

Genetic Correlations Among Several Colony Characters in the Honey Bee (Hymenoptera: Apidae) Taking Queen and Worker Effects into Account

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ABSTRACT In the honey bee, in which the castes depend upon one another, most colony traits may be composed of queen as well as worker effects. The contributions of these two castes were found to be heritable for several characters of economic value. If two colony traits are each composed of queen and worker effects, the genetic correlation between them is therefore composed of the genetic correlation between the queen (r_{Q12}) and the worker effects (r_{W12}), respectively, and the cross-correlation (r_{QW12}) between the queen effects of trait 1 and the worker effects of trait 2 (and reverse). Genetic correlation between partial honey yields within years were estimated to be medium or, between spring and summer productivity, even negative. The genetic relationships between honey and wax production were high ($r_{Q12} = 0.75$, $r_{W12} = 0.72$) but with a negative cross-correlation ($r_{QW12} = -0.86$). Insignificant genetic correlations between honey production and aggressiveness were found (-0.06 , 0.03 , 0.11); the corresponding estimates between honey production and calmness during inspection were even positive (0.31 , 0.36 , -0.34). A selection index simultaneously improving queen and worker effects of several colony traits is proposed.

KEY WORDS Insecta, *Apis mellifera*, genetic correlation, selection indices

RECORDED COLONY CHARACTERS such as honey production and aggressiveness reflect queen effects (laying capacity, pheromone production, etc.) as well as worker effects (hoarding behavior, production of and responsiveness to alarm pheromones, length of life, etc.). Because the common methods (parent-offspring regression, sib analysis, realized heritability) of estimating heritabilities (h^2) and genetic correlations (r_g) do not permit taking this composed character of the colony traits into account, two approaches were used.

Either the estimations of these genetic parameters were restricted to individual queen or worker characters (e.g., corbicular area), which are expected to show a high correlation with the performance of the entire colony (Rinderer et al. 1983; Collins et al. 1984, 1987; Milne 1985a,b,c) or, in the case of colony traits, the influence of one caste was neglected (Pirchner et al. 1962, Soller & Bar-Cohen 1967, Böger 1969, Bar-Cohen et al. 1978, Oldroyd et al. 1987).

Chevalet & Cornuet (1982) proposed considering colony characters in the honeybee as composite traits influenced by both queen and worker bees. An analogy exists in mammals, where traits such as weaning weight depend on the offspring, whose growth is measured, and on its dam, who furnishes the environment during development. Willham

(1963) developed a model that fits this situation, permitting simultaneously the estimation of h^2 values for maternal and offspring influences. Modifying this model to the characteristics of the honey bee, Bienefeld & Pirchner (1990) estimated heritabilities for queen and worker effects for several colony traits. If heritable queen and worker effects influence colony traits, both effects must be taken into account to estimate genetic correlations between such traits.

The objective of the present study was to develop an appropriate method for the estimation of these genetic parameters and the derivation of a selection index suited for honey bees.

Materials and Methods

The breeding societies in Hannover, Weser-Ems, and Hamburg (Federal Republic of Germany), and the Bee Research Institutes in Celle and Kirchhain (Federal Republic of Germany), and Lunz (Austria), provided the data from 5,581 controlled, mated (island mating or artificial insemination) *Apis mellifera carnica* Pollmann colonies from 1960 to 1984. Honey production ($n = 5,342$ records), wax production ($n = 1,724$), the subjective judgment of aggressiveness ($n = 2,770$), calmness during inspection ($n = 2,764$), and spring development ($n = 2,177$) were recorded in accordance with the technical recommendations for performance testing in honey bees as summarized by Ruttner (1972). The scoring system for aggressiveness, calmness during inspection, and spring development ranged

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from 1 (worst) to 4 (best). Details of the traits measured and their descriptive statistics are given by Bienefeld et al. (1989). The breeding society in Hamburg and the institute in Celle provided additional information about the partitioning of the entire honey yield in the spring ($n = 1,890$), summer ($n = 1,872$), and autumn ($n = 1,066$) yields.

