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Original article

First estimate of genetic parameters for the Syrian honey bee *Apis mellifera syriaca*

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Abstract – Population-specific parameters are important for designing breeding programmes, providing insights into the possible genetic gain achieved in the conditions under which the traits were measured. In the present study, 72 beekeepers and three breeding centres provided performance testing results from 1,088 colonies. (Co)variances were estimated by restricted maximal likelihood (REML). Computations were carried out with both REMLF90 and AIREMLF90 software. In this first approach for *Apis mellifera syriaca*, a typical representative of the endangered subspecies of the Middle East, we found that the heritabilities for honey production (H) and gentleness (G) were h_H^2=0.27±0.32 and h_G^2=0.08±0.28, respectively. A negative genetic correlation between the two traits was estimated (r_{HG}=−0.50±0.93).

***Apis mellifera syriaca* / genetic correlation / indigenous population / heritability / Syrian honey bee**

1. INTRODUCTION

Apis mellifera syriaca Buttel-Reepen 1906 is a native honey bee in the eastern Mediterranean region and clusters within the near east races (Ruttner 1988; Ftayeh et al. 1994). The Syrian honey bee (SB) is distributed in Syria, Lebanon, Iraq, Jordan, Palestine and southern Turkey. The SB is well adapted to extreme hot and dry climates (Zaitoun 2000; Zaitoun et al. 2000; Al Ghzawi et al. 2001) and has a superior ability to adapt egg laying to pollen availability and honey flow (Haddad and Fuchs 2004). This honey bee subspecies is well adapted to withstand attacks from the most powerful local predators, such as *Vespa orientalis* and *Merops orientalis* (Blum 1956; Kalman 1973; Ruttner 1988). Moreover, Zaitoun et al. (2001) have reported an extraordinary grooming behaviour in SBs that is assumed to be an important resistance factor towards the ectoparasitic mite *Varroa destructor* (Peng et al. 1987). In spite of these advantages, beekeepers in Syria commonly try to displace the indigenous population with European honey bee races because the local races do not meet the apicultural demands of modern beekeeping. However, European queens also fail to fulfil the expectations of beekeepers under the local conditions because pure European colonies do not produce much more honey than the local breeds under these conditions and hybrids with SBs are not gentle. Moreover, beekeepers have reported high queen losses during the introduction of European queens into the local Syrian colonies, a phenomenon also observed in other countries in the Middle East with requeening practices (Bienefeld et al. 1996). Consequently, selection within the well-adapted local subspecies for characters such as honey production (H) and gentleness (G), reported to be most important for Syrian beekeepers (Zakour and Bienefeld, unpublished data), seems to be the most promising

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approach. However, to date, the results of attempts at selection have been disappointing. Moreover, genetic parameters essential for the design of a breeding programme are lacking for this population. Several genetic parameters are available for the European races (Table I), but just a single one (for the trait honey production) for *A. mellifera meda* from Iran (Mostajeran et al. 2000) is available among the Middle Eastern races. Further, this parameter is based on a small dataset (150 colonies), and consequently, this estimate is subject to a high standard error. Moreover, this estimate results from an experiment designed for this purpose, with standardised colony management and data recording, which tend to reduce environmental variation and consequently result in higher genetic parameters than estimates based on field data from beekeepers.

However, for the design and implementation of a breeding programme, genetic parameters are needed that have been estimated in the conditions under which selection takes place. These kinds of genetic parameters are lacking not only for the Syrian and other Middle

Table I. Heritability estimates for honey production and gentleness characters of various honey bee subspecies.

