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Effects of various breeding strategies on diploid drone frequency and quantitative traits in a honey bee population

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Abstract When selecting in a finite population of honeybees there is a conflict between gain in a quantitative trait and increasing homozygosity, and therefore the frequency of inviable diploid drones. The consequences when using different mating, import, and selection strategies on diploid drone frequency and genetic gain, was explored with Monte Carlo computer simulations.

Within a closed population breeding structure, mass selection gave the highest genetic gain in the quantitative trait, but also the largest increase in percentage diploid drones and queens with unacceptably-low brood viability. Mass selection combined with truncation selection against queens having more than 15% diploid drones gave a comparable genetic gain and was the best strategy of the ones studied to avoid diploid drones. Within-family selection (one replacement per sib group) gave the least genetic gain, and a frequency of diploid drones comparable to random (no) selection. It was intermediate between mass selection and mass selection combined with viability selection concerning the frequency of diploid drones.

Insemination with pooled and homogenized semen originating from all breeder queens (30), as compared to natural mating with 12 randomly-selected drones, had little effect on the genetic gain and on the overall frequency of diploid drones (10 to 15% by generation 20).

The effect of opening the closed breeding population for the import of external queens every generation, by exchanging breeder queens of lowest performance with a corresponding number of new queens (5, 10 and 15 out of 30), was also investigated. Under mass selection (natural mating as well as artificial insemination) the frequency of diploid drones and the proportion of queens discarded were reduced because of low brood viability. However, artificial insemination was superior to natural mating considering the latter criterion. If the imported queens were at the same genetic level for the quantitative trait under selection as the whole breeding population at that generation, or 10% better, the genetic gain was respectively slightly reduced and approximately maintained. If the imported queens were of inferior quality (equal to the initial population) the import of queens slowed genetic progress considerably.

Key words *Apis mellifera* · Closed population
Diploid drones · Inbreeding · Genetic gain
Monte Carlo simulation

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Introduction

The worker population of a honey bee colony consists of different patrilines due to multiple matings of the queen with haploid drones originated from unfertilized eggs. Sex of honeybees is determined by a single multiallelic locus. Heterozygosity results in diploid females (workers or queens). Homozygosity at this sex locus results in diploid drones, but they are removed by the workers at the larval stage (Woyke 1963). Inbreeding, and thereby loss of sex alleles, may lead to weaker colonies with less honey-producing capability due to loss of larvae (Woyke 1980, 1981). This phenomenon may be an important factor explaining why few long-term breeding programs have been reported as being successful. Despite knowledge generated during the last decade (Chevalet and Cornuet 1982; Cornuet and Chevalet 1982; Moran 1984; Moritz; 1984, 1986; Page and Laidlaw 1982 a, b, 1985; Page et al. 1983, 1985), there is need for further theoretical work for optimal designs of honeybee breeding programs under a broad range of conditions. Using a Monte Carlo strategy we have developed a simulation program to predict the effects of various breeding strategies on the diploid drone frequency and on a quantitative trait. The program structure and some of the results it generates are presented. The objective was to establish a simple methodological foundation that can easily be extended to make possible the optimal design of hon-

eybee breeding plans when several single gene traits and polygenic traits are to be improved simultaneously.

Description of the simulation

Program structure

The simulation program follows the breeding structure: establishment of initial breeding population, queen and drone production, optional import of external queens, mating of the queens with drones contributed by all the breeder queens, selection, establishment of new breeder population, etc. Except for the optional import of external queens the structure is similar to the closed population breeding structure described by Page and Laidlaw (1982 a, b, 1985). Input parameters are number of generations of breeding; number of breeder queens in each generation (same for all generations); initial number of sex alleles in the population; number of matings per queen; number of daughter queens to be reared from each breeder queen in each generation (fixed for all generations); the heritability of the quantitative trait under study; the selection strategy to be used for each generation; the strategy for import of external queens; and the number of replicate runs for each initial parameter set.

