Influence of model selection and data structure on the estimation of genetic parameters in honeybee populations

Manuel Du, Richard Bernstein, Andreas Hoppe, and Kaspar Bienefeld

Breeding and Behavior, Institute for Bee Research Hohen Neuendorf, 16540 Hohen Neuendorf, Germany

Abstract

Estimating genetic parameters of quantitative traits is a prerequisite for animal breeding. In honeybees, the genetic variance separates into queen and worker effects. However, under data paucity, parameter estimations that account for this peculiarity often yield implausible results. Consequently, simplified models that attribute all genetic contributions to either the queen (queen model) or the workers (worker model) are often used to estimate variance components in honeybees. However, the causes for estimations with the complete model (colony model) to fail and the consequences of simplified models for variance estimates are little understood. We newly developed the necessary theory to compare parameter estimates that were achieved by the colony model with those of the queen and worker models. Furthermore, we performed computer simulations to quantify the influence of model choice, estimation algorithm, true genetic parameters, rates of controlled mating, apiary sizes, and phenotype data completeness on the success of genetic parameter estimations. We found that successful estimations with the colony model were only possible if at least some of the queens mated controlled on mating stations. In that case, estimates were largely unbiased if more than 20% of the colonies had phenotype records. The simplified queen and worker models proved more stable and yielded plausible parameter estimates for almost all settings. Results obtained from these models were unbiased when mating was uncontrolled, but with controlled mating, the simplified models consistently overestimated heritabilities. This study elucidates the requirements for variance component estimation in honeybees and provides the theoretical groundwork for simplified honeybee models.

Keywords: REML estimates; genetic parameters; honeybees; maternal and direct effects; computer simulation; animal model; mating control

Introduction

Breeding efforts in honeybees, as in other agricultural species, rely on the fact that selection traits are partly determined by genetic features and that superior animals can thus pass on their qualities to their offspring. In order to determine the extent to which this is the case, it is necessary to measure the magnitude of genetic variance as a contributor to the phenotypic variance in a population. Thus, estimates of genetic and residual variance components are important to judge the prospect of success in selective breeding schemes (Lush 1937).

In addition to their importance for evaluating the possibilities for breeding, genetic and residual variance estimates also belong to the input data of best linear unbiased prediction (BLUP) breeding value estimation (Henderson 1975) and are thus an integral part of modern techniques of genetic evaluation, including that of honeybees (Bienefeld et al. 2007; Brascamp and Bijma 2014; Hoppe et al. 2020).

Estimates of variance components in livestock populations typically rely on the animal model (AM), assuming that the phenotype $y_{ij}$ of an individual $j$ in an environment $i$ is determined by a fixed environmental effect $b_i$, a random genetic effect $u_j$ of the individual, and a random residual effect $e_{ij}$:

$$y_{ij} = b_i + u_j + e_{ij}. \quad (AM)$$

Based on this model and the relationships between the involved individuals, the variances of $u_j$ (additive genetic variance, $\sigma^2_A$) and $e_{ij}$ (residual variance, $\sigma^2_e$) are typically estimated as restricted maximum likelihood (REML) values, assuming that $u_j$ and $e_{ij}$ are normally distributed (Patterson and Thompson 1971). There exist several algorithms to derive REML estimates, the two most widely used probably being Expectation Maximization REML (EMREML) (Dempster et al. 1977; Mäntysaari and van Vleck 1989) and Averaged Information REML (AIREML) (Madsen et al. 1994; Johnson and Thompson 1995; Gilmour et al. 1995). The EMREML algorithm is generally deemed reliable to return exact REML estimates; however, it often takes many iterations to converge (Meng and van Dyk 1998; Thompson et al. 2005; Misztal 2008). In contrast, AIREML terminates much faster but also requires a higher degree of regularity of the likelihood function. It may thus fail to yield accurate REML estimates, particularly if the data set is small or irregular (Misztal 2008; Masuda 2019).

The application of the AM to the honeybee bears the problem that, unlike in other livestock species, a phenotype record is usually not attributed to an individual bee but to a colony, i.e. a...
collective of bees with different genetic properties. In particular, the distinction between queen and worker group has proven important, because the same genetic set-up has different influences on a trait, depending on the caste it is expressed in (Bienefeld and Pirchner 1990). The model which to date represents the honeybee biology most accurately was introduced by Brascamp and Bijma (2014), refining several earlier approaches (Chevalet and Cornuet 1982; Bienefeld et al. 1989, 2007). We call this model the colony model (CM). It assumes that for a colony, consisting of a queen and a worker group in an environment, the phenotype is determined by:

\[ y_{iqw} = b_i + u^Q_i + \pi^W_{iq} + e_{iqw}. \quad \text{(CM)} \]

The concept is similar to that of maternal and direct effects in other livestock species (Willham 1963): The genetic effect splits up into a (maternal) queen component \( u^Q_i \) and a (direct) worker component \( u^W_i \). The genetic effect of the worker group, \( \pi^W_{iq} \), is equipped with a bar to indicate that it is formed as the average genetic covariance between queen and worker effects, \( \sigma_{qw}^2 \). While \( \sigma_{qw}^2 \) and \( \sigma_{qq}^2 \) are precisely the variances of \( u^Q_i \) and \( e_{iqw} \), respectively, the variance of \( \pi^W_{iq} \), being the variance of an averaged value, is reduced to \( a_{qw}\sigma_{qw}^2 \), where the reduction factor \( a_{qw} \) is the average relationship between two workers in a colony (Brascamp and Bijma 2014, 2019). If a queen mates freely with many mutually unrelated drones, most of her workers are maternal half-sibs and thus \( a_{qw} \) is little larger than 0.25. In breeding schemes with controlled mating on mating stations, the value for \( a_{qw} \) has been estimated between 0.317 (Brascamp et al. 2018) and 0.427 (Bienefeld et al. 1989).

The CM has yielded unbiased REML estimates of variance components with simulated data (Brascamp et al. 2014; Brascamp and Bijma 2019) and has been applied successfully in the estimation of genetic parameters in real honeybee populations (Bienefeld and Pirchner 1990; Brascamp et al. 2016; Hoppe et al. 2020). However, it turned out that this model has high demands on data quality. In case of imperfect data, algorithms for parameter estimation in honeybees have repeatedly failed to converge or yielded unreasonable results. This was observed for the AIREML algorithm (Andonov et al. 2019; Guichard et al. 2020), as well as older and supposedly more reliable algorithms, including EMREML (William and ESı 1993; Zakour et al. 2012).