Subspecies	Trait	h^2	SE	Method	NTC	Data	Reference
A. mellifera ligustica	H	0.36 0.58	0.16 0.35	REAL VAR_Q	48 64	BR	Soller and Bar-Cohen 1967
		0.54	0.16	MDR	479		Bar-Cohen et al. 1978
A. mellifera carnica	H	0.23	–	VAR_W	55	EX	Pirchner et al. 1960
		0.19	–	MDR	500	–	Vesely and Siler 1964
		0.75	–		12	EX	El-Banby 1967
		0.26_W 0.15_Q	0.10 0.11	REML	5,342	BK	Bienefeld and Pirchner 1990
	G	0.41_W 0.40_Q	0.25				
	H G	0.24 0.08	–		2,864	BK and BR	Willam and Eßl 1993
	H	0.29–0.39 0.14	–	VAR_Q	1,530 2,332	BK	Börger 1969
A. mellifera	G	0.38 0.32	0.05 0.08	OPR OSR	36	EX	Moritz et al. 1987
		0.30–0.57	–	REAL			
		1.28	0.32	OSR[a]			
		1.5	0.20	OPR[a]			
		0.81	0.20	VAR_W			
A. mellifera	H	0.16–0.25	–	–	–	BK	Zawilski 1974
		0.07–0.24	–	REAL	83	EX	Malkow et al. 1976
A. mellifera mellifera	H	0.27	–	–	300	EX	Kriwzow 1976
A. mellifera carpatica	H	0.11–0.18	–	–	–	EX	Grankin 1976
A. mellifera meda	H	0.30	–	INTR	150	EX	Mostajeran et al. 2000

h^2 heritability, *SE* standard error, *H* honey production, *G* gentleness, *NTC* number of tested colonies, *BR* data provided by bee-breeding centres, *BK* data provided by beekeepers, *EX* data obtained from scientific experiment, *W* separate heritability estimates for worker effect, *Q* separate heritability estimates for queen effect, *REAL* realized heritability, *VAR_Q* analysis of variance between queens, *VAR_W* analysis of variance between workers, *MDR* mother–daughter regression, *REML* restricted maximal likelihood, *OPR* offspring–mean parents regression, *OSR* offspring-sire regression, *INTR* intraclass correlation.

[a] Parent data are standardised to the mean value of the offspring.

Eastern honey bee populations but also for populations worldwide. Because the general conditions under which bee breeding takes place in Syria are typical of those for other developing countries in the Middle East and other parts of the world, estimates within an unselected population with a poor tradition in honey bee breeding are likely to be of interest for honey bee-breeding programmes in several countries. Consequently, the present study is aimed at estimating genetic parameters for honey production and gentleness in an unselected honey bee subspecies under conditions usually found in countries that start with breeding programmes in this species.

2. MATERIALS AND METHODS

2.1. Data structure

The theoretical background and the practical methods of performance testing were presented at several meetings in Syria for private bee breeders and staff of bee-breeding centres. In 2009 and 2010, data from 1,088 uncontrolled mated Syrian honey bee colonies (from 41 different Syrian regions) were provided by the Syrian Federation of Chambers of Agriculture. Tested queens were reared at 72 commercial Syrian apiaries and three bee-breeding centres. From the 26 state honey bee-breeding centres, altogether keeping about 2,000 colonies, only three provided (n=209) performance testing data for this study. The remaining 879 test results came from private apiaries. In 2009, 112 of the altogether 806 tested colonies (with unknown genetic relationship) were selected as breeding colonies. In 2010, test results of 282 offspring colonies were available. The average offspring colony number per breeding colony was 2.5. Fifty-eight breeding colonies had just one offspring colony. All colonies involved in this study were assumed to be *A. mellifera syriaca*, but only 6 % of the colonies were examined morphologically for pure breeding. Consequently, we cannot exclude the possibility of hybrid colonies in our dataset. The colonies were kept in Langstroth-type (n=967) and local-type (n=121) hives (Alhafany 1996; Abed 1998). If both types were used at the same apiary, colonies with different hive types were considered as separate apiaries to adjust for this effect. Honey production was estimated by the number of honey combs times a factor of 2.5. Gentleness was recorded subjectively according to Ruttner (1972). The scoring system for gentleness during inspection ranged from 1 (worst) to 4 (best). In most cases, gentleness was observed five times per colony (n=5,668 records), and the average was used for estimating genetic parameters. Because of the non-normal distribution of the gentleness behaviour data, this estimate was conducted with exponentially transformed values. Details describing the data set are summarised in Table II.

2.2. Statistical model

We uses a mixed model with the combined year × apiary effect as a fixed and the queen as a random effect.

$$Y = Xb + Zu + e$$

where Y is the vector of the colony observations; b, u and e are vectors of fixed, random queen and residual effects, respectively, and X and Z are incidence matrices relating observations to b and u, respectively.

