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Heritability of morphological characters used to distinguish European and Africanized honeybees *

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Summary. Identification of "Africanized" honeybees (*Apis mellifera*) is usually achieved by measuring an array of morphological characters. Discriminant functions exist that allow determination of subspecies similarity on the basis of these measurements. Here we compute the heritabilities of the standard character set for ten ecotypes (Table 1) of bees. Heritability is extremely high for body size characters and there is greater genetic variance among ecotypes than within. Heritability is lower, but still very high, for the vein angle characters and hamuli number (Table 3). Heritability was also computed for the same character set for a group of 20 colonies in Venezuela (Table 4). Heritabilities declined by an average of 41% when specimens were reared in nonmaternal environments, but were still extremely high for the body size characters. These results support the continued use of morphological characters as a tool for identifying Africanized bees. They also suggest that multivariate analysis of morphology is useful in evaluating changes in the honeybee genome, and is therefore an effective means of studying the population genetics of honeybees.

Key words: Honeybee – Heritability – Discriminant functions – Taxonomy – Africanized bees

Introduction

Honeybees (*Apis mellifera*) are a widely distributed species. Ruttner (1987) recognizes 24 subspecies, which he calls races. Classification of honeybees according to race is generally achieved by measuring an array of morphological characters. Discriminant functions have been developed by DuPraw (1964, 1965a, b) and Ruttner et al. (1978), which reliably separate honeybee subspecies on the basis of morphology.

Africanized bees are descendants of an introduction of *A. m. scutellata* into Brazil in 1956 (Kerr 1967). These bees are apiculturally undesirable (relative to commercial bees of European origin) due to poor honey production, excessive defensiveness, and a high propensity to swarm (Rinderer 1988). Despite these extreme behavioral differences, Africanized and European bees are physically similar. This has posed a difficult problem for entomological regulators who are charged with responsibility for monitoring the spread of Africanized bees. Discriminant functions have now been developed that provide good separation of Africanized and European bees (Daly and Balling 1978), and even their F_1 hybrids (Rinderer et al. 1990). Greatly simplified procedures, using only a few easily measured characters, have also been developed (Rinderer et al. 1986a). Morphometrics continues to be used in determining the racial similarity of unknown samples of honeybees by both regulators and scientists.

The phenotype of an organism is determined by both genetic and environmental factors. A character that is highly heritable has large genetic variance, but is little influenced by environmental factors. A character that has a low heritability has either low genetic variability or is heavily influenced by environmental variables (Falconer 1981). A discriminant function that is derived from characters of high heritability will provide good resolving power of racial types, and will be robust to environmental variation that may have affected the development of the specimen bees (provided there are significant genetic differences for these characters among racial types). A discriminant function that is derived from characters of

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low heritability will either have poor discrimination of subspecies (due to low additive genetic variance for the character), or will provide inaccurate classification of unknown specimens due to differences induced by the environment in which specimens developed.

Oldroyd and Moran (1983) developed a simple method for estimating heritability, h^2, of honeybee worker characters. Their method exploits the fact that workers in a colony of honeybees headed by a naturally mated queen are a mixture of super-sisters (with a coefficient of relatedness of 0.75) and half-sisters (with a coefficient of relatedness of 0.25) (Page and Laidlaw 1988). The coefficient of average relatedness, r, of all workers is a function of the number of subfamilies present in the colony at the time of sampling. Oldroyd and Moran (1983) assumed the presence of 13 subfamilies in a natural honeybee colony, and therefore recommended a value of $r=0.29$ for estimating h^2. They also showed that if the effective number of matings is greater than 5, (which is very likely), then estimates of r are little altered.

If analysis of variance is used to obtain estimates of the between- and within-queen components of variance for the population of interest, then the intraclass correlation, t (Steel and Torrie 1980), may be determined. The heritability of a character is then estimated as t/r (Falconer 1981; Oldroyd and Moran 1983).