As a remedy, several recent studies used simplified honeybee models for parameter estimations, attributing the entire genetic component of the phenotype either to the queen (queen model, QM) or to the worker group (worker model, WM), while ignoring the other caste (Andonov et al. 2019; Facchini et al. 2019; Guichard et al. 2020, 2021):

\[ y_{iq} = b_i + u^{QM}_i + e^{QM}_{iq}, \quad \text{(QM)} \]

or

\[ y_{iw} = b_i + \pi^{WM}_{iw} + e^{WM}_{iw}. \quad \text{(WM)} \]

These simplified models lead to increased numeric stability of the estimation procedures, also when the data quality is poor (William and ESı 1993; Guichard et al. 2020, 2021). They are easily justified for traits that are clearly attributed to only one caste (de Graaf et al. 2020; Facchini et al. 2021). However, most commercially important honeybee traits, such as honey yield or gentleness, are commonly influenced by the queen and her workers. For these traits it is to date unclear, how parameter estimates that were obtained with the simplified models QM and WM compare to estimates using the complete model CM. Sometimes, \( u^{QM}_i \) from the QM is directly associated with \( u^Q_i \) from the CM, although there exists a general sentiment that \( u^{QM}_i \) likely also captures some worker effect information due to the close relationship between a queen and her workers (Guichard et al. 2020, 2021). The same holds for \( \pi^{WM}_{iw} \) and \( \pi^W_{iq} \). In simulation studies on mammals, it has been shown that neglecting existing maternal effects in parameter estimations can lead to severely biased variance estimates for the direct effects (Robinson 1996; Clément et al. 2001).

Data paucity, which has been made responsible for the failure to estimate genetic variance components under the CM in several honeybee populations, appears in different forms:

- The mating behavior of the honeybee differs from that of other agricultural species. A young queen mates only once, soon after hatching, with several drones from other hives and afterwards uses the collected semen to fertilize eggs for the rest of her life. For the breeder, this mating behavior is typically not observable, leading to uncertain paternity and thus incomplete pedigrees. Several studies for other livestock species have shown that incomplete pedigree information can yield biased estimates of variance components (Cantet et al. 2000; Clément et al. 2001; Id-Lahoucine and Casellas 2017). The situation for the honeybee can be ameliorated by the use of artificial insemination or isolated mating stations, which provide a certain degree of paternal pedigree information (Bienefeld et al. 1989; Brascamp and Bijma 2014; Uzunov et al. 2017). But although it has been shown that these strategies substantially enhance genetic response (Plate et al. 2019b; Du et al. 2021a), many honeybee populations are still bred without or with incomplete mating control (Andonov et al. 2019; De la Mora et al. 2020; Maucourt et al. 2020).

- Apiary sizes play a crucial role in separating fixed and random effects, because colonies from the same apiary are usually attributed the same fixed effect. In comparison to other agricultural species, contemporary groups in honeybees tend to be small (Andonov et al. 2019; Bieńkowska et al. 2020), which is likely to harm the accuracy of estimated genetic parameters (Swalve 1995; Strabel and Swaczkowski 1999; Vasconcelos et al. 2008).

- Performance tests for some honeybee traits, such as the pin test for hygienic behavior, are laborious and therefore not recorded by all breeders, leading to incomplete phenotype data (Hoppe et al. 2020). Studies in other agricultural species have shown that missing phenotype data hampers the estimation of genetic parameters and that the disentanglement of maternal and direct genetic variances is particularly compromised (Gerstmayr 1992; Maniatis and Pollott 2003; Heydarpour et al. 2008).

While it is known that these factors have a negative influence on genetic parameter estimations, it is unclear to what extent this is the case in honeybee populations.

In this study, we derive a theoretical framework that allows the comparison of genetic parameter estimates under the CM with those under the simplified queen and worker models (QM / C19).
and WM). Furthermore, we used simulated data to investigate the influences of model choice, estimation algorithm, controlled mating, apiary size, and phenotype data completeness on the estimation of variance components in honeybee populations.

Theory
Projected contributions and variances

In this section, we discuss what to expect if the simplified models QM and WM are used to estimate variance components from phenotypes that were created according to the CM. Our approach is analogous to the theory of transformed variances in other species, like they appear for example in sire-maternal grandsire models (Kriese et al. 1991). However, to our knowledge, none of the resulting Equations (4a), (4c), (6a), or (6b) have previously been derived for the honeybee.

We start with the QM, which projects all genetic effects onto the queen. A worker group $W_q$ inherits its breeding value $\pi_{w_q}$ from its queen $q$ and the drones $d$ that $q$ mated with:

$$\pi_{w_q} = \frac{1}{2} u_{q}^W + \pi_{d}^W .$$

Note that (diploid) queens transmit only half of their genes to their offspring, while (haploid) drones pass their entire genetic information. Furthermore, no Mendelian sampling is modeled in the inheritance to a worker group because sampling effects for individual workers cancel out when average values are taken. For more details on modeling additive genetic inheritance in honeybees (see e.g. Du et al. 2021b; Kistler et al. 2021). By inserting Equation (1), the model equation of the CM can be rewritten as

$$y_{wq} = b_i + u_{q}^Q + \frac{1}{2} u_{q}^W + \pi_{d}^W + e_{wq}.$$  

The genetic contribution of $q$ to the phenotype, as it is projected by the simplified model QM, is therefore not only $u_{q}^Q$, but

$$u_{q}^{Q\text{(QM)}} = u_{q}^Q + \frac{1}{2} u_{q}^W .$$

Accordingly, the projected residual contribution is

$$\epsilon_{q}^{Q\text{(QM)}} = \pi_{d}^W + e_{wq}.$$  

Note that, we assumed that a queen’s breeding value is independent from the breeding values of the drones she mated with, i.e. no assortative mating. The genetic variance projected to the queen by the QM is thus:

$$\sigma_{A(QM)}^2 = \text{var}(u_{q}^{Q\text{(QM)}}) = \sigma_{A(Q)}^2 + \frac{1}{4} \sigma_{A(W)}^2 + \sigma_{A(W)}^2 .$$

The phenotypic variance for honeybee colonies equals [Brascamp and Bijma 2019; Bernstein et al. 2021, Equation (2)].

$$\sigma_{p}^2 = \text{var}(y_{wq}) = \sigma_{A(Q)}^2 + a_{uq} \sigma_{A(W)}^2 + \sigma_{A(W)}^2 + \sigma_{e}^2 .$$

In consequence, since $u_{q}^{Q\text{(QM)}}$ and $\epsilon_{q}^{Q\text{(QM)}}$ are independent, the residual variance projected by the QM is

$$\sigma_{e(QM)}^2 = \text{var}(\epsilon_{q}^{Q\text{(QM)}}) = \sigma_{p}^2 - \sigma_{A(QM)}^2 = \left(a_{uw} - \frac{1}{4}\right) \sigma_{A(W)}^2 + \sigma_{e}^2 .$$

We now turn to the WM, attributing all genetic effects to the worker group. The calculation of the projected genetic contributions when using this model is more involved, because the worker group’s true breeding value $\pi_{w}$ has nonvanishing covariances with both $u_{q}$ and $\pi_{d}$. We present the resulting formulas here and give their derivations in the appendix:

$$\pi_{w}^{(WM)} = \frac{1}{2a_{uw}} \pi_{q}^2 + \pi_{d}^W ,$$

and

$$\epsilon_{w}^{(WM)} = \left(1 - \frac{1}{4a_{uw}}\right) u_{q}^Q - \frac{1}{4a_{uw}} \pi_{q}^2 + \epsilon_{wq} .$$

Thus, when using the WM to estimate genetic and residual variance components from phenotypes that were created according to the CM, the expected results are:

$$\sigma_{A(WM)}^2 = \frac{1}{a_{uw}} \text{var}(\pi_{w}^{(WM)}) = \frac{1}{4a_{uw}} \sigma_{A(Q)}^2 + \sigma_{A(W)}^2 + \frac{1}{4a_{uw}} \sigma_{A(W)}^2,$$

and

$$\sigma_{e(WM)}^2 = \text{var}(\epsilon_{w}^{(WM)}) = \left(1 - \frac{1}{4a_{uw}}\right) \sigma_{A(Q)}^2 + \sigma_{e}^2 .$$

The projected variances $\sigma_{e(QM)}^2$, $\sigma_{A(WM)}^2$, and $\sigma_{e(WM)}^2$ (but not $\sigma_{A(QM)}^2$) depend on the average relationship of workers, $a_{uw}$, and will thus differ for different mating strategies.