The queens were mated by drones (average 6) of drone-producing sister queens on island mating stations. Polhemus et al. (1950) pointed out that haploid drones can be considered a random sample of identical gametes of their female parent; thus, this female is equivalent to a sire in regular diploid animals. Under such a mating system, it is not possible to assign a female (queen or the "average" worker of a colony) to a single (of several) drone-producing queens. However, because their dam is unique, she is denoted as "sire" (actually "grand-sire") in the pedigree. A total of 5,581 queens was descended from 698 dams (DQ, dams of queens) and from 231 so-called "sires" (SQ, sires of queens) and were mated to drones from 275 sires (SW, sires of workers). Details of the mating scheme of the population analyzed are given by Bienefeld et al. (1989) and Bienefeld & Pirchner (1990).

If two traits are influenced by both queen and worker effects, the calculation of the genetic correlation between these two traits requires the extension presented in Fig. 1. The genetic correlation between the queen effects (r_{Q12}) and the worker effects (r_{W12}), respectively, and the cross-correlation (r_{QW12}) between the queen effects of trait 1 and the worker effects of trait 2 (and reverse, $r_{QW12} = r_{WQ12}$) are computed as

$$r_{Q12} = \frac{\sigma_{Q12}}{\sigma_{Q1} \cdot \sigma_{Q2}} \quad (1)$$

$$r_{W12} = \frac{\sigma_{W12}}{\sigma_{W1} \cdot \sigma_{W2}} \quad (2)$$

$$r_{QW12} = \frac{\sigma_{QW12}}{0.5(\sigma_{Q1} \cdot \sigma_{W2} + \sigma_{Q2} \cdot \sigma_{W1})} \quad (3)$$

where σ_{Q1} , σ_{W1} , σ_{Q2} , and σ_{W2} denote the genetic standard deviation of queen (Q) and worker (W) effects of traits 1 and 2, respectively; and σ_{Q12} and σ_{W12} the covariances between traits 1 and 2, respectively, due to queen and worker effects. σ_{QW12} is the covariance between the queen effects on trait 1 and the worker effects on trait 2 (and reverse, because $\sigma_{QW12} = \sigma_{QW21}$).

The genetic variances and covariances used in formulas 1, 2, and 3 are calculated by a modified method originally proposed by Willham (1963) for estimating heritabilities for composite characters in mammalian species. The maternal (queen effect) genetic influence contributes an environmental effect to the offspring (average worker), but it is also genetic in the sense that the genotypic differences among dams are expressed in the phenotypes of their offspring (Chevalet & Cornuet 1982). Therefore, the phenotypic expression will be influenced

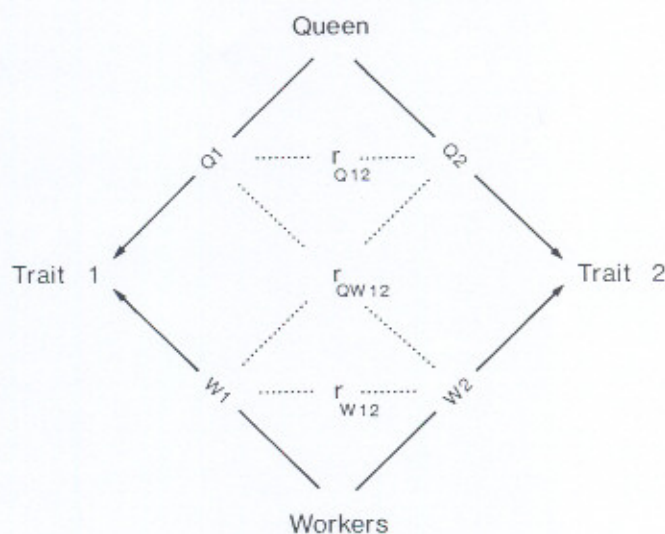


Fig. 1. Genetic correlations if queen and worker effects are involved. Q1, Q2, sum of queen's influences on traits 1 and 2, respectively; W1, W2, sum of worker's influences on traits 1 and 2, respectively; r_{Q12} , genetic correlation between Q1 and Q2; r_{W12} , genetic correlation between W1 and W2; r_{QW12} , genetic correlation between Q1 and W2 or W1 and Q2 (cross-correlation).

by two genetic components which result in a covariance between trait 1 of two colonies (P_{X1} and P_{Y1}):

$$\text{Cov}(P_{X1}, P_{Y1}) = a_{X1}\sigma_{W1}^2 + (a_{X2} + a_{YV})\sigma_{QW1} + a_{WV}\sigma_{Q1}^2 \quad (4)$$

