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Original article

Estimation of heritability of some characteristics of hind legs and wings of honeybee workers (*Apis mellifera carnica* Polm) using the half-sibs method

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Summary — Morphometrical investigations were done on 732 honeybee workers from 44 colonies in the apiary of the Agricultural Institute of Slovenia. Fore- and hind-wing area, cubital index, length of hairs on tergite 5, side surfaces of tibia, femur and metatarsus, and the length of tibial hairs on the prepared hind legs were measured. The total side surfaces of hind-leg and wings were calculated. Investigated characteristics of bees were divided into 2 groups: the first group included hind-leg and wing sizes while the second included hairs and index characteristics. The characteristics from the first group showed more expressed phenotypic and genetic correlation than the characteristics from the second group. All estimated heritabilities were large and significant. In an artificial selection of described properties of bees the selected traits are more or less successfully changed, the unselected characteristics are always a compromise between genetic relationships to the selected trait, and selection due to environment.

population genetics / heritability / biometry / half-sibs method

INTRODUCTION

Morphological characteristics of honeybee workers have been important since honeybee trade started in the middle of the 19th century. Visible characteristics of bees were long a determining factor for the purity of races. New parameters were added to the investigations of the length of proboscis in the 1920s: femur, tibia and metatarsus on the hind leg; length and width of the fore wing; and size of the wax mirror (Alpatov, 1929). Goetze (1940) introduced new parameters into the investigation of morphological traits of bees: wing venation and length of hair. In present practice there are 2 characters: the cubital index and the length of hair on tergite 5 which is useful in discriminating between the European races of bees (Ruttner, 1988). For the detailed investigations of the overlap of different strains and races in genus *Apis*, 40 morphological traits were selected from a greater number of measured characteristics. Traditional descriptive methods of traits of honeybee colonies use the means of colony characters as variables for statistical analysis. At present statistical analyses are mostly done by one of the standard multivariate methods.

The purpose of the work done on many morphometric characteristics of bees has been to improve the production traits of honeybee colonies. In many cases the final result should be to achieve the removal of undesirable strains or hybrids of bees from the production apiaries, and inclusion of the selected stock in the population. Selected bee colonies should be superior to the unselected colonies in honey production, and have reduced swarming and non-stinging behavior. The morphological characteristics that show a close relation to the production traits of colonies are very interesting for beekeepers. One of the most promising characteristics has been the corbicula size (Milne and Pries, 1984). The selection goal, a larger corbicula size, should mean greater pollen pellets from a single worker-bee flight, better pollen supply of the whole family, and greater honey yields (Milne and Pries, 1986). The question is why nature has not provided bees with a larger corbicula area. One of many possible answers could be the pleiotropic effect of the alleles that contribute to the determination of the size of corbicula area.

MATERIAL AND METHODS

Morphometrical investigations were done on 732 honeybee workers from 44 colonies in the apiary Senično–Brdo of the Agricultural Institute of Slovenia. All queen-mothers were unrelated and were mated naturally.

Combs with emerging brood were put into separate boxes in an incubator. One-day-old bees were put into laboratory test cages, with 50 honeybee workers in each cage. Five-day-old bees were anesthetized and killed in an ether atmosphere. Each bee was then numbered to prevent any kind of mistake. The length of hairs on tergite 5 was measured immediately. The hind legs, and fore and hind wings of each bee were prepared. Prepared body parts of honeybee workers were measured under a magnification of 24 on the graphic tablet. Software program *Apis* (Pernuš, 1990) produces raw data prepared for the mixed-model least-squares and maximum likelihood PC–1 programs LSMLMW (Harvey, 1987).

The values of 10 characteristics of each single bee were determined. The side surfaces of the tibia, femur and metatarsus, and the length of the tibial hairs were measured from the prepared hind legs. At the same time the total side surface of the hind leg was calculated. On the fore wing, only the cubutal index (wing venation) and the total surface were measured. The total surface of wing area was also measured on the hind wing. The total surface of wings was calculated from these values.