Methods
Parameter estimation with simulated data

We used the program BeeSim (Plate et al. 2019a) to simulate several honeybee populations over 20 years, for which we then performed genetic parameter estimations. All populations comprised 500 queens per year and each year, 50 two-year old queens were randomly selected to produce ten daughter queens. Both controlled and uncontrolled queen mating strategies were considered. In uncontrolled matings, queens were paired with $n_d = 12$ drones that were produced by a random selection of queens of ages between one and three years. In controlled matings, queens were paired with $n_d = 12$ drones on one of ten isolated mating stations. Each mating station consisted of a sister group of eight drone producing queens, whose dam was randomly selected among the three-year old breeding queens. The respective implementations of controlled and uncontrolled mating were thus identical to earlier simulation studies (Plate et al. 2019b, 2020; Du et al. 2021b). The resulting values of $a_{uw}$ were 0.29 for uncontrolled mating and 0.37 for controlled mating. Six different proportions $p$ of queens undergoing controlled mating were considered ($p = 0.0, 0.2, 0.4, 0.6, 0.8, 1.0$). In populations with mixed controlled and uncontrolled mating of queens, we assumed $a_{uw}$ to be a weighted average between 0.29 and 0.37. Separate simulations were performed for eight traits, reflecting different ratios between genetic and residual variance, as well as different correlations $r_{A(W)}$ between queen and worker group effects (see
Table 1. Genetic parameters of simulated traits.

| Trait | $\sigma^2_{KQ}$ | $\sigma^2_{AQ}$ | $\sigma^2_A$ | $\sigma^2_{E_{QW}}$ | $\sigma^2_{E_{AW}}$ | $\sigma^2_{E_{AW}}$ | $\sigma^2_{E_{QW}}$ |
|-------|-----------------|-----------------|-------------|---------------------|---------------------|---------------------|---------------------|
| T1    | 1               | 2               | 4           | 0.5                 | 0.35                | 2                   | 4.08                | 6.65                | 4.14                |
| T2    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 4.08                | 4.94                | 4.14                |
| T3    | 1               | 2               | 4           | 0                   | 0                   | 6.65                | 4.08                | 5.18                | 4.14                |
| T4    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 1.08                | 4.94                | 1.14                |
| T5    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 1.08                | 3.22                | 1.14                |
| T6    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 1.08                | 3.22                | 1.14                |
| T7    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 1.08                | 3.22                | 1.14                |
| T8    | 1               | 2               | 4           | 0                   | 0                   | 1.5                 | 1.08                | 3.22                | 1.14                |

Results

Plausibility analysis

With the CM, a total of 74.2% of all EMREML runs and 70.7% of AIREML runs passed the plausibility test. While 40.7% of all failed AIREML procedures rendered parameters that lay outside of the admissible intervals, this effect was much rarer for EMREML, where 99.6% of all unsuccessful runs did not converge within 3,000 iterations. The success rates for both algorithms depended heavily on the set-up. The factors with the highest influence proved to be the rates of controlled mating and phenotype data completeness (Fig. 1, a and b). When the majority of queens mated controlled and at least 70% of the phenotype data was complete, almost all (>98%) parameter estimations yielded plausible results. On the other hand, if mating was entirely uncontrolled, 49.2% of EMREML and 99.0% of AIREML procedures failed. Similarly, if only 10% of all colonies had phenotype records, a clear majority of estimation runs failed, even with otherwise favorable parameters. We further observed for both algorithms that larger apiaries yielded better results, traits with small residual variance performed better than traits with large residual variance, and traits with negative correlation between queen and worker effects performed better than traits with zero or positive correlation (Fig. 1, c and d). However, apiary sizes and true genetic parameters were only of secondary importance, with far smaller influences than controlled mating and data completeness.

As expected, the simplified models QM and WM proved more robust than the CM under compromised data quality: Even in settings with poor phenotype coverage ($q \leq 20\%$), the majority of parameter estimations were successful. Here, EMREML performed slightly better than AIREML (Fig. 2, a and b). In both algorithms, we saw a trend that the QM outperformed the WM if mating was predominantly uncontrolled and the opposite for mainly controlled mating. In all settings with at least 50% phenotype data, 99% or more of AIREML procedures with simplified models led to plausible results (not shown). The EMREML results with at least 50% phenotypes were more nuanced. While the QM always yielded success rates over 98%, several estimation procedures under the WM with good phenotype data did not converge in time (Fig. 2c).

Estimation accuracy

Colony model

The following results only consider those estimation runs that passed the plausibility test. The EMREML and AIREML algorithms showed a qualitative difference regarding the rates of successful runs in scenarios without controlled mating. While EMREML yielded plausible results in several cases, virtually all AIREML
procedures failed (Fig. 1, a and b, first columns). In a first step, we thus analyzed the plausible EMREML results in the CM without controlled mating. Many runs led to genetic variance estimates \( r^2_{AQ} \) and \( r^2_{AW} \) that were close to the true parameters (Fig. 3). However, substantial misestimations occurred in all scenarios. Notably, estimation errors for \( r^2_{AQ} \) and \( r^2_{AW} \) were not independent but occurred along distinguishable trajectories. This phenomenon also occurred for the estimates of \( r^2_{AQW} \) and \( r^2_{E} \), albeit less pronounced (not shown). We thus suspect that without controlled mating, the relationship data was insufficient to distinguish queen and worker effects. Consequently, the REML likelihood functions seemed not to have isolated maxima, but values for \( r^2_{AQ} \) and \( r^2_{AW} \) could be exchanged along the trajectories at a constant likelihood. In this case, the concentration of EMREML outputs around the correct values is likely an artifact of starting the procedure with true parameters. The phenomenon depicted in Fig. 3 never occurred when at least some queens mated controlled. Due to the irregular behavior of estimates according to the CM without controlled mating, we excluded these results.

![Fig. 1](image1.png)  
**Fig. 1.** Rates of plausible parameter estimations with EMREML a, c) and AIREML b, d) under the CM. The rates are presented in dependence of percentages \( p \) of controlled mated queens and \( q \) of colonies with phenotype data a, b), as well as in dependence on apiary size and true trait parameters c, d). Lighter background shades signify higher success rates.