Dominance and epistatic effects are assumed to be zero. σ_{W1}^2 and σ_{Q1}^2 symbolize the additive genetic variances for worker and queen effects with respect to trait 1 and σ_{QW1} the additive covariance between these components. The coefficients a_{YX} , a_{XZ} , a_{YV} , and a_{WV} are twice Malecot's (1948) "coefficient de parente" between two randomly chosen workers (X and Y) of different colonies, between the two dams of these workers (V and Z, where V is the dam of workers X and Z is the dam of workers Y), and between the workers of one colony and the queen of the other and vice versa ($a_{YV} = a_{XZ}$). To estimate the three genetic parameters (σ_{Q1}^2 , σ_{W1}^2 , σ_{QW1} or σ_{Q2}^2 , σ_{W2}^2 , σ_{QW2} , respectively) with respect to one trait, at least three different kinds of relatives are required. The structure of the data allowed the estimation of the following four covariances:

- (1) Cov(pHS), covariance between colonies related by the same SW;
- (2) Cov(mHS), covariance between colonies related by the same DQ;
- (3) Cov(O, DQ), covariance between DQ and offspring colonies;
- (4) Cov(O, SW), covariance between SW and offspring colonies.

Covariances 1 and 2 are estimated directly by computing the covariance between ancestors' performance and the weighted (Searle 1971) offspring mean, both corrected for environmental effects (location within year and bee breeder). Observational

Table 1. Theoretical causal components of computed covariances^a

Covariances	Components		
	σ^2_W σ_{W12}	σ^2_Q σ_{Q12}	σ_{QW} or σ_{QW12}
Cov(pHS)	0.1306	0.0000	0.0000
Cov(mHS)	0.0742	0.2968	0.2968
Cov(O, DQ)	0.2134	0.5000	0.6767
Cov(O, SW)	0.2134	0.0000	0.2500

^a Six drone-producing queens per island mating station (notes from the bee breeding societies) and eight drones per queen (Laidlaw 1974, Woyke 1985).

components 3 and 4 are estimated by the "restricted maximum-likelihood" method (Patterson & Thompson 1971) using an SAS (SAS Institute 1985) routine. The statistical model included SQ, DQ within SQ, and SW in addition to environmental effects. Location within year and bee breeder and SQ were considered fixed effects; all others were random. Because of nonnormal distribution, the subjectively scored traits were transformed (e^{variable}).

The expectation of the covariances (see equation 4) in terms of causal components are summarized in Table 1. The coefficients of genetic relationship of the four types of relatives are computed with regard to the peculiarities of bee reproduction and to the circumstances at the island mating stations. Details of the computation are given by Bienefeld et al. (1989).

The causal components (genetic variances and covariances) are estimated as elements of the vector:

$$b = (X'V^{-1}X)^{-1}X'V^{-1}y, \quad (5)$$

where the coefficients in Table 1 are used as a design matrix X; the observational components Cov(pHS), Cov(mHS), Cov(O, DQ), Cov(O, SW) are used as an observation vector y, and the variances of the observational components are used as the diagonal elements of the square matrix V, with off-diagonal elements all zero except for the covariance between pHS and mHS. To estimate σ_{W12} , σ_{Q12} , and σ_{QW12} , only a slight modification of the procedure described above should be considered. In this case, the observation vector y contains covariances between different traits. Because the same

types of relatives are used to estimate these covariances, the same design matrix X (Table 1) can be applied.

Ancestor-offspring covariance between different traits were computed as:

$$0.5[\text{Cov}(A_1, O_2) + (A_2, O_1)], \quad (6)$$

where A_1 and A_2 are the performances of the ancestor colonies with respect to traits 1 and 2, respectively, and O_1 and O_2 are the corresponding means of their offspring colonies. The different numbers of offspring colonies per ancestor were weighted as suggested by Searle (1971).

Covariances between different traits of the so-called paternal (pHS) and maternal (mHS) half-sibs were estimated by a MANOVA procedure (SAS Institute 1985) applying the model given for estimation of covariances of one trait. The variances (variances of bilinear forms) of the estimates, used as diagonal elements in V, were also calculated by the method of Searle (1971). The standard errors of the genetic parameters (r_{Q12} , r_{W12} , r_{QW12}) were approximated by a method given by Kendall & Stuart (1969) using Taylor series.

Solving of the equations of the type given in formula 5, the weighted ancestor-offspring covariances and standard errors of the genetic parameters were programmed using SAS (SAS Institute 1985) matrix routines.

