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619. Genetic analysis of royal jelly production and behaviour traits of honeybees

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Abstract

To improve their honeybee population, the royal jelly producers focus their selection objectives on both production and colony behaviour traits to maintain a sustainable production. To estimate genetic parameters for all these traits, a dataset from the French royal jelly producers group including records collected from 1,347 colonies was analysed using ReML methodology applied to animal models. Heritability estimates for royal jelly production traits were moderate while estimates for colony behaviour traits (gentleness, non-swarming behaviour, spring development, non-sanitary susceptibility and feed autonomy during hollow of honey flow) ranged from low estimates (0.10 ± 0.10 for non-swarming behaviour) to very high estimates (0.68 ± 0.10 for feed autonomy). Unfortunately, the dataset was too small to obtain reliable estimates for the genetic correlations between production and behaviour traits.

Introduction

Royal jelly production requires highly selected strains of honeybees to be profitable for beekeepers. Therefore, French royal jelly producers belonging to the 'GPGR' group conduct a collective breeding program with data recording since 2011. This very specific production requires a full-time work for a beekeeper taking care of only about a few dozen of colonies. Therefore, information to be analysed even after ten years of data collection is based on less than 1,500 colonies with performance testing, which corresponds to a very small dataset size for any analysis in quantitative genetics. Due to its very high economic value, the main trait of interest for the beekeepers is the amount of royal jelly produced per colony. However, beekeepers have also to consider various colony behaviour traits in order to maintain sustainable production conditions. First of all, the colonies being visited often, it is important that the bees are not too aggressive. The non-swarming tendency and the absence of susceptibility to disease are all the more important traits than royal jelly production relies on small size apiaries for which any colony loss has major economic impact. In addition, feed self-sufficiency becomes a major issue for colony survival and productivity in the context of climate change, the lack of floral resources being increasingly felt even during the production season. Beyond the risk of colony loss, the overall dynamics of the colonies will be lower and the production penalized for colonies with little feed autonomy. For all these reasons, it is important to develop a multicriteria breeding program considering jointly production and behaviour traits. The aim of the study was therefore to estimate genetic parameters for the main traits of interest for royal jelly producers to better orient the breeding program.

Materials & methods

Honeybee population. The French Royal Jelly Producers Group 'GPGR' is carrying out a breeding program at the national scale to select improved honeybees for their very specific production. Although data collection started in 2011, only records from years 2013 to 2021 were kept for the analysis because data have only been homogeneously recorded since 2013. Our dataset included records for 1,347 queens of which 808 were open mated and 539 were mated by artificial insemination and were potential breeding queens (BQs). Each year, a new generation of queens was produced from a pool of 9 BQs on average born the previous year. Those breeding queens came from 6 bee breeders that have been working together since

2011. Each year, 8 to 18 different beekeepers have been involved in performance testing of an average of 12 BQs' daughters to select the drone-producing queens (DPQs) of the next generation. Generation interval is therefore 2 years on the sire path.

Performance testing. Queen performance test starts after the first colony wintering, when all workers are daughters of the tested queen (Büchler *et al.*, 2013). Beekeepers initiate royal jelly production for the tested queens as early as possible in the season, generally between April and May, depending on the year and the area. To do so, each hive has a queenless part in which queen cells with young larvae (stage L1) are introduced. Then, every 3 days, beekeepers harvest the royal jelly produced and introduce new queen cells with young larvae. For each colony, amount of royal jelly is recorded for the first two harvests in the season (respectively named P1 and P2) and the mean production ($PROD=(P1+P2)/2$) is also analysed.

Regarding behaviour traits, gentleness (GENT), non-swarming tendency (SWAR) and spring colony development (DEVE) are assess according to the COLOSS BEEBOOK recommendations (Büchler *et al.*, 2013) with a visual score ranging from 1 (worst score) to 4 (best score). In order to assess overall disease resistance (SANI) and feed autonomy (AUTO) during hollows of honey flow in the production season, beekeepers evaluate their colonies with scores ranging also from 1 to 4 almost every three days at harvest time. SANI and AUTO were analysed considering information collected the days with the worst average scores within apiary.

Genetic parameters estimation. BLUP animal genetic models were used to fit the data using BLUPF90 and its AIREMLF90 program was used to estimate genetic parameters based on the inverse of a relationship matrix derived from an R program based on Brascamp and Bijma (2014, 2019) methodology and software. To build this matrix, we assumed that each queen was mated to 8 drones bred either by a single DPQ for artificially inseminated queens or by 100 unrelated DPQs for open mated queens. Genetic parameters were initially estimated with a model considering both direct (Worker effect) and maternal (Queen effect) random genetic effects in the model describing any phenotype y_{ijk} for colony k along with the fixed effect of the contemporary group CG_{ij} constituted by the combined environmental effects of apiary i and year j :

$$y_{ijk} = \mu + CG_{ij} + Worker_k + Queen_k + e_{ijk}, \text{ with } \mu \text{ the overall average and } e_{ijk} \text{ the residual effect.}$$

For all the behaviour traits, the ReML algorithm did not converge and, therefore, a simple model was used only accounting for the contemporary group fixed effect and a single random genetic effect as a colony effect combining both worker and queen effects (Du *et al.*, 2022):

$$y_{ijk} = \mu + CG_{ij} + Colony_k + \epsilon_{ijk}, \text{ with } \mu \text{ the overall average and } \epsilon_{ijk} \text{ the residual effect.}$$

For production traits (P1, P2 and PROD), heritability estimates were obtained for both the direct genetic effect (h^2_d) and the maternal genetic effect (h^2_m), as well as the genetic correlation between the two effects (r_{dm}). The simple colony effect model produced a unique estimate of heritability for a synthetic colony trait (h^2_c). Genetic correlations between production and behaviour traits were calculated under this simple model.