The initial breeding population is established as follows. Each breeder queen has:

(1) two different sex alleles drawn from a uniform probability distribution;

(2) an additive genotypic value (G_i) of the polygenic trait obtained by sampling from a standard normal probability distribution N(0,1). For simplicity the initial additive genetic standard deviation is set to 1. Thus the value of the predicted genetic progress is given directly in terms of initial additive genetic standard deviations;

(3) a distribution of sex alleles in her spermatheca generated by drawing randomly one allele for each individual mating from a uniform probability distribution;

(4) an additive genotypic value for each of the queens (equivalent to sire) having contributed to her spermatheca through their haploid drones. It is assumed that the drones and the breeder queens initially are from populations having identical distributions of genotypic values. Thus the genotypic values associated with the sires are also distributed as N(0,1). (These values are algorithmically associated with specific sex alleles.)

The next generation is described by creating the specified number of daughter queens from each breeder queen. For each daughter queen, one sex allele is chosen randomly from the two carried by her mother (dam), and the other allele is chosen randomly from the sex alleles (sperm types) represented in the spermatheca of the dam. Homozygous sex alleles are not allowed. Each daughter queen is then given a genotypic value (G_i) by adding one half the value of the dam, one half the genotypic value of the sire chosen(i.e., one of the breeder queens in the previous generation), and a term representing the effect of allelic recombination,

$$G_i = 0.5\ G_d + 0.5\ G_s + G_a \quad (1)$$

where G_d and G_s are respectively the genotypic value of the dam and the sire. G_a is a stochastic variable representing the contribution due to allelic recombination. It is distributed as $(0.5c)^{1/2}N(0, V_a)$ where c is a factor adjusting for the effect of inbreeding on allelic recombination (Wright 1921; Foulley and Chevalet 1981). It is given by

$$c = 1–0.5\ (F_d + F_s) \quad (2)$$

where F_d and F_s are respectively the inbreeding coefficients of the dam and the sire. The additive genetic variance is set to unity ($V_a = 1$). To simplify, the mean value of the inbreeding coefficient for each generation is used. The mean inbreeding values are obtained by double tagging the initial sex alleles so that each type of sex allele in the initial population has ten different origins. For each of the queens in the whole breeding population in a given generation, the proportion of pairs of sex alleles drawn from respectively her genome and her spermatheca that are of identical origin is calculated. This proportion is interpreted as the mean inbreeding coefficient of the daughters (workers and queens) of the queen, and the mean value of the inbreeding coefficient for a given generation is determined as the mean for all queens. Using the mean values instead of using individual values leads to less-variable genotypic values and therefore more conservative estimates of the genetic progress.

The phenotypic value (P_i) of each queen is then determined by adding an environmental effect (E_i) to her genotypic value:

$$P_i = G_i + E_i \quad (3)$$

where E_i is a stochastic variable distributed as $N\{0,[(1–h^2)/h^2]\}$. The variance of the environment term follows directly from the definition of heritability [$h^2 = V_a/(V_a+V_e)$] when it is expressed in terms of the initial additive genetic variance (V_a). Environmental variance is considered stable throughout the generations of a simulation.

Two different mating strategies are given, representing respectively natural mating at a mating station and instrumental insemination with pooled and homogenized semen containing an equal share from the drones of each breeder queen (Kaftanoglu and Peng 1980; Moritz 1983). With natural mating each queen is mated by repeatedly randomly sampling a sire among the breeder queens for the specified number of times. In each sample one sex allele is chosen randomly from the two carried by the sire. In addition, each sex allele (or the sperm type associated with it) is given a genotypic value equal to half the value of the sire. With instrumental insemination each queen is mated as twice the number of breeder queens so that each of them contribute with both its sex alleles to the spermatheca of each new queen.

After finishing the mating, the program establishes the new generation of breeder queens by selecting on the phenotypic values according to the initially-chosen selection strategy.