All members of the honeybee colony are relatives. Two generations coexist as a unit. The queen and several father drones present as sperm in a sperm storage organ (spermatheca) are the parent generation. The offspring generation represents workers and drones. Female offspring from a single drone represent a super-sister group. Two workers originating from different fathers and a common mother are half sisters (Harbo and Rinderer, 1980). For the single honeybee colony, as a mix of many groups of honeybee worker super-sisters, the most likely pedigree coefficient of the relationship could be estimated. It should have a definite value which is characteristic for the half sisters ($r = 0.25$) and for the super-sisters ($r = 0.75$). If it is assumed that each group of super-sisters (= subfamily) consists of a very large number of bees with equal numbers of each subfamily, the expected colony relationship should be (Laidlaw and Page, 1984):

$$R = \frac{1}{4} + \frac{1}{2 * k} \qquad [1]$$

where: R: expected colony relationship; k: predicted number of subfamilies.

The exact determination of subfamily numbers was in most cases impossible. The number of matings, the short-term insemination effective number, has to be estimated. In our further analyses, the expected colony relationship of 0.296 was used. The value suits the short-term insemination effective number of 11. It was predicted that subfamilies would be at the same frequency.

Half sisters originate from the same mother, but from different fathers and have 25% common variability or an additive variance component of the genetic variance. Super-sisters have 75% additive variance component, and a further 50% variation due to dominance (Collins, 1986). The intraclass correlation coefficient (t) could be estimated for all cases: for half sibs 25%; for super-sibs 75%; for the whole bee colony more than the value of the expected colony relationships. The heritabilities and correlations were estimated using the prediction of the value of the average intraclass correlation coefficient of 0.32.

The LSMLMW PC–1 version computer program (Harvey, 1987) was used to run half-sib analysis of variance of worker bees from the same investigated colony. Model 2 of cited program runs Henderson's method 3 and estimates the genetic, phenotypic and environmental correlations between investigated traits, and their heritabilities.

The simple model used was:

$$Y_{ij} = \mu + \alpha_i + \varepsilon_{ij} \qquad [2]$$

Y_{ij}: estimated value of the desired characteristic of bees;

μ: common mean;

α_i: random influence of colony;

ε_{ij}: remainder.

The heritability was estimated using:

$$h^2 = \frac{\frac{1}{0.32} \bullet \sigma_s^2}{\sigma_s^2 + \sigma_{col}^2} \qquad [3]$$

where σ_s^2: sire – queen variance component; σ_{col}^2: colony variance component.

The standard error of h^2 was estimated by the formulae given by Swiger *et al* (1964) and Tallis (1959, cited by Harvey, 1987). Phenotypic and genetic correlations with their standard errors were estimated by the method of Falconer (1981). Environmental correlation was estimated by the formula cited by Harvey (1987).

Common environment inside a colony increases the similarity between relatives and increases the difference between bee colonies. The values of genetic parameters estimated from the above-cited model are probably slightly overestimated.

RESULTS AND DISCUSSION

For a clearer explanation of the given results the characteristics of bees could be divided into 2 groups: the first group of hind-leg and wing sizes and the second group of hair and index characteristics.

The body parts of hind legs and wings (except the femur) show similar phenotypic correlations between them (see table I). All the values are positive and above zero. Femur size is closely related to the whole hind-leg size only. The tibia show more expressed correlation to the metatarsus, whole hind-leg, fore- and hind-wing area and to the total surface of wings. The data on metatarsus were even more positive than the characteristics of the wings and hind-legs investigated. Similar expressed correlations are present for fore- and hind-wing area, and at total wing surface.

Characteristics from the second group show lower values around zero. Cubital index is negatively correlated to almost all body parts of the hind leg and wing areas. The phenotypic correlation of hairs is positive but small, in relation to all the characteristics of the bees investigated.