![Fig. 2](image2.png)  
**Fig. 2.** a) Rates of plausible EMREML runs with \( \leq 20\% \) colonies with phenotype data under the models QM, WM and CM. b) As (a), but with AIREML. c) Rates of plausible EMREML procedures under the WM presented in dependence of percentages \( p \) of controlled mated queens and \( q \) of colonies with phenotype data.

![Fig. 3](image3.png)  
**Fig. 3.** Heatmap of estimate bias for \( \sigma^2_{AQ} \) and \( \sigma^2_{AW} \) with the CM and EMREML without controlled mating. \( \sigma^2_{AQ} \) and \( \sigma^2_{AW} \) that were close to the true parameters (Fig. 3).
from all further analyses, even when the results passed the plausibility test.

When at least 50% of the colonies had phenotype data, EMREML estimates for $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, $\sigma_{\text{AW}}^2$, and $\sigma_{E}^2$ were on average unbiased (Fig. 4, a and b), with slight differences between settings. When only 20% or fewer of the colonies had phenotype records, we observed biased parameter estimates. The genetic variances $\sigma_{\text{A}1}^2$ and $\sigma_{\text{A}2}^2$ were on average overestimated by 0.27 and 0.64, respectively (Fig. 4c), while the genetic covariance $\sigma_{\text{AW}}^2$ and the residual variance $\sigma_{E}^2$ were on average underestimated by 0.45 and 0.07, respectively (not shown). However, these biases were not caused by a general shift of parameter estimates, but by an excess of outliers in one direction, leading to skewed distributions. In all cases, the mode of the biases of estimated (co)variances, i.e. the distribution maximum and thus the most likely outcome for a single parameter estimation, was close to zero. When using the AIREML algorithm instead of EMREML, we obtained closely resembling results, whence we omit a detailed presentation and only provide Supplementary Fig. 1 as the AIREML counterpart to Fig. 4.

Despite the overall similar behavior of EMREML and AIREML results, both algorithms generally converged to nonidentical values. The median absolute differences between EMREML and AIREML estimates for $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, $\sigma_{\text{AW}}^2$, and $\sigma_{E}^2$ were 0.09, 0.16, 0.10, and 0.04, respectively. In 56.6% of all scenarios where both algorithms yielded plausible results, the EMREML output for $\sigma_{\text{A}1}^2$ was closer to the true parameter value. The corresponding percentages for $\sigma_{\text{A}2}^2$, $\sigma_{\text{AW}}^2$, and $\sigma_{E}^2$ were 54.2%, 57.0%, and 52.5%. This marginal superiority of EMREML estimates was also reflected in slightly lower realized standard errors, i.e. quadratic means of differences between estimated and true values, for the respective variance components. In addition to the realized standard errors, AIREML allows to intrinsically predict standard errors from the inverse averaged information matrix (Madsen et al. 1994; Meyer and Houle 2013). All three types of standard errors were generally in good accordance, with a slight tendency of the predicted standard errors to overestimate their realized counterparts (Fig. 5).

The excess of outliers in parameter estimations with < 20% data, which had caused the biases described above, resulted in vastly increased standard errors. These were also recognized inherently by AIREML. When we restricted our analysis to data sets with at least 50% recorded phenotypes, we found a clear scheme: Throughout, the residual variance $\sigma_{E}^2$ was estimated the most accurately (overall EMREML standard error 0.12) followed by $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, $\sigma_{\text{AW}}^2$, and $\sigma_{E}^2$ (standard errors 0.30, 0.33, and 0.55). Variance components were estimated more precisely, when the residual variance was smaller (traits T5 to T8). This difference showed strongest for $\sigma_{A1}^2$, where standard errors were halved in comparison to the traits T1 to T4. Among traits with equal residual variance, those with stronger negative correlation between effects were estimated more accurately. The rate of controlled mating had a strong effect on the estimates of genetic (co)variances, but only little influence on estimates of $\sigma_{E}^2$. Particularly when only 20% of all queens mated on mating stations, the standard errors for $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, and $\sigma_{\text{AW}}^2$ were much increased. As in the plausibility analysis, the influence of apiary sizes on the standard errors of variance estimates was small; yet we saw a trend that larger apiary sizes led to slightly better results.

**Queen and worker models**

Both the QM and WM performed best when mating was uncontrollable, i.e. precisely where parameter estimation with the CM failed. Under free mating conditions, EMREML estimates of $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, and $\sigma_{\text{AW}}^2$ with the QM were unbiased (Fig. 6a), whereas estimates for $\sigma_{\text{A}1}^2$, $\sigma_{\text{A}2}^2$, and $\sigma_{\text{AW}}^2$ with the WM showed a slight tendency to underestimate residual contributions (Fig. 6b). Unlike in the CM, completeness of phenotype data had almost no influence on the bias (not shown).

We observed biased results when controlled mating was introduced (Fig. 6, c and d). In contrast to the biases under the CM with incomplete phenotype data (Fig. 4c), these biases were not caused by excessive outliers. Instead, the results of the EMREML runs varied around shifted values and both the QM and WM showed a clear trend to overestimate genetic variances and underestimate residual variances, and thus made traits appear more heritable than they actually were. Biases for all traits were similar in absolute numbers and therefore relatively more severe when the residual variance $\sigma_{E}^2$ was low or the covariance $\sigma_{\text{AW}}^2$ between queen and worker effects was negative. The biases also occurred when only part of the queens mated controlled but were less pronounced then (not shown).

Like in the parameter estimations with the CM, standard errors were smaller when phenotype data was more complete (Table 2). Similarly, traits with smaller residual variance were estimated with smaller errors as were traits with stronger negative correlation between queen and worker effects. Throughout, the standard errors for trait T1 ($\sigma_{E}^2 = 4$, $\sigma_{\text{AW}}^2 = 0.5$) were about four times as high as those for trait T8 ($\sigma_{E}^2 = 1$, $\sigma_{\text{AW}}^2 = -1$). When
corrected for the described bias, the standard errors for variance component estimates with (partly) controlled mating were very similar to those with uncontrolled mating. Furthermore, as in the CM, the influence of the apiary size was detectable but small.

Standard errors for the residual variances ($\sigma^2_{Q(M)}$ and $\sigma^2_{W(M)}$) were similar when estimations were performed with either model. Standard errors for $\sigma^2_{A(M)}$ were on average slightly lower than a third of the standard errors for $\sigma^2_{A(Q)}$, indicating that $\sigma^2_{A(M)}$ and $\sigma^2_{A(W)}$ could be estimated with similar accuracy.

As in the CM, AIREML estimates showed very similar behavior to EMREML results. Therefore, we again restrict ourselves to providing Supplementary Fig. 2 as the analog to Fig. 6.