Results

Performance statistics. Most of the queens have recorded data on all traits (Table 1). AUTO is the exception because its evaluation started in 2017 and only 733 records have been used in the analysis. During the production period considered, the average royal jelly produced was 32.9 g per harvest day and colony (Table 1).

Table 1. Performance statistics for production at first (P1), second (P2) harvests, and in average (PROD) and scores for gentleness (GENT), swarming (SWAR), sanitary status (SANI), colony development (DEVE) and feed autonomy (AUTO).

Trait	All tested queens			Open mated queens			Artificially inseminated queens		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
Production traits (g)									
P1	1,293	31.0	16.2	772	27.8	15.2	521	35.7	16.4
P2	1,298	34.9	18.0	775	30.8	16.9	523	41.0	18.0
PROD	1,293	32.9	15.9	772	29.3	14.8	521	38.3	15.9
Behaviour traits (score ranging from 1 to 4)									
GENT	1,114	2.97	0.64	639	2.94	0.68	475	3.00	0.58
SWAR	1,018	3.51	0.71	593	3.45	0.80	425	3.59	0.56
SANI	1,269	3.21	0.70	755	3.09	0.68	514	3.93	0.70
DEVE	961	2.98	0.88	602	3.00	0.87	359	2.95	0.89
AUTO	733	2.03	0.94	396	2.10	0.97	337	3.11	0.51

Genetic parameters. Table 2.a shows that moderate to strong estimates of direct heritability were derived for all the production traits while estimates of maternal heritability were low and not significantly different from zero. In addition, strong negative genetic correlations between direct and maternal effects were estimated, but with extreme standard error values (ranging from 0.7 to 1.9). With a colony effect model, heritability for any production trait was moderate. The genetic correlation between P1 and P2 was strong (0.66) and their genetic correlations with PROD was not significantly different from 1 (Table 2.b).

Heritability for behaviour traits ranged from low estimates for SWAR to very high estimates for GENT and AUTO (Table 3). Apart from SWAR, all values were significantly different from zero. At the only exception of the negative estimates of the genetic correlations between DEVE and production traits, correlations between all other colony behaviour traits and production traits could not be considered as reliable (strong difference between L1 and L2 estimates) and/or significantly different from zero.

Table 2. Genetic parameters across production traits.

Trait	a. Worker-Queen model			b. Colony model		
	h^2_d	H^2_m	r_{dm}	P1	P2	PROD
P1	0.41±0.18	0.07±0.07	-0.65±1.90	0.32±0.11	0.66±0.34	0.88±0.33
P2	0.54±0.17	0.14±0.10	-0.66±0.74		0.41±0.10	0.94±0.14
PROD	0.52±0.17	0.12±0.09	-0.68±1.22			0.38±0.10

Table 3. Heritability of behaviour traits and genetic correlations with production traits.

	GENT	SWAR	SANI	DEVE	AUTO
Heritability	0.65±0.10	0.10±0.10	0.27±0.10	0.52±0.13	0.68±0.10
Correlation with P1	na ¹	0.31±0.86	-0.03±0.48	-0.73±0.28	-0.76±0.22
Correlation with P2	0.57±0.24	0.29±0.66	0.53±0.36	-0.58±0.39	-0.09±0.34
Correlation with PROD	0.12±0.32	0.30±1.45	0.03±0.42	-0.67±0.30	-0.31±0.33

¹ na = ReML did not converge for this parameter.

Discussion

Royal jelly production showed a relatively high heritability at the colony or direct worker genetic effect level, which confirms earlier results (Phocas *et al.*, 2017) on the same historical population and the possibility of improving production performance. Estimates of heritability for behaviour traits were less consistent across analyses since Phocas *et al.* (2017) estimated quite different values for GENT (0.40), SWAR (0.40) and SANI (0.10), but considering a different genetic model than the colony one. Nevertheless, apart from swarming tendency, our results are therefore encouraging to integrate behaviour traits in the breeding program. However, correlations between production and behaviour traits were clearly not reliable. Phocas *et al.* (2017) found a significant negative genetic correlation (-0.71 ± 0.14) between PROD and SANI, while this correlation appeared now to be null or even positive depending on the production trait considered.

Last but not the least, it is important to notice that the estimates of genetic correlation between direct and maternal effects were strongly negative. The huge standard errors of these estimates give evidence that the structure and size of our dataset was clearly insufficient to disentangle worker and queen genetic effects in the colony performance. While it imposes caution on the true value of direct-maternal genetic correlation, it is however interesting to notice that our estimates are close to estimates derived for larger datasets on other bee populations and traits (Brascamp *et al.*, 2018). Our results confirm the ones based on simulated data from Kistler *et al.* (2022) and the importance of very large datasets to get reliable estimates of genetic parameters. Therefore, we are facing many uncertainties for implementing robust breeding programs for small honeybee populations.

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