The trends of genetic correlation are similar to the phenotypic trends (table II). Of the first group only the femur size is less correlated to the other investigated characteristics. The correlation to the whole hind-leg size is an exception. The

Table I. Phenotypic correlations of lateral tibia area (TI), lateral femur area (FE) and lateral metatarsus area (ME), and sum of all 3 values (HL); surface of hind (HW) and fore wings (FW) and total surface of wings (HW + FW); cubital index (CI); length of corbicula hairs (LH/TI) and length of hairs on tergite 5 (LH/T5) from 732 worker bees from the apiary at Senično-Brdo.

	TI	*FE*	*ME*	*HL*	*HW*	*FW*	*HW + FW*	*CI*	*LH/TI*	*LH/T5*
TI	–	0.004	0.378	0.693	0.322	0.325	0.381	–0.06	0.048	–0.08
FE		–	0.145	0.634	0.085	0.150	0.145	0.01	–0.01	0.054
ME			–	0.672	0.314	0.400	0.429	–0.10	0.024	0.133
HL				–	0.344	0.416	0.455	–0.07	0.035	0.091
HW					–	0.424	0.778	–0.05	0.072	0.069
FW						–	0.899	–0.07	0.099	0.018
HW + FW							–	–0.07	0.103	0.045
CI								–	0.084	0.005
LH/TI									–	–0.10

Table II. Genetic correlations of 10 morphological characteristics of 732 honeybee workers from the apiary at Senično-Brdo.

	TI	*FE*	*ME*	*HL*	*HW*	*FW*	*HW + FW*	*CI*	*LH/TI*	*LH/T5*
TI	–	0.161	0.223	0.808	0.561	0.360	0.478	–0.141	0.077	–0.192
	–	±0.172	±0.160	±0.061	±0.125	±0.145	±0.130	±0.171	±0.190	±0.266
FE		–	0.020	0.584	0.009	0.198	0.147	0.093	0.131	0.658
		–	±0.181	±0.118	±0.187	±0.171	±0.175	±0.184	±0.202	±0.257
ME			–	0.646	0.551	0.598	0.646	–0.325	0.060	0.294
			–	±0.105	±0.130	±0.113	±0.105	±0.165	±0.195	±0.257
HL				–	0.576	0.553	0.623	–0.170	0.134	0.167
				–	±0.125	±0.121	±0.108	±0.174	±0.193	±0.279
HW					–	0.581	0.808	–0.362	0.160	0.164
					–	0.120	±0.063	±0.167	±0.198	±0.278
FW						–	–0.949	–0.199	0.064	–0.070
						–	±0.018	±0.170	±0.192	±0.281
HW+FW							–	–0.284	0.108	0.033
							–	±0.166	±0.192	±0.281
CI								–	0.208	–0.266
								–	±0.194	±0.308
LH/TI									–	–0.278
									–	±0.425

metatarsus size is closely related to almost all the characteristics of the first group. Similar values are also present for the wing characteristics. Unexpectedly high values of the first group cause changes in almost all characteristics upon selection of a single trait described. Selective increase of the corbicula size, for example, influences the enlargement of the whole hind leg and the wings.

The genetic correlation of the cubital index to the tibia size is negative but nonsignificant. The significant negative genetic correlations to the metatarsus size, hind and fore-wing area, and the sum of wing surfaces are also remarkable. The negative genetic correlation to the hind-leg size is situated at the limit of statistical significance. The selective changing of cubital index has a certain influence on the largeness of the wings and hind legs of honeybee workers: smaller cubital index and larger wings and legs. Hair length on the tibia shows an almost non-significant correlation to the other characteristics. An exception is only the positive relation to the cubital index. The situation is similar to the length of hairs on tergite 5. A significant positive correlation is present in relation to the femur and metatarsus size. Concerning racial characteristics, the length of hairs on tergite 5 might be more suitable for the purification of bee races *(carnica vs mellifera)* than the cubital index. The genetic correlations to the hind-leg size and wing surface is less well expressed in this case.

All the estimated heritabilities (see table III) are large and significant. Additive variability was increased because of the dominant deviation of super-sisters, the common environment and the maternal effects of the family nest. The amount of variability was rather overestimated in relation to the variability between colonies. This affects the large estimates. Nevertheless the values are usable as orientation estimates.