Since the queens are ordered within traits, the bivariate mixed queen model is as follows:

$$\begin{pmatrix} Y_H \\ Y_G \end{pmatrix} = \begin{pmatrix} X_H & 0 \\ 0 & X_G \end{pmatrix} \begin{pmatrix} b_H \\ b_G \end{pmatrix} + \begin{pmatrix} Z_H & 0 \\ 0 & Z_G \end{pmatrix} \begin{pmatrix} u_H \\ u_G \end{pmatrix} + \begin{pmatrix} e_H \\ e_G \end{pmatrix}$$

The relatedness matrix defines a covariance structure for the respective additive genetic effects of both traits (Mrode 1996; Lynch and Walsh 1998). It is assumed that

$$\mathrm{var}\begin{pmatrix} a_H \\ a_G \\ e_H \\ e_G \end{pmatrix} = \begin{pmatrix} a_{HH}A & a_{HG}A & 0 & 0 \\ a_{GH}A & a_{GG}A & 0 & 0 \\ 0 & 0 & e_{HH} & e_{HG} \\ 0 & 0 & e_{GH} & e_{GG} \end{pmatrix}$$

where A is the numerator relationship matrix, which is symmetric, and its diagonal element for queen i is equal to $1+F_i$ (Henderson 1976a, b), where F_i is the inbreeding coefficient of queen i (Wright 1922) and is

always 0 under our conditions of uncontrolled mating. The off-diagonal elements constitute the coefficient of the relationship between queens *i* and *j*. The tested colonies used in the analyses stemmed from uncontrolled matings; this means that the pedigree information is only available on the maternal side, which may result in an underestimation of genetic relatedness. The required inverse of the numerator relationship matrix A^{-1} was calculated according to the Henderson (1976a) and Dempfle (1989) algorithm. The computing technique has been fully described by Bienefeld and Pirchner (1990).

In the above matrix, a_{HH}, a_{GG} and $a_{HG}=a_{GH}$ are the elements of additive genetic variance and the covariance matrix for queen effects; e_{HH}, e_{GG} and $e_{HG}=e_{GH}$ are the elements of variance and the covariance matrix for the residual effects. (Co)variances were estimated by restricted maximal likelihood (REML) using REMLF90 and AIREMLF90 software, as presented by Misztal et al. (2002). The programme was run until a convergence criterion of (10^{-11}) was reached.

The standard errors of heritability and of genetic correlation were calculated with formulae 1 and 2 (see below), respectively (the approach of Lynch and Walsh 1998).

Formula 1, standard error for heritability:

$$\mathrm{SE}_{\mathrm{H}}^{2} = \left[\left(\frac{h^2}{a}\right)\left\{\left(1-h^2\right)^2\mathrm{var}(a) - 2\left(1-h^2\right)h^2\mathrm{cov}(a,e) + \left(h^2\right)^2\mathrm{var}(e)\right\}\right]^{1/2}$$

Formula 2, standard error for genetic correlation:

$$\mathrm{SE}_r = r\left[\frac{\mathrm{var}(a_{\mathrm{H}})}{4a_{\mathrm{H}}^2} + \frac{\mathrm{var}(a_{\mathrm{G}})}{4a_{\mathrm{G}}^2} + \frac{\mathrm{var}(a_{\mathrm{HG}})}{a_{\mathrm{HG}}^2} + \frac{\mathrm{cov}(a_{\mathrm{H}},a_{\mathrm{G}})}{2a_{\mathrm{H}}a_{\mathrm{G}}} - \frac{\mathrm{cov}(a_{\mathrm{H}},a_{\mathrm{HG}})}{a_{\mathrm{H}}a_{\mathrm{HG}}} - \frac{\mathrm{cov}(a_{\mathrm{G}},a_{\mathrm{HG}})}{a_{\mathrm{G}}a_{\mathrm{HG}}}\right]^{1/2}$$