Results

The genetic relationship between the partial yields of honey performances are given in Table 2. The genetic correlations of queen and worker effects were low to medium and negative in the relationship between spring and summer performances. The covariances between queen and worker effects (cross-correlation) of these partial yields were positive, whereas the corresponding estimates for the other combinations were zero or negative. The genetic correlation between the queen and worker effects of honey and wax production were distinctly positive but were negative between queen and worker influences on the other trait (Table 3).

All three genetic correlations between honey production and aggressiveness were close to zero.

Table 2. Genetic correlations between partial honey yields

Honey flow season	Genetic correlation ($r \pm SE$)			
	Summer		Autumn	
	Worker	Queen	Worker	Queen
Spring				
Worker	-0.45 ± 0.38	0.38 ± 0.39	0.35 ± 0.28	-0.49 ± 0.37
Queen		-0.43 ± 0.44		0.65 ± 0.48
Summer				
Worker			0.02 ± 0.15	-0.06 ± 0.20
Queen				0.17 ± 0.25

Table 3. Genetic correlations between honey production and other traits of economical importance

Colony characters	Genetic correlation		
	$r_w \pm SE$	$r_Q \pm SE$	$r_{QW} \pm SE$
Wax	0.72 \pm 0.64	0.75 \pm 0.74	-0.86 \pm 0.66
Aggressiveness	0.03 \pm 0.52	-0.06 \pm 0.69	0.11 \pm 0.58
Calmness	0.36 \pm 0.35	0.31 \pm 0.64	-0.34 \pm 0.48
Spring development	-0.03 \pm 0.44	0.18 \pm 0.64	-0.03 \pm 0.52

The genetic correlation between honey production and calmness were, except in the case of the cross-correlation, positive. Spring development does not show much genetic relationship to honey production.

Discussion

There are always many more difficulties in estimating genetic correlations with satisfactory small standard errors than heritabilities (Pirchner 1979). This holds especially true in our case, characterized by (for this purpose) a relatively small data set and (compared with the standard method) the rather involved estimation. The genetic correlations estimated show large standard errors, permitting one only to judge tendencies. However, corresponding with the results shown in Table 2, Soller & Bar-Cohen (1967) also found, by conventional estimation methods, phenotypic (-0.16) as well as genetic (-0.3) negative relations between spring and summer honey production.

Generally, Dickerson (1962) pointed out that genotype-environment interaction, also found in colony performances of honey bees (Louveaux et al. 1966, Bar-Cohen et al. 1978), tend to lower genetic correlations. The adaptability of colonies with prolific or economic, early, or deferred colony development depends strongly on the actual honey flow condition (Böger 1969), which causes this genotype-environment interaction and therefore problems in breeding of a multipurpose honey bee (Louveaux et al. 1966).

In addition, a greater susceptibility to nosema (Adam 1982) and increased swarming tendency (Ruttner 1983) of early-developing colonies, which may depress the colony performance in later honey flow periods, reduce the usefulness of such genotypes.

The genetic correlations between queen and worker effects of honey and wax production, respectively, are expectedly highly positive but are distinctly negative with respect to the cross-correlation between queen and worker effects. Bienefeld & Pirchner (1990) found medium heritabilities and a strong negative correlation between queen and worker effects for honey ($r_{QW1} = -0.88$) and wax production ($r_{QW2} = -0.96$), respectively. These strong negative relationships between queen and worker effects on identical characters in combination with the positive correlation between the queen ($r_{Q12} = 0.72$) and worker effects ($r_{W12} = 0.75$)

of honey and wax production, result in this negative cross-correlation ($r_{QW12} = -0.86$).

Also, Sugden & Furgala (1982) considered as faulty the belief of some beekeepers that aggressiveness and productivity of honeybees are related. So far, only the lack of this relationship has been published (Sugden & Furgala 1982, Szabo 1982, Bienefeld 1989). This low phenotypic relationship between these most important characters in honey bee breeding involved an insignificant genetic correlation (Table 3). The genetic correlation between honey production and calmness during inspection was positive, which raises hopes for breeding gentle and productive honeybees without the difficulties to be expected from antagonistic relationships.