In this paper we use the technique of Oldroyd and Moran (1983) to estimate the heritabilities of all characters used to produce the Daly and Balling (1978) discriminant scores, for ten populations of honeybees. In a second analysis, the heritabilities of these same characters were estimated for an experimental "population" of bees that had been cross-fostered into different rearing environments. This analyis provides a measure of the upward bias in heritability estimates obtained by the Oldroyd and Moran (1983) method, which stems from the confounding of common rearing environment and dam effects, such as consistent operator biases during measurement.

Materials and methods

Analysis 1. h^2 estimates from various bee populations

Data sets comprising the 25 morphological characters used for the Daly and Balling (1978) morphometrical procedure were available from our laboratory's collection. Each data set represents 25 morphological measurements of approximately ten bees collected from each of 5–80 colonies in a defined region, or of a recognized ecotype. A description of each collection is given in Table 1.

Each character in each ecotype was analyzed using a one-way analysis of variance of queen effects. The heritability and standard error of heritability (SE) were then computed (Oldroyd and Moran 1983).

To investigate the proportion of genetic variation found within and between ecotypes, a nested analysis of variance (in which queens were nested within ecotypes) was performed for each character. These analyses were used to estimate between- and within-population variance components. The proportion of total phenotypic variance contributed by ecotypes and by queens within-ecotypes was computed for each character by methods outlined in Table 2.

Table 1. Description of bee samples studied

Country	n	Description
Argentina	47	Feral populations from provinces of Tucuman and Salta
Yugoslavia	16	Multiply mated queens from fourth generation selections of *A.m. carnica* for tolerance to *Varroa* spp.
Mexico	25	Feral and rustic colonies collected in northern Mexico prior to Africanization
Kenya & Tanzania	27	Rustic colonies of *A.m. monticola* collected from Mt. Meru, Mt. Elgon, Mt. Kilimanjaro, and Mt. Kenya
Saudi Arabia	20	Feral bees of *A.m. yeminitica*
United States	30	Queens from random domestic colonies in the Baton Rouge area taken to Venezuela where worker bees were reared
Brazil	43	Feral colonies from the Rio de Janeiro area
Venezuela	80	Feral colonies from the state of Portugesa
Southern Africa	5	Feral colonies of *A.m. scutellata* from Kenya and South Africa

Table 2. Computation of between- and within-population variance components

Source	*df*	Mean square	Composition of mean square[a]
Between ecotypes	$e-1$	MS_E	$\sigma_W^2+k\sigma_Q^2+qk\sigma_E^2$
Between queens (within ecotypes)	$\sum_{i=1}^{e}(q_i-1)$	MS_Q	$\sigma_W^2+k\sigma_Q^2$
Within queens	$\sum_{i=1}^{e}\sum_{j=1}^{n_i}(k_{j(i)}-1)$	MS_W	σ_W^2

[a] The coefficients k and q are adjusted for unequal sample sizes

e = number of ecotypes
q_i = number of queens in the i^{th} ecotype ($i=1, 2, 3, \ldots, e$)
$k_{j(i)}$ = number of workers sampled from the j^{th} queen in the i^{th} ecotype ($j=1, 2, 3, \ldots, n_i$)
V_T = total phenotypic variance $=\sigma_T^2$ $=\sigma_W^2+\sigma_Q^2+\sigma_E^2$
V_E = variance among ecotypes $=\sigma_E^2$
V_Q = variance among queens within ecotypes $=\sigma_Q^2$
V_{WQ} = variance within queens $=\sigma_W^2$
P_Q = proportion of total phenotypic variance due to queens with ecotypes $=V_Q/V_T$
P_E = proportion of total phenotypic variance due to ecotypes $=V_E/V_T$

Table 3. Heritabilities of 25 morphological characters from ten honeybee populations, and the proportion of overall variance attributable to ecotypes and queens within ecotypes