If new material in the actual generation is to be imported, the program imports the specified number of queens by exchanging them with the breeder queens of lowest performance from those previously selected. Two options are given for assigning genotypic values to the new imported breeder queens. The first is to randomly select the values from the distribution of the genotypic variance of the quantitative trait of the initial population. This option simulates the effect of importing new queens without taking their genotypic value into account. The second option is to let the new breeder queens have phenotypic mean values in a specified proportion (r) of the mean phenotypic value of the whole breeding population before selection for the actual generation. The genotypic value (G_i) of each new imported queen is then calculated as

$$G_i = r\bar{P} + G_{imp} \quad (4)$$

where P is the mean phenotypic value of the breeding population before selection (i.e., an estimate of the genotypic value), and G_{imp} is a stochastic variable with the same variance as the initial additive genetic standard deviation [i.e., as N(0,1)].

Imported queens are given sex alleles by randomly selecting two alleles for each queen from the initial sex allele distribution. The spermathecae of imported queens are given the same sex allele distributions as the selected breeder queens they replace. This condition mimics a procedure where candidates for import are mated with the same drone material as the other breeder queens.

After the selection and import processes have been completed, the program uses the selected queens to establish a new breeding population and it performs the breeding, mating, import, and selection routines in the offspring population. This is done for the specified number of generations. The whole process is repeated with identical initial parameter values in the first generation for a specified number of replications.

Parameter values and breeding strategies used in the simulations

The results reported below were based on the following parameter values: number of generations of breeding = 20; number of breeder queens in each generation = 30; number of daughters per breeder queen in each generation = 5–20; initial number of sex alleles = 15 (Adams et al. 1977; Cornuet and Aries 1980); initial genetic variance $V_a = 1$; heritability of the quantitative trait = 0.3. A fixed value of h^2 was used in all simulations. In order to predict the genetic progress of a trait with moderate heritability the value was set to 0.3.

Estimates of heritabilities for honey production seem to average about this value (Pirchner et al. 1962; Vesely and Siler 1963; Soller and Bar-Cohen 1967; Bar-Cohen et al. 1978; Bienefeld and Pirchner 1990).

The mating strategies were artificial insemination with pooled and homogenized semen from drones provided by all breeder queens, as well as natural mating. In the case of natural mating the number of matings per queen was fixed and set at 12 (Koeniger 1986) for most simulations. In general it was also assumed that the breeder queens contributed equal numbers of drones to the drone pool and that the drones had an equal probability of mating with a virgin queen. However, in one study these premises were relaxed by varying the number of matings randomly between 8 and 15, and by letting each breeder queen's relative contribution to the common drone pool vary randomly within a range of 1 to 20.

Four different selection strategies were studied. These were within-family selection by selecting the daughter queen with the highest phenotypic value for each breeder queen (within family), mass selection by selecting the new breeder queens ignoring familial relationships (mass), mass selection combined with selection for high brood viability (so that no new breeder queens were allowed to give a frequency of diploid drones greater than 0.15) (mass + viability), and finally random selection of new breeder queens (random). The limit 0.15 was chosen according to apparent practice in a commercial closed population breeding program (Cobey and Lawrence 1988). See the Discussion for further details.

Three import strategies were studied, the imported breeder queens (5, 10 and 15) having either a genetic mean value as in the original base population, or equal to the actual breeding population, or at 110% of the mean of the actual breeding population. The import was performed every generation.

The number of replicate runs for each initial parameter and strategy set was 20.