However, there are certainly some problems, which can be summarized as follows:

- The selection should be applied to the improvement of queen and worker effects simultaneously (Chevalet & Cornuet 1982).
- There are negative correlations between queen and worker effects for colony characters, lowering selection response for each trait (Bienefeld & Pirchner 1990).
- Several colony characters (honey production, aggressiveness, calmness during inspection, swarming tendency, winter hardiness, etc.) must be considered, each having a different importance to beekeepers (Bienefeld 1987).
- Genetic correlation between queen and worker effects of different selection traits and the corresponding cross-correlations should also be considered.

Cornuet & Chevalet (1987) published a selection index for the improvement of one trait which makes use of additional (honey performance) information from related colonies. However, the optimum selection criterion, when several characters are to be improved, was derived by Smith (1936) and Hazel (1943). The objective of selection is referred to as "merit," and the breeding value for merit is to be symbolized by I . The selection index to be constructed for the improvement of merit is

$$I = b_1P_1 + b_2P_2 + \dots + b_mP_m,$$

where P_m are phenotypic measurements of m characters on which selection is to be based, and b_1 to b_m are the corresponding weighting factors to be determined. Information from relatives can be included in the index, so that P 's can be measurements from relatives. Based on a paper by Henderson

(1963), Van Vleck (1970) extended the selection procedure for several economic traits each having direct (e.g., calf effects with respect to the trait weaning weight) and maternal (influence by its dam) genetic components. Analogous to the modification of Willham's (1963) model for estimation of genetic parameters in honeybees, the index variant of Van Vleck (1970) permits a selection procedure considering queen and worker effects of several colony traits simultaneously. Selection involving m colony characters, each with a worker (g_w) and a queen (g_Q) genetic components, is assumed to be for total genetic economic value defined as $H = v'g$, where g can be represented as a $2m \times 1$ partitioned vector of genetic values; i.e.,

$$g' = (g_1 | g_2 | \dots | g_m) \text{ with } g_i = (g_{wi} | g_{Qi}),$$

where each g_i consists of values for worker and queen genetic effects for trait i , and v as the corresponding $2m \times 1$ partitioned vector of economic values; i.e.,

$$v' = (v_1 | v_2 | \dots | v_m) \text{ with } v_i = (v_{wi} | v_{Qi})$$

are economic values for worker and queen genetic effects for each trait.

Available for use in selection are measurements on the m traits for N relatives. For convenience, only the case where the same traits are used for information that is economically important will be considered. Other traits (e.g., spring development) could also be used, and extension to those situations is not difficult. Thus the data vector x , a $mN \times 1$ vector, can be described by the partitioned vector:

$$x' = (x_1 | x_2 | \dots | x_N),$$

where $x_i = (x_{i1} | x_{i2} | \dots | x_{im})$ is the observation vector of the m traits on the i th relative. Without loss of generality, the elements of x will be assumed to have zero means and phenotypic variance-covariance matrix $P = E(xx')$ of order mN .

Similarly, assume the elements of g to have zero means and a genetic variance-covariance matrix $G = E(gg')$ of order $2m$. As is true for the usual case of one genetic component per trait, the right-hand sides of the equations giving the best weights for the elements of x represent the additive genetic covariance between the workers providing the information and the workers (and potential queens) of the colony to be evaluated and on the genetic variances and covariances of the traits. In addition, there will be terms containing the additive relationships of the dams of the colonies with the records, to the workers of the colony being evaluated, as well as genetic covariances among the worker and queen genetic components. It can be shown that the necessary relationships can be represented by a $2m \times mN$ matrix which may be partitioned as

$$A = (A_1 | A_2 | \dots | A_N),$$

where each submatrix i is a $2m \times m$ matrix of the form

$$A_i = \begin{bmatrix} a_i & 0 & \dots & 0 \\ a_{id} & 0 & & 0 \\ 0 & a_i & & 0 \\ 0 & a_{id} & & 0 \\ \vdots & \vdots & & \vdots \\ 0 & & & a_i \\ 0 & & & a_{id} \end{bmatrix}$$

where a_i is the additive genetic relationship between the i th workers and the workers of the colony being evaluated, and similarly, a_{id} is the corresponding relationship between the dam of the i th workers and the workers (of the colony) being evaluated.

The weights for the elements of x , which will maximize the correlation between the index criterion (I) and aggregate breeding value (H), will be denoted as the $1 \times mN$ partitioned vector

$$b' = (b_1 | b_2 | \dots | b_N)$$

corresponding in structure to the data vector.

The equations for b maximizing the correlation between index and breeding value can be written as $Pb = A'Gv$, which yields, in index weights, $b = P^{-1}A'Gv$. The index criterion for selection is then $I = b'x$.

