of heredity today. However, the inheritance of many traits included in livestock-breeding programs is more complex and cannot be described with a model based on two genes and four alleles. In the past, it has been suggested to use such models for complex traits such as hygienic behavior (Rothenbühler, 1964). This approach does not allow meaningful results and raises expectations among beekeepers that do not correspond with reality.

Most traits are influenced by a lot of genes (polygeny). Therefore, the concepts of quantitative genetics should be applied in selection. The obtained results (heritability, breeding values, and genetic gain) are specific to the populations studied and cannot be transferred to other populations. For which traits of a particular population genetic gain is possible can only be determined with a careful evaluation of the field.

Selection is a complex and costly process and does not provide short-term solutions. Other processes (e.g., control of colony health state, beekeeping practice, treatments, etc.) solve some issues more quickly. For example, having an own nuc production can reduce the need to select non-swarming colonies. Another example: honey production can be increased more easily with a higher number of colonies or by migrating to areas with more honey resources than by selecting colonies that produce more honey. However, after adjusting the management of the apiary to the production target, a long-term genetic gain can be achieved by cumulating improvements from year to year. Selection then provides a long-term solution to improve performance in the apiary. This requires a rigorous framework to be effective: it is essential to record the routinely work (collection of performance data, etc.) and to promote partnerships between researchers, technical specialists, and beekeepers to guide this approach. If so, this genetic strategy enables successful selection of healthy and locally adapted honey bees.

Disclosure Statement

The authors report there are no competing interests to declare.

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