Discussion
Observations with the CM
This simulation study confirms several observations from parameter estimation studies with real data. The simplified models QM and WM proved indeed numerically more robust than the more complex model CM. In particular, we showed that a reliable parameter estimation with the CM is impossible in the absence of controlled mating. This has been claimed in several instances in the literature (Zakour et al. 2012; Andonov et al. 2019), but so far only on the basis of singular failed attempts of parameter estimation.

Furthermore, missing phenotype records made the estimation algorithms prone to produce outlier results, far off the correct values, likely caused by flat likelihood functions, whose maxima were difficult to determine. For instance, the genetic covariance between queen and worker effects was often estimated strongly negative even though this was not justified. In the past, genetic covariances between queen and worker effects in honeybee populations have been estimated strongly negative (Bienefeld and Pirchner 1990), but recently—possibly due to more complete data records—these negative covariances appeared less pronounced (Hoppe et al. 2020).

Lastly, the predicted standard errors from the inverse averaged information matrix in AIREML proved to be reasonable. Thus, it appears good practice to discard variance component estimates if the standard error exceeds the estimated value, as it was done by Willam and Eßl (1993) or Andonov et al. (2019).

Observations with the QM and WM
Our derivations of projected variances provide the theoretical base for genetic parameter estimations with the QM and WM. When mating was uncontrolled, estimated parameters and projected variances matched well. Under controlled mating, we detected a bias, but still, in most cases the projected variances provided a better description of the genetic estimates than comparing them to $\sigma^2_{A(Q)}$ and $\sigma^2_{A(W)}$, respectively (Guichard et al. 2020, 2021). Consequently, the projected variances $\sigma^2_{A(M)}$ and $\sigma^2_{A(W)}$ should also be used in the numerator of heritability definitions when comparing parameter estimates across models.

The biased results with the QM and WM under controlled mating were the most striking observations with these models. We attribute them to the following modeling issue. Random residual effects for different colonies are usually thought to be independent, and we also assumed this for the projected residual effects $e^2_{Q(M)}$ and $e^2_{W(M)}$. In the QM, the projected residual effect has a component $u_{W(i)}$, coming from the drones a queen mated with.

It is possible to extend the models QM and WM to account for residual covariances, similar to the considerations in (Bijma 2006). However, this complicates the models and it is unclear, how numerically robust such extended models are with poor data.
Implications for real data analysis

Model choice

In populations with uncontrolled mating, parameter estimates with the CM seem impossible and the models QM and WM appear as viable alternatives. In view of the biases in the WM, also with uncontrolled mating (Fig. 6b), the QM appears slightly superior. It provides a general idea of how heritable a trait is in a population. However, it is unclear, how genetic parameters that were received from the QM or WM should be integrated into modern strategies of genetic evaluation. In any case, without controlled mating, the genetic progress in breeding programs will be slow (Plate et al. 2019b; Du et al. 2021a). When using the QM and WM in populations with controlled mating, one should bear in mind that the genetic influence on a trait is likely to be overestimated.

Guichard et al. (2020, 2021) used both the QM and WM to estimate genetic parameters in honeybee populations and received estimates for $\sigma_2^{A(QM)}$, $\sigma_2^{E(QM)}$, $\sigma_2^{A(WM)}$, and $\sigma_2^{E(WM)}$. At first glance, it might appear possible to use the system of linear Equations (4a),
Early dependent (because unfortunately, this is not possible, since the equations are line-
arily dependent (because \( \sigma^2_{A;w} + \sigma^2_{E;w} = a_{ww}\sigma^2_{A;w} + \sigma^2_{E;w} \)). Estimating reliable genetic parameters was hard when many phenotype records for a trait were missing. In practice, it is thus advisable to restrict the estimation procedure to a sub-
population in which phenotype records are well-represented. Similarly, suitable sub-populations may be chosen to exclude overly small apiaries.

**Estimation algorithms**

The general properties of the EMREML algorithm being robust but slow and AIREML being faster but unstable when applied to regular data were reflected in this study. Estimating genetic parameters for a real population is typically not time sensitive. The higher success rate (Fig. 1) and slightly higher accuracy (Fig. 5) of EMREML thus suggest a prima facie superiority of this algorithm. However, Fig. 3 shows that the great numeric stability of EMREML can also come as a disadvantage. In situations where the data quality is insufficient to yield meaningful results, EMREML still produces reasonable output, leading to a false sense of security. The failure of AIREML to produce plausible results is an indicator for data quality problems. We therefore recommend to use both algorithms in parallel in order to obtain genetic parameter estimates at a maximum reliability.

**Limitations of the study**

In addition to the factors considered in this study, there are further parameters which affect variance component estimations and complicate the process in reality. In our simulations, queens were randomly chosen for reproduction, whereas many real populations undergo directional selection. With complete phenotype and pedigree data, selection has been shown to have no negative impact on REML parameter estimations in other species. However, in connection with missing parental information, biases can occur (Hofer 1998; Cantet et al. 2000).

In our simulations, phenotype records and pedigree information were partly incomplete, but they were always correct. In practice, misassignments of records can easily occur. In a study on cassava (Manihot esculenta), Yabe et al. (2018) found changed variance components resulting from mislabeled phenotypes, and several studies showed that incorrect pedigree entries have great influence on the estimation of genetic \((\sigma^2)\)variances (Lee and Pollak 1997; Parlato and van Vleck 2012). When estimating variance components in practice, it is thus paramount to screen the data for inconsistencies. For example, breeders may incorrectly report honey yields of 0 kg, when they did not measure the trait (Brascamp et al. 2016). With the emergence of breeding-relevant SNP panels for the honeybee (Spotter et al. 2012; Jones et al. 2020; Momeni et al. 2021) it may become easier to detect pedigree mistakes.

In addition to genetic effects of queens and worker groups and residual effects, further random effects may be relevant in honeybee populations and ignoring them can affect parameter estimates. For example, Andonov et al. (2019) modeled a random effect for the interaction between performance test year and apiary. Furthermore, several studies have shown an improved performance of locally adapted honeybees over imported stock (Buchler et al. 2014; Kovacić et al. 2020), suggesting the presence of random genotype × environment effects (Costa et al. 2012a,b). Adding meaningful random effects to the CM, QM, or WM can be beneficial, because reality is modeled more accurately. However, models with more random effects are more complex and thus have higher demands on data quality (Masuda 2019).

Our model assumes that genetic and residual variances homogeneously apply to all combinations of apiaries and years. In reality, this may not be the case (Hill et al. 1983; Guzzo et al. 2018; Hoppe et al. 2020). Heterogeneous variances impede the estimation of genetic parameters, because the model does not fit to the data. Various strategies to mitigate this problem have been developed (Vasscher and Hill 1992; van der Werf et al. 1994). However, with the exception of (Hoppe et al. 2020), studies on genetic parameters in honeybees mostly ignore such strategies. We think that further research on heterogeneous variances in honeybees can increase the success rates of parameter estimations.