Character	Populations																		Proportion	
	Argentina		Yugoslavia		Mexico		Southern Africa		Kenya & Tanzania		Mexico		Venezuela		Brazil		United States		Saudi Arabia		P_E	P_Q
	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE		
Forewing length	1.58	0.36	1.18	0.49	1.42	0.45	1.89	1.19	1.85	0.46	1.42	0.45	1.15	0.28	1.44	0.35	0.89	0.30	1.59	0.55	0.61	0.17
Forewing width	1.46	0.34	1.09	0.46	1.36	0.44	2.13	1.31	1.12	0.32	1.36	0.44	1.63	0.29	1.68	0.40	0.73	0.26	1.55	0.54	0.51	0.21
Hindwing length	1.22	0.30	1.62	0.62	1.15	0.39	0.37	0.41	1.65	0.42	1.16	0.39	1.38	0.25	1.07	0.28	1.31	0.39	1.25	0.45	0.55	0.15
Hindwing width	1.48	0.35	0.83	0.39	1.03	0.36	1.73	1.10	0.89	0.27	1.03	0.36	1.33	0.25	1.36	0.34	1.14	0.35	1.87	0.35	0.55	0.16
Number of hamuli	0.33	0.14	0.29	0.21	0.58	0.25	0.63	0.54	0.60	0.21	0.58	0.25	0.34	0.11	0.58	0.19	0.69	0.25	0.39	0.22	0.02	0.13
Angle 29	0.50	0.17	0.74	0.35	0.93	0.33	1.13	0.80	0.69	0.23	0.93	0.33	0.51	0.13	0.53	0.18	0.64	0.24	0.25	0.18	0.24	0.13
Angle 30	0.42	0.15	0.91	0.40	0.79	0.30	1.11	0.78	0.83	0.26	0.78	0.30	0.53	0.14	0.63	0.20	0.68	0.25	0.02	1.12	0.17	0.14
Angle 31	0.45	0.16	0.58	0.30	0.68	0.27	0.86	0.65	1.08	0.31	0.68	0.27	0.64	0.15	0.38	0.15	0.87	0.29	0.15	0.15	0.21	0.14
Angle 32	0.83	0.23	0.76	0.36	0.94	0.33	0.92	0.69	1.73	0.24	0.94	0.33	0.61	0.15	1.15	0.30	1.26	0.38	0.30	0.19	0.40	0.15
Angle 33	0.63	0.19	0.52	0.28	0.68	0.27	0.86	0.66	0.46	1.18	0.68	0.27	0.76	0.17	0.68	0.21	0.50	0.21	0.98	0.38	0.23	0.15
Angle 34	0.56	0.18	0.31	0.22	0.96	0.34	0.86	0.66	0.66	0.22	0.96	0.34	0.77	0.17	0.62	0.20	0.66	0.24	0.79	0.33	0.26	0.15
Angle 35	0.46	0.16	0.29	0.21	0.60	0.25	0.04	0.24	0.55	0.20	0.60	0.25	0.95	0.19	0.16	0.11	0.78	0.27	*	–	0.07	0.16
Angle 36	0.67	0.20	0.67	0.33	0.56	0.24	0.66	0.55	0.40	0.17	0.56	0.24	0.86	0.18	0.63	0.20	0.43	0.19	0.77	0.32	0.19	0.15
Angle 38	0.73	0.21	0.65	0.32	0.66	0.27	0.72	0.59	0.75	0.24	0.66	0.27	0.52	0.13	1.08	0.28	0.99	0.32	0.47	0.24	0.12	0.17
Angle 39	0.67	0.20	0.45	0.26	0.87	0.32	2.52	1.51	0.46	0.18	0.87	0.32	0.67	0.15	0.84	0.24	0.73	0.26	0.40	0.22	0.14	0.19
Cubital vein B	0.78	0.22	0.39	0.24	0.81	0.30	0.71	0.58	0.12	0.12	0.81	0.30	0.96	0.19	0.53	0.18	1.00	0.32	*	–	0.06	0.14
Cubital vein A	0.58	0.18	0.50	0.28	0.86	0.32	0.38	0.41	0.74	0.24	0.86	0.32	0.69	0.16	0.42	0.16	0.94	0.31	0.20	0.17	0.27	0.14
Tibia length	1.26	0.30	0.46	0.26	1.59	0.50	1.45	0.96	1.13	0.37	1.59	0.50	1.67	0.29	1.26	0.32	1.21	0.37	1.28	0.46	0.52	0.19
Femur length	1.54	0.36	0.56	0.29	1.37	0.44	1.68	1.08	1.60	0.42	1.37	0.44	1.64	0.29	1.57	0.38	1.12	0.35	1.43	0.50	0.66	0.14
Basitarsis length	1.13	0.28	0.37	0.24	1.44	0.46	1.21	0.84	1.19	0.33	1.45	0.46	1.28	0.24	1.66	0.39	1.01	0.32	1.00	0.38	0.51	0.17
Basitarsis width	1.32	0.32	1.19	0.49	1.12	0.38	1.50	0.99	0.88	0.27	1.12	0.38	1.03	0.20	0.89	0.25	1.38	0.41	0.96	0.37	0.31	0.22
Third sternum length	1.41	0.33	0.69	0.33	1.56	0.49	1.45	0.96	1.13	0.32	1.56	0.49	1.37	0.25	1.52	0.37	0.73	0.26	1.28	0.46	0.54	0.17
Wax mirror length	1.32	0.32	0.48	0.27	1.02	0.36	2.04	1.26	1.32	0.32	1.02	0.36	0.85	0.18	1.20	0.31	0.52	0.21	1.47	0.51	0.49	0.16
Wax mirror width	1.47	0.34	0.22	0.19	1.13	0.38	0.50	0.47	1.32	0.36	1.13	0.38	1.41	0.26	1.25	0.32	0.92	0.30	1.55	0.54	0.69	0.11
Distance between wax mirrors	0.76	0.21	0.62	0.31	0.49	0.22	1.15	0.81	0.66	0.22	0.49	0.22	0.89	0.18	0.85	0.24	1.23	0.37	0.81	0.33	0.24	0.18