When x and g have a multivariate normal distribution, this solution maximizes genetic improvement in H for truncation selection on I and the expected genetic improvement is proportional to the standard deviation (σ_1) of I :

$$\sigma_1 = (b'Pb)^{0.5}.$$

The correlated response in the i th component of g is

$$\Delta g_{ki} = \frac{ib'(A'G)_i}{\sigma_1},$$

where k refers to either the worker or queen component of trait i , $(A'G)_i$ is the i th column of $A'G$, and i is the intensity of selection, assumed to be 1.

Records (honey production X_{11} , aggressiveness X_{12}) from the colonies to be evaluated, and corresponding records of "full-sib colonies" (X_{21} , X_{22}) and paternal half-sib colonies (X_{31} , X_{32}), are available to predict the breeding value of potential young queens from the colony to be evaluated for both queen and worker effects on the traits mentioned. The expression "full-sib colonies" stands for colonies, the queens of which descended from the same dam (DQ) and were sired by the same drone-producing queens (SW). Paternal half-sib colonies share only the same paternal descent (same SW). Genetic relationships between queens $a(Q)$, worker groups $a(W)$, and between queens and worker groups $a(QW)$, respectively, of various related colonies used, are given in Table 1 or were calculated (in the case of full-sib colonies) by the method of Bienenfeld et al. (1989).

Indices FS and HS symbolize so-called full-sib and paternal half-sib colonies, respectively.

Phenotypic and genetic parameters required for P and G, respectively, and taken from Bienefeld (1988a) and are summarized in Table 4.

The b values of the selection index are obtained by solving the matrix equations as given in the appendix. Economic values are assumed to be 5 for honey production and about 0.25 (considering the transformation) of this value (Bienefeld 1987) for aggressiveness. They are assumed to be identical for queen and worker effects.

It should be stressed, first, that economic values, especially for aggressiveness (by saving time or by making accessible new honey flow possibilities in densely populated areas) are rather speculative, and second, that compensation between traits is feasible over only a limited range of colony aggressiveness. The economic value for aggressiveness (0.05) takes into account that phenotypic and genetic parameters were estimated by transformed values (e^{variable}), causing a range (2.7–54.6) quite different from that of the original scoring scale (1–4).

Using the parameters and the economic values mentioned, the index becomes

$$I = 0.28X_{11} + 2.05X_{12} + -0.36X_{21} \\ + 0.04X_{22} + -0.04X_{31} + 0.20X_{32},$$

where X_{11} is the honey production of the colony to be evaluated, X_{12} is the aggressiveness of the colony to be evaluated, X_{21} is the honey production of full-sib colonies, X_{22} is the aggressiveness of full-sib colonies, X_{31} is the honey production of paternal half-sib colonies, and X_{32} is the aggressiveness of paternal half-sib colonies. The expected correlated responses per generation relative to an intensity of selection = 1 and $\sigma_I = 6.67$, are:

$$\Delta g_{w1} = 1.05 \text{ kg}, \Delta g_{Q1} = 0.27 \text{ kg} \\ \text{(honey)}$$

$$\Delta g_{w2} = 6.73, \Delta g_{Q2} = -4.93 \\ \text{(aggressiveness)}$$

Because the generation interval was found to be 3.9 yr (Bienefeld 1988b), the progress per year is a quarter of the above values. The length of the generation interval in the population analyzed is caused by performance testing normally lasting 2 yr and by the fact that selection on males is based on the dams of the drone-producing queens. Because such gentle colonies (insignificant aggressiveness) was scored high (4) and vicious colonies (distinct aggressiveness) low (1), the negative value with respect to the genetic change of queen effects means a deterioration. This is caused by the lower economic value of this trait and the negative genetic covariance between queen and worker effects. Considering the absolute level of genetic change in this trait, one must notice that these values are given in transformed units.