In our simulations, all traits were normally distributed, which is an a priori assumption of REML estimates. But for many honeybee traits, this assumption is unrealistic. In particular for behavioral traits, like gentleness, which are measured on a discrete scale from one to four, observed distributions typically deviate significantly from normality (Brascamp et al. 2016; Andonov et al. 2019). Thus, Andonov et al. (2019) suggested to use Gibbs sampling based on a threshold model (van Tassel et al. 1994; Tsuruta and Misztal 2006) instead of REML estimates for genetic parameters in these traits.

Finally, we assumed relationships to be calculated according to Brascamp and Bijma (2014) with averaged values for worker groups. In the literature, parameter estimations in honeybees are often performed by modeling worker groups as single individuals (Ehrhardt et al. 2010; Zakour et al. 2012; Andonov et al. 2019; Maucourt et al. 2020). In this case, the diagonal entry of a noninbred worker group in the relationship matrix is one, as opposed to 0 for WM. Thus, diagonal entries of the alternative relationship matrices will on average be higher. As shown by Legarra (2016), estimated genetic variances with these relationship models will thus be higher.
generally be lower. This expectation is in accordance with the results of a simulation study by Brascamp et al. (2014).

Intuitively, it may seem obvious that modeling a worker group as a single bee is biologically less accurate than the averaging ansatz of Brascamp and Bijma (2014). But for some traits, such as gentleness, this is not so clear. Due to alarm pheromone release, the sting of a single bee triggers aggressive behavior of the entire colony even though the majority of workers may have a docile pre-disposition (Nouvian et al. 2016). The ideal way to model worker groups is likely to be trait-dependent and requires further research.

Data availability
The complete data from all parameter estimations is uploaded on figshare at https://doi.org/10.5061/dryad.1nh54n. The source code of the simulation program BeeSim is available at https://doi.org/10.5061/dryad.1nh54n.

Supplemental material is available at G3 online.

Funding
This work was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—(462225818 to Manuel Du) and by the German federal states of Brandenburg, Berlin, Sachsen, Sachsen-Anhalt, and Thüringen.

Conflicts of interest statement
The authors declare no conflict of interest.

Literature cited
Aitken AC. On Bernoulli’s numerical solution of algebraic equations. Proc R Soc Edinb. 1927;46:289–305.
Andonov S, Costa C, Uzunov A, BergomI D, Misztal I. Modeling honey yield, defensive and swarming behaviors of Italian honey bees (Apis mellifera ligustica) using linear threshold approaches. BMC Genet. 2019;20(1):78.
Bernstein R, Du M, Hoppe A, Bienefeld K. Simulation studies to optimize genomic selection in honey bees. Genet Sel Evol. 2021;53(1):64.
Bernstein R, Plate M, Hoppe A, Bienefeld K. Computing inbreeding coefficients and the inverse numerator relationship matrix in large populations of honey bees. J Anim Breed Genet. 2018;135(4):323–332.
Bienefeld K, Ehrhardt K, Reinhardt F. Genetic evaluation in the honeybee considering queen and worker effects—A BLUP-animal model approach. Apidologie. 2007;38(1):77–85.
Bienefeld K, Pirchner F. Heritabilities for several colony traits in the honeybee (Apis mellifera carnica). Apidologie. 1990;21(3):175–183.
Bienefeld K, Reinhardt F, Pirchner F. Inbreeding effects of queen and worker on colony traits in the honey bee. Apidologie. 1989;20(5):439–450.
Bierkowska M, Łoś A, Węgrzynowicz P. Honey bee queen replacement: an analysis of changes in the preferences of Polish beekeepers through decades. Insects. 2020;11(8):544.
Bijma P. Estimating maternal genetic effects in livestock. J Anim Sci. 2006;84(4):800–806.
Brascamp EW, Bijma P. Methods to estimate breeding values in honey bees. Genet Sel Evol. 2014;46:53.
Brascamp EW, Bijma P. A note on genetic parameters and accuracy of estimated breeding values in honey bees. Genet Sel Evol. 2019;51(1):71.

Brascamp EW, Veerkamp RF, Bijma P. Estimation of genetic parameters and breeding values in honey bees. In: Proceedings of the 10th World Congress on Genetics Applied to Livestock Production. Canada: Vancouver, 2014.
Brascamp EW, Willam A, Boigenzahn C, Bijma P, Veerkamp RF. Heritabilities and genetic correlations for honey yield, gentleness, calmness and swarming behaviour in Austrian honey bees. Apidologie. 2016;47(6):739–748.
Brascamp EW, Willam A, Boigenzahn C, Bijma P, Veerkamp RF. Correction to: heritabilities and genetic correlations for honey yield, gentleness, calmness and swarming behaviour in Austrian honey bees. Apidologie. 2018;49(4):462–463.
Büchler R, Costa C, Hatjina F, Andonov S, Meixner MD, Conte YL, Uzunov A, Berg S, Bienkowska M, Bouga M, et al. The influence of genetic origin and its interaction with environmental effects on the survival of Apis mellifera L. colonies in Europe. J Apicult Res. 2014;53(2):205–214.
Cantet RJC, Birchmeier AN, Santos-Cristal MG, de Avila VS. Comparison of restricted maximum likelihood and Method R for estimating heritability and predicting breeding value under selection. J Anim Sci. 2000;78(10):2554–2560.
Chevalet C, Cornuet JM. Étude théorique sur la sélection du caractère production de miel chez l’abeille. Apidologie. 1982;13(1):39–65.
Clément V, Bibé B, Verrier E, Elesen JM, Manfredi E, Bouaj J, Hanocq F. Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. Genet Sel Evol. 2001;33(4):369–395.
Costa C, Büchler R, Berg S, Bienkowska M, Bouga M, Bubalo D, Charistos I, Conte YL, Drazic M, Dyhrwa Y, et al. A Europe-wide experiment for assessing the impact of genotype-environment interactions on the vitality and performance of honey bee colonies: experimental design and trait evaluation. J Apicult Sci. 2012a;56(1):147–158.
Costa C, Lodesani M, Bienefeld K. Differences in colony phenotypes across different origins and locations: evidence for genotype by environment interactions in the Italian honeybee (Apis mellifera ligustica)? Apidologie. 2012b;43(6):634–642.
de Graaf DC, Laget D, De Smet L, Boüaert DC, Brunain M, Veerkamp RF. Brascamp EW. Heritability estimates of the novel trait ‘suppressed in ovo virus infection’ in honey bees (Apis mellifera). Sci Rep. 2020;10(1):14310.
De la Mora A, Emaen B, Morfin N, Borges D, Eccles L, Kelly PG, Goodwin PH, Guzman-Novoa E. Selective breeding for low and high Varroa destructor growth in honey bee (Apis mellifera) colonies: initial results of two generations. Insects. 2020;11(12):864.
Dempster AP, Laird NM, Rubin DB. Maximum likelihood from incomplete data via the EM algorithm. J R Stat Soc B. 1977;39(1):1–38.
Du M, Bernstein R, Hoppe A, Bienefeld K. A theoretical derivation of response to selection with and without controlled mating in honey bees. Genet Sel Evol. 2021a;53(1):17.
Du M, Bernstein R, Hoppe A, Bienefeld K. Short-term effects of controlled mating and selection on the genetic variance of honeybee populations. Heredity (Edinb). 2021b;126(5):733–747.
Ehrhardt K, Büchler R, Bienefeld K. Genetic parameters of new traits to improve the tolerance of honeybees to Varroa mites. In: Proceedings of the 9th World Congress on Genetics Applied to Livestock Production. Germany: Leipzig, 2010.
Facchini E, Bijma P, Pagnacco G, Rizzi R, Brascamp EW. Hygienic behaviour in honeybees: a comparison of two recording methods and estimation of genetic parameters. Apidologie. 2019;50(2):163–172.
Facchini E, De Iorio MG, Turri F, Pizzi F, Laurino D, Porporato M, Rizzi R, Pagnacco G. Investigating genetic and phenotypic variability of
queen bees: morphological and reproductive traits. Animals. 2021;11(11):3054.