3. RESULTS

The average honey production was 8.9±4.0 kg, with significant differences (F=265.6, P=<0.0001) between colonies kept in Langstroth-type (9.4±3.7 kg) or in local-type (2.6±1.1 kg) hives. The average score for gentleness was 1.5±0.5 (Table II) which represents highly aggressive colonies on the scale of Ruttner (1972). Gentleness was also significantly different between colonies (F=24.0, P=<0.0001) kept in Langstroth-type (1.6±0.5) or local-type hives (1.3±0.5). The additive genetic variance and covariance for H and G (a_{HH}, a_{GG} and $a_{HG}=a_{GH}$, see Section 2 for definition) were estimated to be 1.0718, 0.2683 and −0.3208, respectively. The corresponding estimates for the residuals (e_{HH}, e_{GG} and $e_{HG}=e_{GH}$) were 2.8827, 3.1535 and 0.0033, respectively.

The estimated heritability of honey production had a medium value of h_H^2=0.27±0.32. The heritability of gentleness score was estimated to be lower (h_G^2=0.08±0.28). The genetic correlation between honey production and gentleness was found to be negative (r_{HG}=−0.50±0.93).

4. DISCUSSION

The peculiarities of honey bee genetics and biology, such as the haplodiploid state, multiple mating of queens and eusociality, which result in combined contributions of queens and workers to

Table II. Descriptive statistics of traits measured in 2009 and 2010.

Year	Trait	N	$\overline{X}$	S	Minimum	Maximum
2009	Honey production (kg)	806	8.5	3.32	0.5	23.8
	Gentleness		1.5	0.40	1	3.1
2010	Honey production (kg)	282	10.2	2.58	1	20.0
	Gentleness		1.5	0.42	1	3.1

N number of tested Syrian honey bee colonies, $\overline{X}$ mean, S standard deviation, *Gentleness* scored subjectively from 1 (worst) to 4 (best).

colony performance, and the strong negative genetic correlation between the contributions of each caste (Bienefeld and Pirchner 1990, 1991; Liu and Smith 2000), result in serious problems for correctly estimating genetic parameters in this species. In addition, when comparing our estimates with the parameters listed in Table I, one has to consider that these estimates differ greatly depending on the statistical method used, data source (experimental or from beekeepers' performance tests) and extreme differences in data set sizes.

However, by averaging the heritability for honey production over all studies performed on European races, an average h^2 (0.32) for honey production has been found, which is slightly higher than our value (0.27) estimated under practical apicultural conditions in Syria. Heritabilities of this magnitude indicate that selection should be effective.

Bienefeld et al. (2008) found a highly significant genetic gain (0.5 % per year) with respect to honey production in the German *A. mellifera carnica* population. However, this genetic response was promoted by genetic evaluation, which considers separate heritabilities for queen and worker effects on honey production and the negative genetic correlation between queen and worker effects (Bienefeld et al. 2007). The structure of the data provided by the Syrian beekeepers (uncontrolled mating of the queens and, consequently, missing paternal pedigree information) does not allow estimation of the heritabilities of the impact of the two honey bee castes separately and the correlation between them.

For characters associated with gentleness, the experimental data of Moritz et al. (1987) resulted in moderate to extremely high (out of range) heritabilities (0.3–1.5), and these data are therefore not useful for comparisons. By using the same Ruttner (1972) scoring method in a pure-bred *A. mellifera carnica* population, Bienefeld and Pirchner (1990) found, with their somewhat more complex approach (considering both queen and worker effects), higher h^2 values (0.41 and 0.40) for worker and queen effects, respectively, and a negative genetic correlation (r_{QW}=−0.91±0.15) between them. The estimate for the Syrian population (0.08±0.28) is much lower. However, this h^2 value is identical to an estimate for the combination of calmness and gentleness published by Willam and Eßl (1993) for an *A. mellifera carnica* population under selection. In other taxa, different estimates of heritability for the same character in the same species have been found to show a wide range of variation, some of which might reflect real differences between populations or the conditions under which they are studied (Falconer 1981). Usually, the non-selected Syrian honey bee population are expected to show a larger genetic variation and, consequently, a higher h^2. However, due to the consideration of the (negative) covariance in the study of Bienefeld and Pirchner (1990) between queen and worker effects, the parameters are not directly comparable. Willham (1963) pointed out that a negative genetic correlation between mother (in our case, queen) and offspring (worker) effects causes that sufficient genetic variance with respect to mother and offspring effects is not being translated into the equivalent variability of the phenotypic (whole colony) variance. This is likely to lower the heritability, if

estimated by methods neglecting the negative covariance. Moreover, the method of measuring gentleness was introduced shortly before the performance testing started. The lack of experience of the beekeepers is likely to increase the phenotypic variation, so that the ratio of genetic and phenotypic variance, the heritability, is predicted to be smaller.