* Cannot be estimated due to negative variance components

Table 4. Heritabilities of 25 characters commonly used to distinguish Africanized bees from European bees in a European and an Africanized sample of colonies at the same site in Venezuela. The bees were reared in their maternal colony and in four different rearing environments (see text)

Character	Maternally reared				Reared in four different environments			
	Africanized		European		Africanized		European	
	h^2	SE	h^2	SE	h^2	SE	h^2	SE
Forewing length	2.18	0.99	1.87	0.87	0.63	0.23	0.48	0.24
Forewing width	2.15	0.98	2.17	0.99	0.91	0.41	0.59	0.28
Hindwing length	1.52	0.73	1.12	0.59	0.79	0.37	0.15	0.10
Hindwing width	1.53	0.74	1.77	0.83	0.73	0.34	0.53	0.26
Number of hamuli	0.87	0.49	0.48	0.35	0.55	0.27	0.66	0.31
Angle 29	0.41	0.31	1.11	0.58	0.46	0.23	0.92	0.42
Angle 30	0.84	0.47	1.13	0.59	0.72	0.33	0.98	0.45
Angle 31	0.51	0.35	0.91	0.51	0.62	0.29	0.40	0.20
Angle 32	1.19	0.61	1.12	0.59	0.82	0.38	1.21	0.54
Angle 33	0.43	0.32	0.19	0.24	0.55	0.27	0.38	0.20
Angle 34	1.21	0.61	0.31	0.28	0.77	0.36	0.35	0.18
Angle 35	0.36	0.29	0.51	0.36	0.49	0.24	0.29	0.16
Angle 36	1.16	0.60	0.27	0.27	0.90	0.41	0.17	0.11
Angle 38	1.16	0.60	0.75	0.45	0.96	0.43	0.58	0.28
Angle 39	1.11	0.58	1.00	0.54	0.15	0.10	0.65	0.31
C.I. vein B	1.30	0.65	1.10	0.58	0.80	0.39	0.93	0.43
C.I. vein A	0.94	0.52	0.66	0.41	0.85	0.37	0.36	0.19
Tibia length	1.87	0.87	0.34	0.30	0.94	0.43	0.17	0.11
Femur length	1.95	0.90	0.35	0.30	0.93	0.42	0.19	0.12
Trochanter length	2.17	0.98	1.04	0.56	1.37	0.60	0.46	0.23
Trochanter width	1.41	0.69	0.51	0.36	1.26	0.56	0.43	0.22
Sternite length	0.66	0.41	1.65	0.79	0.34	0.18	0.53	0.26
Wax mirror length	0.96	0.52	0.22	0.25	0.11	0.08	0.50	0.25
Wax mirror width A	1.15	0.59	0.62	0.40	0.26	0.15	0.14	0.10
Wax mirror width B	0.44	0.32	0.97	0.53	0.70	0.33	0.76	0.36