Lateral tibia surface shows high genetic determination near to the value 1.00. This result confirms the findings of Milne (1986). A similar estimate of heritability was found in the metatarsus and hind-leg size, fore-wing area, wing surface and hairs on tergite 5. The group with medium to high estimates of heritability consist of femur size, hind-wing area and cubital index. The value present at cubital index confirms the formerly estimated values of Rihar (1972) and William (1991). The length of hairs on the tibia express medium heritability.

Environmental correlations arise from the fact that members of the same family are more likely to share similar environmental sites than members of different families (Bulmer, 1985). This represents a serious problem in the interpretation of correlated variables between individuals in a honeybee colony. Simultaneity of ontogenetic development of bees in a temporally fluctuating environment, and common conditions inside the colony nest could be explained as a kind of maternal environment.

Table III. Estimated heritabilities of 10 morphological characteristics based on 732 honeybee workers from 44 colonies from the apiary at Senično-Brdo (h^2 + se).

TI	*FE*	*ME*	*HL*	*HW*	*FW*	*HW + FW*	*CI*	*LH/TI*	*LH/T5*
1.343	0.642	0.937	0.955	0.683	1.163	1.067	0.745	0.374	1.265
± 0.181	± 0.140	± 0.166	± 0.167	± 0.144	± 0.178	± 0.174	± 0.150	± 0.105	± 0.299

The values of environmental correlation in table IV could be understood as a measure of how much of the interclass correlation is due to relatives having a common environment. It is evident that tibia size is negatively environmentally correlated to the metatarsus size, fore-wing area and to the wing surface; the same is true for the relation of hind-wing area to hind-leg size. The length of hairs on tergite 5 is also affected by environmental correlation of metatarsus and fore wings. Cubital index, as a characteristic of fore wing, is environmentally correlated to the forewing area, to the total surface of wings, and surprisingly, to the length of hairs on tergite 5. The given values suggest that the model used for evaluation of heritability is slightly inexact in our case.

Moritz (1991) compared the wing venations of samples of *Apis mellifera carnica* dating back to 1911 and that of the modern carniolan bee in Germany. Modern *carnica* is a hybrid between the former carniolan bee and *Apis mellifera mellifera* despite the desired racial characteristics of *carnica*. Similar differences probably exist between populations of *carnica* from Slovenia, its original territory, and Germany. Breeding of *carnica* in both countries certainly results in morphologically different bee strains.

The size of honeybee workers is limited first by environmental conditions which influence the gene pool of the population, and second by the maternal conditions of the bee family. Every honeybee population is approaching the optimal compromise between negatively correlated maternal and direct effects (Bienefeld, 1988). Heterozygous loci, which determine the size of hind legs and wings, are preferable because of selection due to the environment.

Selective fixation of alleles, which takes part in the analysis of characteristics of hind legs and wings, is from the point of view of our investigation most questionable. Because of the Hardy–Weinberg law of gene frequencies, a durable random drift is present in the selection process. Fixed alleles are more or less removed from further selection. In other words: natural selection runs parallel to the breeding work inside closed populations. It always forces the exact determining frequencies of alleles at each single place (apiary). In the artificial selection processes the selected traits are more or less successfully changed and the unselected characteristics are always a compromise between ge-

Table IV. Environmental correlations of 10 morphological characteristics of 732 honeybee workers from the apiary at Seničino-Brdo.

	TI	*FE*	*ME*	*HL*	*HW*	*FW*	*HW + FW*	*CI*	*LH/TI*	*LH/T5*
TI	–	0.414	–0.87	>1.00	0.653	–0.53	<–1.0	–0.27	0.013	0.506
FE		–	0.861	>1.00	0.235	0.087	–0.15	–0.19	–0.14	0.356
ME			–	>1.00	–0.90	>1.00	>1.00	>1.00	–0.06	<–1.0
HL				–	<–1.0	>1.00	>1.00	0.725	–0.27	0.289
HW					–	0.415	–0.61	0.738	–0.02	0.440
FW						–	<–1.0	–0.56	–0.18	–0.60
HW + FW							–	<–1.0	–0.02	–0.12
CI								–	–0.06	–0.39
LH/TI									–	–0.10

netic relationships to the selected trait and natural selection.