In contrast to Bienefeld and Pirchner (1991) and Willam and Eßl (1993), who found insignificant, but even slight positive genetic correlations between honey production and gentleness in a pure-bred *A. mellifera carnica* population in Germany and in Austria, respectively, the corresponding estimate of correlation in the Syrian honey bee population is estimated to be negative ($r_{HG}=-0.50\pm0.93$). This negative genetic correlation might be explained by partial hybridisation within the Syrian honey bee population (Zakour and Bienefeld, unpublished data). Heterosis has been found to result in higher honey production, but lower gentleness (Ruttner 1968). Alternatively, the negative genetic correlation might be attributable to the natural selection of Syrian honey bees under unique Syrian geographical and environmental conditions, as a type of adaptation of this subspecies to its local environment. Lerner (1950) and Falconer (1981) have pointed out that if selection is applied to two traits simultaneously, then pleiotropic genes that affect both characters in the desired direction will be acted upon strongly by selection and brought rapidly towards fixation, whereas pleiotropic genes that affect one character favourably and the other adversely will be influenced much less by selection and will remain at intermediate frequencies, so that subsequently the genetic correlation between the two characters becomes negative. However, the standard error of our genetic correlation estimate is large and so a more detailed interpretation of the negative relationship between honey production and behaviour should await further studies with a larger and controlled-mated population.

Finally, genetic diversity is generally assumed to be an important barrier against changing environmental conditions (Le Conte and Navajas 2008). The worldwide displacement of several subspecies of *A. mellifera* (Jensen et al. 2005; Meixner et al. 2010) by two European subspecies, *A. mellifera carnica* and *A. mellifera ligustica*, is unacceptable. However, the import of these European races documents the discontent of beekeepers with the local population in many countries. The poor honey production and aggressive behaviour of the Syrian honey bee population found in this study are likely to explain this discontent. But poor performance and aggressive behaviour of the Syrian honey bees are also affected environmentally, as exemplary shown by significant hive type effects on both traits. We have no experimental data on these hive type effects and could only speculate about the causes. However, it was necessary considering apiaries at which different hive types were simultaneously used as separate apiaries to adjust for this significant effect in the statistical model.

Our study provides evidence that, even in the absence of well-established infrastructure and education of beekeepers, honey production and, with some restrictions, gentleness are inherited to a degree that indicates a genetic advantage for these traits. In view of these heritabilities, a much more favourable approach would be to select well-adapted local races for higher productivity and more gentle behaviour than to adapt European races to a harsh environment and a new predator situation in their new home. The European races are not adapted to the extreme environment, but the races of the Middle East are. Additionally, we do not have estimates of the heritability of adaptation to this environment or the genetic correlation between adaptation and productivity, but the reported heritability of honey production may favour the selection of local breeds for higher productivity rather than foreign races for adaptation. If the performance tests and selection for productivity are done under Syrian conditions, the bees may not lose their adaptation to the local environment. Several autochthonous honey bee subspecies are facing extinction (Meixner et al. 2010; De la Rúa et al. 2009), and consequently, breeding programmes designed to improve these

subspecies to meet the demands of beekeepers should be accompanied by efficient checks for pure-bred status and an import ban on foreign honey bee races.

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Première estimation de paramètres génétiques pour l'abeille syrienne *Apis mellifera syriaca*

***Apis mellifera syriaca* / corrélation génétique / population indigène / héritabilité / abeille syrienne**

Erste Schätzung genetischer Parameter für die syrische Honigbiene *Apis mellifera syriaca*

***Apis mellifera syriaca* / genetische Korrelation / genetische Parameter / Heritabilität / syrische Honigbiene**

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