Aanalysis 2. The effect of cross-fostering on h^2 estimates

The data used for this analysis were described by Rinderer et al. (1986b). In that study, measurements of the morphological characters used to produce the Daly and Balling (1978) discriminant scores were obtained from Africanized and European bees. For each queen, offspring workers were reared in their own colonies and in a colony of the opposite race. For both sets of rearing conditions, half of the specimens was reared in a comb that had been produced by Africanized bees, while the other half was reared in a comb of larger cell size that had been produced by European bees. All colonies were headed by open-mated queens. Data from ten colonies of European bees and ten colonies of Africanized bees are analyzed here, with approximately ten workers sampled per colony.

Results

World populations

Estimates of heritability and their standard errors are given in Table 3 for each character for each ecotype. For nearly all ecotypes, heritability of size characters was very high, while the number of hamuli and vein angle characters had moderate to high heritability. The estimates for southern Africa should be treated with caution, as the sample size is too low for a valid estimate of heritability. Since the Yugoslavian population had been subject to artificial selection, assumptions about colonial relatedness may be invalid.

The proportions of the total phenotypic variance (for all populations combined) that are attributable to ecotype effects, P_E, were high for nearly all characters. Exceptions to this generality were the number of hamuli, length of cubital vein B, and wing vein angles 38 and 39 (Table 3). Less than 10% of the total variation in these characters was attributable to race. The proportion of total phenotypic variance due to queens within ecotypes, P_Q, was smaller than the proportion due to ecotypes P_E in 20 of the 25 characters (Table 3). In general, body size characters showed much higher P_E relative to P_Q compared to the vein angle characters.

Effect of cross-fostering

Estimates of heritability and their standard error are given for each character in Table 4. These statistics are computed for specimens of both ecotypes (Africanized and European) reared in the maternal comb in their maternal colony, and then for specimens reared in the four

different environments. The Spearman rank correlation between the heritabilities estimated for maternally reared bees and bees reared in four environments is 0.64 ($P<0.001$) for the Africanized specimens and 0.51 ($P<0.01$) for the European specimens. The mean heritability of all characters of both ecotypes was 1.03 (SD = 0.57) for the maternally reared specimens and 0.61 (SD = 0.30) for specimens reared in four environments. Thus, the additional environmental variance and breaking up of common maternal covariance caused an average decline in h^2 of about 41%.

Discussion

Theoretically, narrow-sense heritability cannot exceed unity, since this would imply that greater than 100% of total phenotypic variation was due to additive genetic variation. Estimates of heritability can exceed unity through experimental and estimation error, or if one of more of the assumptions used in producing them are incorrect. Several of the present population estimates exceed unity, which indicates that there may be elements of methodical upward bias that have contributed to them.