Various influences of environment make genetically different populations of bees quickly and easily. It could be further predicted that the selection of bees from the same gene pool under different environmental conditions using the same selection program results in a different genetic stock for several generations. The environment–genotype interaction at the selection of a single morphological characteristic of bees could disturb the achievement of main selection goal: higher honey yields. The share of selection due to environment is great and must be taken into consideration in all selection programs.

Résumé — Estimation de l'héritabilité de quelques caractères des pattes postérieures et des ailes chez les ouvrières d'abeilles (*Apis mellifera carnica* Polm) par la méthode des demi-fratries. Les études morphométriques ont porté sur les pattes postérieures et les ailes de 732 ouvrières d'abeilles prélevées dans 44 colonies du rucher Senicno-Brdo de l'Institut d'agriculture de Slovénie. Les paramètres suivants ont été mesurés sur les pattes préparées : surfaces latérales du tibia, du fémur et du métatarse, longueur des poils du tibia, surface latérale totale de la patte postérieure. Pour l'aile antérieure, seuls l'index cubital (ic) de la vénation alaire et la surface totale ont été calculés. En outre, on a mesuré la surface de l'aile postérieure et, à partir de ces valeurs, estimé la surface totale des 2 ailes. Pour chaque abeille, 10 caractères ont donc été déterminés. Le coefficient de parenté le plus approché et la parenté croissante entre les colonies ont été évalués. Les évaluations des héritabilités et des corrélations ont été faites en supposant un coefficient de corrélation intraclasses moyen de 0,32. On a évalué les corrélations génétiques, phénotypiques et environnementales entre les caractères étudiés, et leurs héritabilités. Pour une explication plus claire, les caractères peuvent être divisés en 2 groupes : un premier regroupant les mensurations de la patte postérieure et des ailes et un second les mesures des poils et de l'ic.

Les segments de la patte postérieure (sauf le fémur) et les ailes présentent entre eux des corrélations phénotypiques semblables (tableau I). Toutes les valeurs sont positives. Les caractères du second groupe présentent des valeurs plus faibles autour de zéro. L'ic est corrélé négativement avec presque tous les segments de la patte postérieure et les surfaces alaires. La corrélation phénotypique des poils est plus ou moins positive, mais néanmoins en étroite relation avec tous les autres caractères étudiés. Le métatarse est étroitement corrélé avec les poils et l'ic et aussi avec les autres caractères du premier groupe.

Les corrélations génétiques montrent les mêmes tendances que les corrélations phénotypiques (tableau III). Des valeurs étonnamment élevées du premier groupe provoquent des modifications de presque tous les caractères après sélection d'un seul caractère. Dans le second groupe, la corrélation génétique négative de l'ic avec de nombreux caractères du premier groupe est remarquable. La modification sélective de l'ic a une influence certaine sur la taille de l'aile et de la patte postérieure des ouvrières – plus l'ic est petit et plus l'aile et l'abeille sont grandes. La longueur des poils du tibia présente des corrélations à la limite de la signification avec les autres caractères.

Toutes les héritabilités évaluées sont élevées et significatives (tableau II). La taille de la variabilité intracolonies est surévaluée par rapport à la variabilité intercolonies. Cela affecte des évaluations élevées.