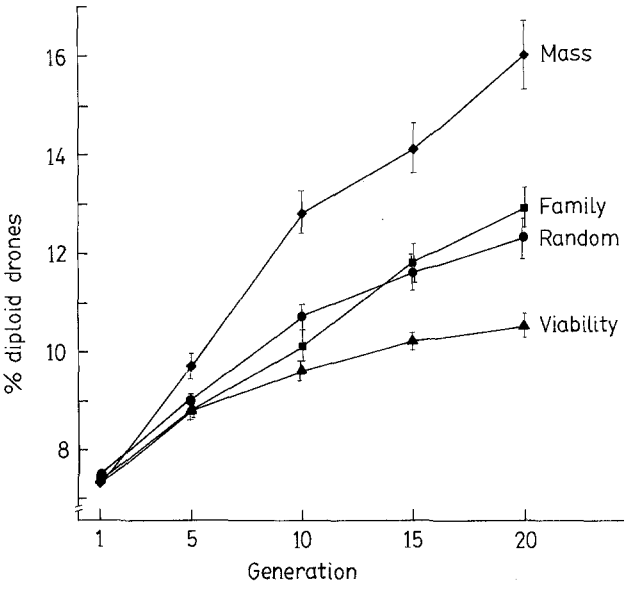

Fig. 1 Average percentage diploid drones (±SE) per colony for the given generations with 30 breeder queens, each contributing 15 daughters for testing in each generation, 15 sex alleles of equal frequency in the initial population, a heritability of 0.3, and natural mating at an isolated mating station was performed with 12 matings per queen. *Family*, *Mass*, *Viability* and *Random* represent respectively: within family selection, mass selection, mass selection combined with selection for brood solidness (> 85% brood viability), and random selection. The results are based on 20 repetitive runs with the same parameter set

Results

The program predicts that within a closed population breeding program (CPBP) pure mass selection gives the largest increase of the proportion of diploid drones, whereas mass selection combined with selection for high brood viability gives a frequency of diploid drones even less than random selection (Fig. 1). Furthermore, insemination with pooled and homogenized semen is predicted to have no significant effect compared to natural mating under these circumstances (data not shown).

For many of the strategies (selection and mating) the average percentage of queens (±SE) in the test population within a CPBP that will have a brood viability less than 85% in a given generation is predicted to be of the order of a 2% increase per generation (Fig. 2). After ten generations of natural mating and mass selection, nearly 40% of the queens will have values beyond the limit. Note that insemination with homogenized semen delays the process for many generations. But, except for mass + viability selection, the difference between natural mating and instrumental insemination is marginal after 20 generations. For mass + viability selection the insemination strategy is predicted to give a considerably better result than natural mating up to at least 20 generations. Results for the insemination strategy fluctuate more than for natural mating, which is indicated by larger standard errors for this trait.

When relaxing the mating premises in the case of natural mating by letting the number of matings per queen

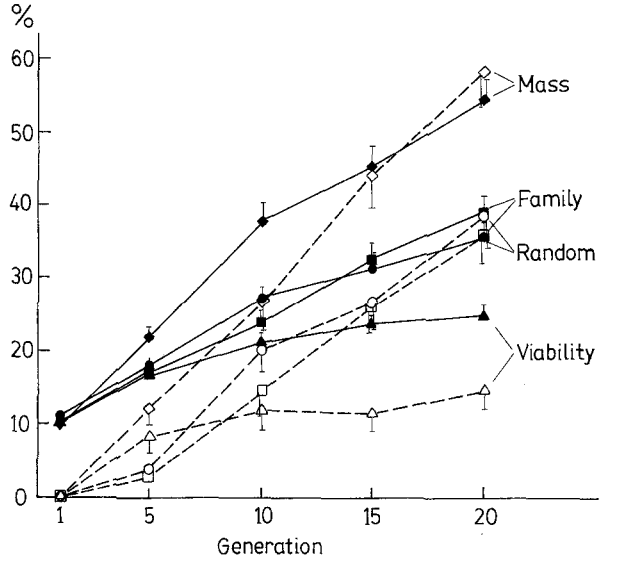

Fig. 2 Average percentage of queens (±SE) from the test population that will have more than 15% diploid drones among its progeny at given generations. *Solid marks* correspond to natural mating, *open marks* to instrumental insemination with pooled and homogenized semen contributed by the 30 breeder queens. See legend to Fig. 1 for further information

vary randomly between 8 and 15 (instead of 12), and letting each breeder queen's relative contribution to the common drone pool vary randomly between 1 and 20 (instead of being equal), the program predicts only slightly differ-