Gerstmayr S. Impact of the data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. J Anim Breed Genet. 1992;109(1–6):321–336.

Gilmour AR, Thompson R, Cullis BR. Average Information REML: an efficient algorithm for variance parameter estimation in linear mixed models. Biometrics. 1995;51(4):1440–1450.

Guichard M, Droz B, Brascamp EW, von Virag A, Neuditschko M, Dainat B. Exploring two honey bee traits for improving resistance against Varroa destructor: development and genetic evaluation. Insects. 2021;12(3):216.

Guichard M, Neuditschko M, Soland G, Fried P, Grandjean M, Gerster S, Dainat B, Bijma P, Brascamp EW. Estimates of genetic parameters for production, behaviour, and health traits in two Swiss honey bee populations. Apidologie. 2020;51(5):876–891.

Guzzo N, Sartori C, Mantovani R. Heterogeneity of variance for milk, fat and protein yield in small cattle populations: the Rendena breed as a case study. Livest. Sci. 2018;213:54–60.

Henderson CR. Best linear unbiased estimation and prediction under repeated measures: application of the EM algorithm. J Am Stat Assoc. 1987;82(397):97–105.

Hill WG, Edwards MR, Ahmed MKA, Thompson R. Heritability of related growth traits in Hereford and Brangus bulls. J Anim Sci. 1991;69(2):478–489.

Henderson CR. Best linear unbiased estimation and prediction under repeated measures: application of the EM algorithm. J Am Stat Assoc. 1987;82(397):97–105.

Hill WG, Edwards MR, Ahmed MKA, Thompson R. Heritability of milk yield and composition at different levels and variability of production. Anim Sci. 1983;36(1):59–68.

Hofer A. Variance component estimation in animal breeding: a review. J Anim Breed Genet. 1998;115(1–6):247–265.

Hoppe A, Du M, Bernstein R, Tiesler FK, Kärcher M, Bienefeld K. Substantial genetic progress in the international Apis mellifera carnica population since the implementation of genetic evaluation. Insects. 2020;11(1):768.

Id-Lahoucine S, Casellas J. Impact of incomplete pedigree data and independent culling level pre-selection on the genetic evaluation of livestock: a simulation study on lamb growth. Livest Sci. 2017;198:76–81.

Johnson DL, Thompson R. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and Average Information. J Dairy Sci. 1995;78(2):449–456.

Jones JC, Du ZG, Bernstein R, Meyer M, Hoppe A, Schilling E, Ableitner M, Jüling K, Dick R, Strauss AS, et al. Tool for genomic selection and breeding to evolutionary adaptation: development of a 100K single nucleotide polymorphism array for the honey bee. Ecol Evol. 2020;10(13):6246–6256.

Kistler T, Basso B, Phocas F. A simulation study of a honeybee breeding scheme accounting for polyandry, direct and maternal effects on colony performance. Genet Sel Evol. 2021;53(1):71.

Kovačić M, Puskadžija Z, Dražić MM, Uzunov A, Meixner MD, Büchler R. Effects of selection and local adaptation on resilience and economic suitability in Apis mellifera carnica. Apidologie. 2020;51(6):1062–1073.

Kriese LA, Bertrand JK, Benyshek LL. Age adjustment factors, heritabilities and genetic correlations for scrotal circumference and related growth traits in Hereford and Brangus bulls. J Anim Sci. 1991;69(2):478–489.

Laird N, Lange N, Stram D. Maximum likelihood computations with repeated measures: application of the EM algorithm. J Am Stat Assoc. 1987;82(397):97–105.

Lee C, Pollak EJ. Influence of sire misidentification on sire × year interaction variance and direct-maternal genetic covariance for weaning weight in beef cattle. J Anim Sci. 1997;75(11):2858–2863.

Legarra A. Comparing estimates of genetic variance across different relationship models. Theor Popul Biol. 2016;107:26–30.

Lush JL. Animal Breeding Plans. Ames, IA: Iowa State Public Press; 1937.

Mäntysaari E, van Vleck LD. Restricted maximum likelihood estimates of variance components from multitrait sire models with large number of fixed effects. J Anim Breed Genet. 1989;106(1–6):409–422.

Madsen P, Jensen J, Thompson R. Estimation of (co)variance components by REML in multivariate mixed linear models using average of observed and expected information. In: Proceedings of the 5th World Congress on Genetics Applied to Livestock Production. Canada: Guelph; 1994.

Maniatis N, Pollott GE. The impact of data structure on genetic (co)-variance components of early growth in sheep, estimated using an animal model with maternal effects. J Anim Sci. 2003;81(1):101–108.

Masuda Y. Introduction to BLUPF90 Suite Programs. Athens, GA: University of Georgia; 2019.

Maucourt S, Fortin F, Robert C, Giovenazzo P. Genetic parameters of honey bee colonies traits in a Canadian selection program. Insects. 2020;11(9):587.

Meng XL, van Dyk D. Fast EM-type implementations for mixed effects models. J R Statist Soc B. 1998;60(3):559–578.

Meyer K, Houle D. Sampling based approximation of confidence intervals for functions of genetic covariance matrices. In: Proceedings of Association Advertisement Animal Breeding Genetics. Napier, New Zealand; 2013. p. 523–526.

Misztal I. Reliable computing in estimation of variance components. J Anim Breed Genet. 2008;125(2):89–99.

Misztal I, Tsuruta S, Strabel T, Auvray B, Druet T, Lee DH. BLUPF90 and related programs (BGF90). In: Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. France: Montpellier; 2002.

Momčil J, Parejo M, Nielsen RO, Lang J, Montes I, Papoutsis L, Farajzadeh L, Bendixen C, Cáuia E, Darrieu J-D, et al. Authoritative subspecies diagnosis tool for European honey bees based on ancestry informative SNPs. BMC Genomics. 2021;22(1):101.

Nouvian M, Reinhard J, Giurfa M. The defensive response of the honeybee Apis mellifera against Varroa destructor. Insects. 2020;11(7):404.

Ober-Trilm A, van Vleck LD. Effect of parentage misidentification on estimates of genetic parameters for milk yield in the Mediterranean Italian buffalo population. J Dairy Sci. 2012;95(7):4059–4064.