If the coefficient of relatedness, r, is underestimated, then heritability estimates will be inflated since $h^2 = t/r$. If heterotic effects contribute to the expression of the character, then some nonadditive genetic variance will contribute to the intraclass correlation and inflate h^2. The importance of these biases decline as the number of subfamilies per colony increases, and they are assumed to be minimal for naturally mated queens, since r rapidly approaches 0.25 after the number of matings exceeds five (Oldroyd and Moran 1983). Moritz and Klepsch (1985) used full and half-sib analysis to estimate the heritability of 5 of the 25 characters evaluated here, in a population of *A. m. capensis*, and demonstrated that dominance effects contributed little to genetic variance for those characters. Roberts (1961), Oldroyd and Moran (1987), and Rinderer et al. (1990), while demonstrating the presence of nonadditive genetic effects for several honeybee morphological characters, also demonstrated that these effects are small relative to additive effects.

The greatest potential bias comes from increased covariance of colony members stemming from common rearing environment rather than common genes. Table 4 provides estimates of the heritability of 25 morphological characters measured on specimens reared in their maternal colony, and for the same genotypes reared in four different environments. If each specimen were reared in a separate random, or single uniform environment, then common maternal environments would not contribute to the intraclass correlation. Thus, the intraclass correlation would more accurately reflect the ratio of additive genetic variance to total phenotypic variance. While the four environments used by Rinderer et al. (1986b) cannot be regarded as random, they tend to maximize the amount of environmental variance to which each genotype was exposed, and reduce the amount of environmental covariance common to sibs. Different rearing environments reduced the heritabilities by an average of 41%. This may represent the approximate upward bias in heritability of morphological characters estimated by sib analysis due to common maternal effects. However, this is probably an overestimate, since the environmental variance present in Rinderer et al.'s (1986b) experiment may be larger than is found nturally.

The ten natural populations examined (Table 3) all displayed very high heritabilities for the body size characters, and moderate to high heritabilities for vein angle and hamuli number characters. The present estimates of heritability of number of hamuli are similar to those estimated using sib analysis by Oldroyd and Moran (1983), and using regression by Gonçalves and Stort (1978). Our estimates of the heritability of vein angles are generally lower than those determined by Moritz and Klepsch (1985), while our estimates of lengths of body parts are very similar. Vein angles are difficult to measure and errors of measurement may contribute to "environmental" variance and reduce heritability.

Over 60% of the total phenotypic variance in wing widths and lengths was due to variance among ecotypes. The remaining variance within races for these characters is almost all genetic. These characters are therefore very satisfactory for discriminating ecotypes: they are highly heritable and have a high level of genetic variability among ecotypes. Simplified procedures for identifying honeybee ecotypes (Rinderer et al. 1986a) focus on these characters, as they have high discriminating power and are simple to measure. We show here that they are also extremely heritable, which further supports their use in studying the population genetics of honeybees.

Angles 35, 38, 39, the length of cubital vein B, and the number of hamuli have relatively lower heritability than the other characters and only low variability among ecotypes (Table 3). The proportion of total phenotypic variance attributable to queens within ecotypes exceeded the variability among ecotypes for these five characters. The use of these characters for distinguishing ecotypes is unlikely to add much useful information to a discriminant function.

The very high heritability of morphological characters in honeybees is probably a reflection of the stable environment in which they are reared. Regardless of the physical location of a colony or its food sources, the rearing and development environment (from egg to adult) of a honeybee is extraordinarily uniform. Larvae are fed similar food and are kept at uniform temperature, regardless of the conditions that prevail outside the

colony. Thus, any phenotypic variability among specimens tends to be genetic rather than environmental in origin. Morphological characters are therefore very suitable for distinguishing Africanized and European honeybees. The rapidity with which such determinations may be made (Rinderer et al. 1986a), and the fact that morphology reflects many interacting aspects of much of the genome, suggests that, in the medium term, morphology may remain the method of choice for identifying honeybee subspecies and for studying dynamic genetic changes within and among populations of honeybees.

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