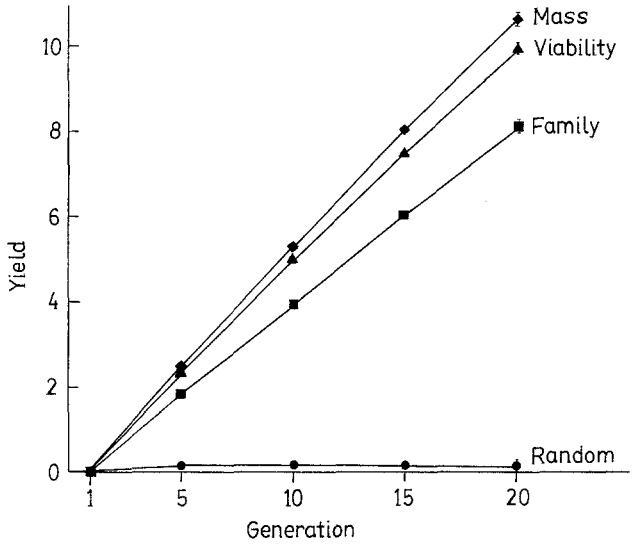

Fig. 3 Expected genetic gain (±SE) in a quantitative trait for the specified generations with natural mating. Measures are in units of the additive genetic standard deviation of the initial population. See legend to Fig. 1 for further description of parameter values

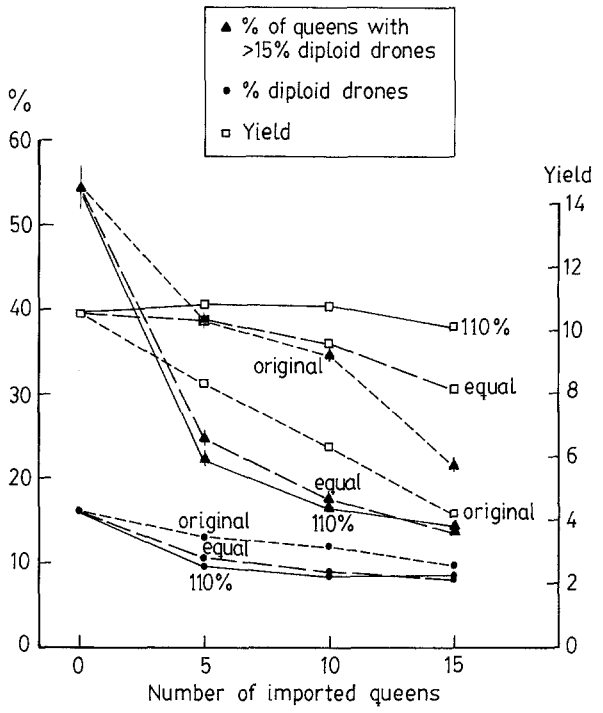

Fig. 4 Effect of importing new genetic material. Mean percentage of diploid drones (±SE), the mean percentage of queens (±SE) that have more than 15% diploid drones among their progeny, and the expected mean genetic gain (±SE) of a single quantitative trait after 20 generations of mass selection is given. Information from Figs. 1, 2 and 3 at the 20th generation is given as a reference (0 queens imported). Results are given for imported breeder queens having either a genetic mean value as in the original base population, or equal to the actual breeding population, or at 110% of the mean of the actual breeding population. Imported queens were mated with drones from the same population as the other breeder queens. General parameters are described in Fig. 1. The selection strategy was mass selection. There was import of new genetic material each generation. When the SE was smaller than the mark in the Figure, it was not drawn

ent results. For example, in is case of mass + viability selection the effect on the percentages of diploid drones is < 1% and the proportion of queens that have a brood viability less than 85% are < 4% (data not shown).

A somewhat counter-intuitive prediction is that there is a marginal difference between pure mass selection and the mass + viability selection strategies concerning expected genetic progress within a CPBP (Fig. 3). As expected from Page and Laidlaw (1985), and predicted by Moritz (1986), the genetic progress of within-family selection is predicted to be somewhat less than for mass and mass+viability selection. But the difference is not large. Insemination with pooled and homogenized semen gave genetic gains not significantly different from natural mating (data not shown).