Patterson HD, Thompson R. Recovery of inter-block information when block sizes are unequal. Biometrika. 1971;58(3):545–554.

Plate M, Bernstein R, Hoppe A, Bienefeld K. Comparison of infinitesimal and finite locus models for long-term breeding simulations with direct and maternal effects at the example of honeybees. PLoS One. 2019a;14(3):e0213270.

Plate M, Bernstein R, Hoppe A, Bienefeld K. The importance of controlled mating in honeybee breeding. Genet Sel Evol. 2019b;51(1):74.

Plate M, Bernstein R, Hoppe A, Bienefeld K. Long-term evaluation of breeding scheme alternatives for endangered honeybee subspecies. Insects. 2020;11(7):404.

Robinson DL. Models which might explain negative correlations between direct and maternal genetic effects. Livest. Prod. Sci. 1996;45(2–3):111–122.

Spötter A, Gupta P, Nümburg G, Reinsch N, Bienefeld K. Development of a 44K SNP assay focussing on the analysis of a varroa-specific defence behaviour in honey bees (Apis mellifera carnica). Mol Ecol Resour. 2012;12(2):329–332.
Strabel BT, Szwaczkowski T. The use of test day models with small size of contemporary groups. J Anim Breed Genet. 1999;116(5):379–386.

Swalve HH. The effect of test day models on the estimation of genetic parameters and breeding values for dairy yield traits. J Dairy Sci. 1995;78(4):929–938.

Thompson R, Brotherstone S, White IMS. Estimation of quantitative genetic parameters. Philos Trans R Soc Lond B Biol Sci. 2005;360(1459):1469–1477.

Tsuruta S, Misztal I. THRGIBBSF90 for estimation of variance components with threshold and linear models. In: Proceedings of the 8th World Congress on Genetics Applied to Livestock Production. Brazil: Belo Horizonte; 2006.

Uzunov A, Brascamp EW, Büchler R. The basic concept of honey bee breeding programs. Bee World. 2017;94(3):84–87.

van der Werf JHJ, Meuwissen THE, de Jong G. Effects of correction for heterogeneity of variance on bias and accuracy of breeding value estimation for Dutch dairy cattle. J Dairy Sci. 1994;77(10):3174–3184.

van Tassell CP, Van Vleck LD, Gregory KE. Bayesian analysis of twinning and ovulation rates using a multiple-trait threshold model and Gibbs sampling. J Anim Sci. 1998;76(8):2048–2061.

Vasconcelos J, Santos F, Bagnato A, Carvalheira J. Effects of clustering herds with small-sized contemporary groups in dairy cattle genetic evaluations. J Dairy Sci. 2008;91(1):377–384.

Visscher PM, Hill WG. Heterogeneity of variance and dairy cattle breeding. Anim Sci. 1992;55(3):321–329.

Willam A, Eßi A. Schätzung von Populationsparametern für verschiedene Merkmale bei der Honigbiene (Apis mellifera carnica). Apidologie. 1993;24(4):355–364.

Willham RL. The covariance between relatives for characters composed of components contributed by related individuals. Biometrics. 1963;19(1):18–27.

Yabe S, Iwata H, Jannink JL. Impact of mislabeling on genomic selection in cassava breeding. Crop Sci. 2018;58:1470–1480.

Zakour MK, Ehrhardt K, Bienefeld K. First estimate of genetic parameters for the Syrian honey bee Apis mellifera syriaca. Apidologie. 2012;43(5):600–607.

Communicating editor: G. de los Campos
Appendix

We calculate, which part of a colony’s phenotype $y_{iwm}$, formed according to the CM, is projected to the worker group’s genetics if the simplified model WM is used for the analysis. Therefore, the random contributions to the phenotype, $r_{iwm} = u_q^Q + \pi^w + e_{iwm}$, have to be split up into a part that can be expressed in terms of $\pi^w$ and $\pi^Q$ thus is attributed to the worker group, and a part that is uncorrelated to these variables and is thus interpreted as a residual. In analogy to Equation (1), the worker group’s breeding value for the queen effect, $\pi^Q_w$, is inherited from the queen $q$ and the drones $d$ that mated with $q$:

$$\pi^Q_w = \frac{1}{2} u_q^Q + \sigma_q^2.$$

With $\text{var}(\pi^Q_w) = a_{uw} \sigma_q^2$ and $\text{var}(u_q^Q) = \sigma_q^2$. Equation (7) yields (because $u_q^Q$ and $\pi^Q_w$ are independent):

$$\text{var}(\pi^Q_w) = \left(a_{uw} - \frac{1}{2}\right) \sigma_q^2.$$

As the following calculation shows, $\pi^Q_w$ is therefore uncorrelated to the linear combination $u_d^Q = \frac{1}{2} u_q^Q + \frac{1}{2} \sum_{a_d} \pi^Q_d$:

$$\text{cov}(\pi^Q_w, u_d^Q) = \text{Eq.} \frac{1}{4} \text{cov} \left(\frac{1}{2} u_q^Q + \frac{1}{2} \pi^Q_d \right) \left( a_{uw} - \frac{1}{2} \right) \sigma_q^2.$$

Indeed, also $\pi^w$ is uncorrelated to $u_d^Q$:

$$\text{cov}(\pi^w, u_d^Q) = \frac{1}{4} \sigma_q^2 - \frac{1}{4} a_{uw} - \frac{1}{2} \left( a_{uw} - \frac{1}{2} \right) \sigma_q^2 = 0.$$

Thus, by writing $u^Q_w$ as

$$u^Q_w = \frac{1}{2a_{uw}} - \frac{1}{2a_{uw}} \pi^w + \frac{1}{2a_{uw}} \pi^Q_d + \left(2 - \frac{1}{2a_{uw}}\right) \frac{1}{2} u_q^Q - \frac{1}{2a_{uw}} \pi^Q_d \quad \text{w}$$

we arrive at the desired decomposition

$$r_{iwm} = u^Q_w + \pi^w + e_{iwm} \quad \text{w}$$

with $\pi^{\text{WM}}$ and $e^{\text{WM}}$ as defined in Equations (5a) and (5b).

The above considerations can be formulated more concisely in the language of Hilbert spaces. An inner product of random effects with expectation zero is defined by

$$\langle v, w \rangle = \sum_{a_d} \text{cov}(v, w).$$

Then $\pi^{\text{WM}}$ is the orthogonal projection of the combined random effects $r_{iwm} = y_{iwm} - p_i$ onto the subspace spanned by $\pi^Q_w$ and $\pi^w$. An orthogonal basis of this subspace is given by the Gram-Schmidt procedure and consists of $v_1 = \pi^Q_w$ and $v_2 = \pi^w - \pi^{\text{WM}}$. Then, $\pi^{\text{WM}}$ can be calculated as

$$\pi^{\text{WM}} = \langle v_1, r_{iwm} \rangle \langle v_1, v_1 \rangle + \langle v_2, r_{iwm} \rangle \langle v_2, v_2 \rangle,$$

and

$$e^{\text{WM}} = r_{iwm} - \pi^{\text{WM}}.$$