Des facteurs du milieu différents produisent rapidement et facilement des populations génétiquement différentes. On peut prédire que la sélection d'abeilles à partir d'un même groupe génétique, avec le même programme de sélection, conduira dans des conditions de milieu différentes à des souches génétiquement différentes.

génétique des populations / héritabilité / morphométrie / méthode des demi-fratries

Zusammenfassung — Schätzung der Erblichkeit einiger Merkmale der Hinterbeine und Flügel von Arbeitsbienen (*A m carnica* Polm) nach der Methode der Halbgeschwister. An 732 Arbeitsbienen aus 44 Völkern des Bienenstandes Senicno-Brdo des Slowenischen Agrarinstitutes wurden morphometrische Untersuchungen der Hinterbeine und Flügel der Bienen durchgeführt. An den präparierten Hinterbeinen wurden die seitlichen Oberflächen von Schenkel, Schiene und Fersenglied, sowie die Länge der Schienenborsten gemessen. Dazu wurde die gesamte Außenfläche des Hinterbeins berechnet. Vom Vorderflügel wurden nur der Cubitalindex des Geäders und die Gesamtfläche gemessen. Außerdem wurde die Fläche des Hinterflügels gemessen und aus diesen Werten die gesamte Fläche beider Flügel bestimmt. Für jede einzelne Biene wurden die Werte von 10 Merkmalen erfaßt. Es wurden der am besten angenäherte Verwandtschafts-koeffizient und die anzunehmende Verwandtschaft zwischen den Völkern geschätzt. Die Schätzungen der Heritabilitäten und der Korrelationen wurden unter der Annahme eines mittleren Intra-Klassen-Korrelationskoeffizienten von 0,32 vorgenommen. Es wurden die genetischen, phänotypischen und Umweltkorrelationen zwischen den untersuchten Merkmalen und ihren Heritabilitäten geschätzt. Zur besseren Erklärung können die Merkmale in zwei Gruppen geteilt werden: Die erste Gruppe mit den Größenmaßen von Hinterbein und Flügeln, die zweite Gruppe mit den Merkmalen der Borsten und des Cubitalindex.

Die Glieder der Hinterbeine (ausgenommen Oberschenkel) und die Flügel zeigen unter sich ähnliche phänotypische Korrelationen (Tabelle I). Alle Werte sind positiv über Null. Die Merkmale der zweiten Gruppe weisen niedrigere Werte um Null auf. Der Cubitalindex ist mit beinahe allen Teilen der Hinterbeine und mit den Flügelflächen negativ korreliert. Die phänotypische Korrelation der Borsten ist mehr oder weniger positiv, jedoch gering im Verhältnis zu allen anderen untersuchten Merkmalen der Bienen. Das Fersenglied (Metatarsus) ist eng mit den Borsten und dem Index korreliert und ebenso mit den anderen Merkmalen aus der ersten Gruppe.

Die Trends der genetischen Korrelationen sind ähnlich wie die der phänotypischen (Tabelle III). Unerwartet hohe Werte der ersten Gruppe verursachen Veränderungen von beinahe allen Merkmalen nach Selektion eines einzigen Merkmals. In der zweiten Gruppe ist die negative genetische Korrelation des Cubitalindex zu vielen Merkmalen der ersten Gruppe bemerkenswert. Die selektive Veränderung des Cubitalindex hat einen gewissen Einfluß auf die Größe der Flügel und Hinterbeine der Arbeitsbienen — je kleiner der Cubitalindex, desto größer Flügel und Beine. Die Borstenlänge auf der Tibia zeigt beinahe unsignifikante Korrelationen zu den anderen Merkmalen.

Alle hier geschätzten Heritabilitäten sind hoch und signifikant (Tabelle II). Die Höhe der Variabilität innerhalb der Völker wurde im Verhältnis zur Variabilität zwischen den Völkern eher überschätzt. Dies beeinflußt die hohen Schätzungen.

Verschiedene Umwelteinflüsse erzeugen rasch und einfach genetisch unterschiedliche Populationen. Man kann weiter voraussagen, daß die Selektion von

Bienen aus derselben genetischen Gruppe mit demselben Selektionsprogramm unter verschiedenen Umweltbedingungen zu genetisch unterschiedlichen Stämmen führen wird.

Bienengenetik / Heritabilität / Morphometrie / Methode der Halbgeschwister

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