By varying the number of daughters tested per breeder queen, and keeping the number of breeder queens constant at 30, it was found that between 15 and 20 daughters per breeder queen seem to be sufficient to harvest most of the potential genetic progress under the given circumstances (after 20 generations), not considering testing costs (data not shown).

The mean percentage of inbreeding of the queens in the test populations after 20 generations was found to vary between 10 and 15% (data not shown) in accordance with Fig. 1.

As expected, import of queens every generation reduced the frequency of diploid drones and the proportion of queens discarded because of low brood viability (Fig. 4). If the queens imported were at the same genetic level for the quantitative trait under selection as the breeding population, or 10% better, the genetic gain was slightly reduced or approximately maintained. If the queens were of inferior quality (equal to the initial population) the import of queens slowed genetic progress considerably.

The effect of equipping each imported breeder queen with sex alleles randomly selected only among those alleles that had been lost from the population gave results very similar to those depicted in Fig. 4 (data not shown).

Very little difference for mean percentage of diploid drones and genetic gain was found when making use of artificial insemination instead of natural mating. However, there was a dramatic reduction of the number of queens with brood mortality greater than 15% (data not shown).

Discussion

The program employed does not account for the fact that a trait such as overall honey production is likely to decrease with decreasing brood viability. However, the percentage of diploid drones may have to reach a considerable level before it has any detectable impact on honey production.

Woyke (1980) found no difference in honey production between colonies with 75% and 100% brood viability despite the fact that the former group had only 93% of the worker population in summer compared to the latter. This indicates that the acceptable level of diploid drones may be increased somewhat compared to our 15% limit. The mean percentage of queens in the test population that will have more than 25% diploid drones among their offspring is dramatically lower compared to keeping the level at 15% according to our program. However, Woyke's results may be somewhat misleading since the observations were made on rather weak colonies (30 000 bees for the 100% group) and under poor honey-flow conditions compared to ordinary conditions in many places (12 kg surplus honey). Under what is characterized as bad conditions, the differences due to brood viability are more pronounced (Woyke 1981). These experiments should therefore be repeated with stronger colonies under good as well as bad honey-flow conditions. If a significant inverse relationship exists between honey production and percentage of diploid drones under favourable conditions, a compensation for this should be in the form of an additional term in equation (3) accounting for the loss of honey production as a function of brood viability. This can be done with the help of a model of honey production dynamics (Omholt 1986, 1992). It is worthwhile to note that by not accounting for such a relationship the predicted brood viability would be lower than what would be the case when honey production is the trait that was actually selected for. For traits such as defensive behaviour, such a lack of compensation is unlikely to play a significant role, but with regard to the tendency of swarming it may be of some importance.

Furthermore, if there is an inverse relationship between the quantitative trait and brood viability, a lack of compensation may mask the fact that the mass + viability selection strategy described will outperform pure mass selection in a real breeding program since several thousand more bees may be present in the colonies selected with the former strategy.

Concerning the slight effect of relaxing the mating premises with respect to drone contributions, it should be noted that these results are based on the assumption that the quantitative trait being selected for is not linked to traits determining the number of matings, or which drones mate with the queens. In this case the differences will certainly be somewhat greater and it may mask the real difference between natural mating and insemination. As long as there are no data that may help to resolve this issue it would be premature to incorporate such a connection in the program.

The program does not account for the possibility of interaction between genotypic value and environment. If such interaction is important then the way phenotypic values are calculated for the new queens in each generation is misleading. This may cause the program to select queens that would not have been selected for under real-life conditions. This phenomenon is apparently a real one (Milne 1985), but due to paucity of data there is no reason at this stage to try to model it properly. It should be noted that within-family selection may be better than mass or mass + viability selection in this respect because within-family selection will avoid loss of genotypes that will not perform very well under a wide range of environmental conditions.

The program considers the quantitative trait to be analogous with an ordinary morphological trait of the queen. This is of course a simplification. A colony trait should rather be thought of as the sum of the direct effect of the queen, the contributions of the workers, and the effect of the environment (Chevalet and Cornuet 1982). Assuming the same patrilines for the colonies, however, it can be shown that the genetic variance among colonies is mainly due to queen genotype, and not the genotypes of drones with which she mated (see Appendix).