In addition to the problems in the application of indices based on inaccurate genetic parameters (Lin 1978, Hayes & Hill 1981), there is a lack of knowl-

Table 4. Phenotypic and genetic parameters (from Bienefeld 1988a)

Parameters	Trait	
	Honey (1)	Aggressiveness (2)
Within each trait		
Phenotypic variance	$\sigma^2_{P1} = 53.7$	$\sigma^2_{P2} = 95.2$
Genetic variance (worker)	$\sigma^2_{W1} = 14.3$	$\sigma^2_{W2} = 39.1$
Genetic variance (queen)	$\sigma^2_{Q1} = 8.1$	$\sigma^2_{Q2} = 38.9$
Genetic covariance (queen/worker)	$\sigma^2_{W1Q1} = -9.5$	$\sigma^2_{W2Q2} = -35.4$
Between both traits		
Phenotypic covariance	$\sigma_{P12} = 3.9$	
Genetic covariance (worker)	$\sigma_{W12} = 0.8$	
Genetic covariance (queen)	$\sigma_{Q12} = -1.0$	
Genetic covariance (queen/worker)	$\sigma_{QW12} = 2.3$	

edge of useful economic weighting factors. The relative economic value for each trait depends upon the profit increment to be expected for each unit of improvement in that trait. If additional feed and labor costs are associated with increased production for either trait, the increased cost per unit should be discounted.

Further research should also analyze whether equal weighting of queen and worker effects are most appropriate. For mammalian species, Van Vleck (1976) suggested there is no reason to believe that the net economic values of offspring and maternal genetic effects are equal, even though the final phenotypic product naturally has only a single market value per unit. The biological inputs are likely to differ. For example, in the case of honey production, the net value of direct genetic effects may depend on the workers' efficiency in collecting nectar, whereas a large part of the costs of the maternal component consists of the efficiency of the queen in producing workers. Perhaps it is more efficient to focus the selection on more efficient workers than on queens able to produce large colonies that consume much honey.

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Appendix

The selection index weights were found as:

$b = P^{-1}A'Gv$, where

$$G = \begin{bmatrix} \sigma^2_{W1} & \sigma_{QW1} & \sigma_{W12} & \sigma_{QW12} \\ \text{Symmetric} & \sigma^2_{Q1} & \sigma_{QW12} & \sigma_{Q12} \\ & & \sigma^2_{W2} & \sigma_{QW2} \\ & & & \sigma^2_{Q2} \end{bmatrix}$$

$$A = \begin{bmatrix} 1 & 0 & 0.24 & 0 & 0.13 & 0 \\ 0.5 & 0 & 0.43 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0.24 & 0 & 0.13 \\ 0 & 0.5 & 0 & 0.43 & 0 & 0 \end{bmatrix}$$

$$P = \begin{bmatrix} \sigma^2_{P1} & U_1 & a(W)_{HS}\sigma^2_{W1} & \sigma_{P12} & U_{12} & a(W)_{HS}\sigma_{W12} \\ & U_1 + (\sigma^2_{P1} - U_1)n^{-1} & a(W)_{HS}\sigma^2_{W1} & U_{12} & U_{12} + (\sigma^2_{P12} - U_{12})n^{-1} & a(W)_{HS}\sigma_{W12} \\ & & a(W)_{HS}\sigma_{W1} + V_1 & a(W)_{HS}\sigma_{W12} & a(W)_{HS}\sigma_{W12} & a(W)_{HS}\sigma_{W12} + V_{12} \\ & \text{Symmetric} & & \sigma^2_{P2} & U_2 & a(W)_{HS}\sigma^2_{W2} \\ & & & & U_2 + (\sigma^2_{P2} - U_2)n^{-1} & a(W)_{HS}\sigma^2_{W2} \\ & & & & & a(W)_{HS}\sigma^2_{W2} + V_2 \end{bmatrix}$$

$U_1 = a(W)_{FS}\sigma^2_{W1} + a(Q)_{FS}\sigma^2_{Q1} + 2a(QW)_{FS}\sigma_{W1Q1}$; $U_2 = a(W)_{FS}\sigma^2_{W2} + a(Q)_{FS}\sigma^2_{Q2} + 2a(QW)_{FS}\sigma_{W2Q2}$. $U_{12} = a(W)_{FS}\sigma_{W12} + a(Q)_{FS}\sigma_{Q12} + 2a(QW)_{FS}\sigma_{W1Q2}$. $V_1 = [\sigma^2_{P1} - a(W)_{HS}\sigma^2_{W1}]p^{-1}$, $V_2 = [\sigma^2_{P2} - a(W)_{HS}\sigma^2_{W2}]p^{-1}$, $V_{12} = [\sigma_{P12} - a(W)_{HS}\sigma_{W12}]p^{-1}$, n , number of full-sib information sources (8), p , number of parental half-sib information sources (20); the other symbols are given in the text or in Table 4.