It should be noted that even though the genotypic value of the queen may be more confounded with the paternal component of the genotype of the worker bees with natural mating (Page and Laidlaw 1985), the heritability values will not be very different from instrumental insemination.

Trusting average values obtained from a simulation may be dangerous when it comes to practical implementation and one should be careful not to violate too many central premises of the program. For example, it may turn out that by using advanced statistical techniques when analysing the test data, one may outperform the program in selecting the best queens. In order to test the program's efficiency in this connection the number of daughters selected from each breeder queen was registered for mass selection and for mass + viability selection, both with natural mating, for several single runs with the parameter set described in the legend to Fig. 1. It turned out that up to seven queens were selected from a single breeder queen, but that the number of contributing breeder queens never fell below 14 out of a total number of 30.

Very few breeding programs will go on for 20 generations. The consequences of a breeding strategy after five generations may be more relevant for practical purposes. For example, the use of artificial insemination to avoid unacceptable proportions of queens discarded for brood viability reasons could be desirable, even if this is not ultimately a better strategy.

A convenient feature of the Monte Carlo approach presented here is that it combines the population genetics and the quantitative genetics of honeybees in a simple way compared to more classical approaches, while at the same time being flexible enough to handle a whole range of conditions encountered in practical bee breeding. For example, due to its basic structure our simulation program can rather easily be expanded to include options for mating with drones obtained from a single or a few colonies inside or outside the breeding population, as well as options for simultaneous selection of single gene traits and several polygenic traits with positive as well as negative genetic correlations. In this way, considerable insight into honeybee breeding may be obtained by moderate effort.

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Appendix

A honeybee colony trait (h) may be thought of as a sum of contributions (Chevalet and Cornuet 1982) from the direct genotypic effect of the queen (Q), the mean of the workers' genotypic contribution ($\bar{W}$), and the sum of the environmental effects on the colony trait (E), so that $h = Q+\bar{W}+E$. The variance of the colony trait [var (h)] (including only the additive terms of Chevalet and Cornuet) is then equal to var (Q) + cov (Q,W) + 2 $\bar{\varphi}$ var (W) + var (E), where the first term is the variance of the direct queen effect, the second the covariance term defined to be the additive genetic covariance between the queen and worker trait within one diploid individual, the third the variance of a worker's additive contribution to the total variance multiplied by a coefficient 2 $\bar{\varphi}$, and the last term is the variance of the environment contribution to the colony trait.

The coefficient is dependent on the effective number of drones mated to the queen (f), and on their mean kinship coefficient (θ) (Chevalet and Cornuet 1982), so that $2\bar{\varphi} = [3+(f-1)(1+2\theta)]/4f = 1/4 + (1+(f-1)/2f]$. Their expression is here split into the contribution of the queen (1/4) and the contribution of the drones (last term) to the variance of the workers' mean genotype.

If one queen is the mother of all workers, her contribution is always 0.25 of the worker trait variance. If the number of drones mated to a queen increases, or they are less related, the drones' contribution to the between-colony variance is reduced. The two terms are equal if the effective number of drones is two per queen for unrelated drones ($\theta=0$).

With 30 breeder queens the kinship coefficient is primarily dependent on the inbreeding coefficient in the actual population, the average kinship being introduced because of the limited number of queens contributing drones being only 1/60. Assuming an inbreeding coefficient somewhat less than 10%, the kinship coefficient may therefore be set to $\theta=0.10$. With f = 12 drones per queen, the drones' contribution is then 0.09 of the worker trait variance, compared to the queen's 0.25. With instrumental insemination f = 60, and the drones' contribution is even less.

The overall genetic variance of the colony trait is therefore likely to be dominated by the queen's genotype, firstly through her direct influence on the trait, secondly through the genetic covariance of the queen trait and the worker trait (which may be positive or negative, but always less than the variance of either trait), and thirdly by contributing much more of the direct genetic variance of the workers compared to the drones.

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