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A HERITABILITY ESTIMATE OF HONEY BEE HOARDING BEHAVIOR

Charles P. MILNE, Jr. (1)

Department of Environmental Biology
University of Guelph
Guelph, Ontario, Canada N1G 2W1

SUMMARY

The removal of sugar syrup from vials and storage in honey comb by caged honey bees is apparently an economically important trait. This hoarding behavior and honey production are significantly correlated phenotypically. The heritability of honey bee hoarding behavior was estimated from the variance components of half-sib families. Worker hoarding behavior was determined for 100 free-mated queens which were the daughters of 14 queens. Hoarding behavior heritability was estimated from this nested model to be 0.187 ± 0.029. This indicates that selection for increased hoarding behavior is possible, and, depending upon the genetic correlation, there may be a correlated response in honey production.

INTRODUCTION

Honey bee worker hoarding behavior is apparently an economically important characteristic (MILNE, 1980 ; ROTHENBUHLER *et al.*, 1979). Colonies whose workers hoard more sugar syrup in cages produce more honey than those hoarding less. This investigation was undertaken to estimate the heritability of the honey bee worker hoarding behavior using sib group covariances. The heritability is the ratio of the variance component due to additive genetic effects to the total phenotypic variance in a population. It is a valuable parameter to determine because it provides an estimate of the relative importance of genetic and environmental factors and it is valuable in designing and evaluating selection programs to improve hoarding behavior and honey production.

MATERIAL AND METHODS

Fourteen queens were randomly chosen to be mothers. Several daughter queens were raised from each mother. These daughters were marked and placed into 2-frame nucleus colonies at one apiary which had about 110 colonies within a 3 km radius. This experiment was performed over two years, about half the daughters were

(1) Present address : Department of Molecular Biology and Genetics, University of Guelph, Guelph, Ontario, Canada NIG 2 W 1.

raised and tested each year. In the fall, between 4 and 10 daughters from each mother had mated and were laying. The hoarding behavior was determined for each of the 100 daughters by assembling 6 (or 5 if the colony lacked sufficient brood) test cages of 50 newly emerged workers, a small piece of dark comb (5 300 ± 100 mm^2) and vials of water and sugar syrup (MILNE, 1980). The cages were held at 35 °C and about 50 % R.H. in a dark incubator. The measure of hoarding behavior was the gm sugar syrup/bee/day removed from the vials on days 7-9 inclusive after placing the bees in the cage.

The statistical model used to partition the sources of variance was :

$$Y_{ijk} = \mu + M_i + D_{(ij)} + S_{(ij)k}$$

where : Y_{ijk} = k th observation (cage) on worker progeny of the j th daughter of the i th mother,

μ = population mean,

M_i = effect of the i th mother,

$D_{(ij)}$ = effect of the j th daughter of the i th mother,

$S_{(ij)k}$ = effect of the k th sample (cage) of worker progeny of the j th daughter of the i th mother.

A one-way analysis of variance was performed on the nested model to estimate the variance components. The heritability (h^2) of hoarding behavior was calculated from the formulae developed by MILNE and FRIARS (1984) for queen free-mated to an average of 17 drones :

$$\hat{h}^2_D = \frac{\left(\frac{68}{19}\right)\hat{\sigma}^2_D}{\hat{\sigma}^2_D + \hat{\sigma}^2_e} \quad (1)$$

$$\text{S.E.}\ (\hat{h}^2_D) = \frac{4\sqrt{\text{var}\ (\hat{\sigma}^2_D)}}{\hat{\sigma}^2_M + \hat{\sigma}^2_D + \hat{\sigma}^2_e} \quad (2)$$

where : $\hat{\sigma}^2_D$ = between daughter variance component estimate,

$\hat{\sigma}^2_e$ = between individual worker variance component estimate,

$\hat{\sigma}^2_M$ = between mother variance component estimate,

S.E. $(\hat{h}^2_D)$ = standard error of heritability.

RESULTS

The distribution of hoarding behavior test results for the 504 cages was skewed to the right, or toward higher amounts hoarded (coefficient of skewness = 1.054). A square root transformation removed the majority of the skewness (coefficient of skewness = 0.258).

In order to estimate $\hat{\sigma}^2_e$ from $\hat{\sigma}^2_s$ (the between sample or cage variance component estimate), it is necessary to discover the number of bees in the cage which engage in hoarding behavior. Two hoarding cages were assembled and each cage was filled with 50 newly emerged workers. The workers were from two colonies and each bee was marked with a numbered plastic disc for observation. On day 6, the cages were provided with a weighed vial and placed in an incubator with a glass front. For the next 3 days, the duration of the hoarding behavior, the holes in the vial were watched continually under a dim red light. The number of each bee feeding with her proboscis was

recorded. Table 1 lists the results of this experiment. In cage 1, 25 bees never removed syrup from the vial, and 37 never hoarded syrup in cage 2. During the 3 days, 118 and 65 total feedings were observed in cages 1 and 2, respectively. From the amount of syrup removed from the vial, 8.3943 and 4.5270 gm for cages 1 and 2, the average amount of syrup removed per feeding was 0.07114 and 0.06965 gm for cages 1 and 2, respectively. The average number of feedings observed for the hoarders in cages 1 and 2 was 4.72 and 5.00, respectively. From the number of bees never seen removing syrup from the vial, 25 and 37, an estimate of 20 bees performing the hoarding behavior in the cage of 50 workers was used to calculate $\hat{\sigma}_e^2$ from $\hat{\sigma}_s^2$, by the formula $\hat{\sigma}_e^2 = 20\ \hat{\sigma}_s^2$.

TABL. 1. — *Results of observing the hoarding behavior of marked workers in cages*

		Cage 1	*Cage 2* (1)
Gm syrup hoarded		8.3943	4.5270
Gm hoarded/bee/day		0.05710	0.03622
Number of workers which fed from the syrup vial this number of times	0 :	25	37
	1 :	12	4
	2 :	1	1
	3 :	3	3
	4 :	1	1
	5 :	2	0
	6 :	0	0
	7 :	2	0
	8 :	0	1
	9 :	0	1
	10 :	1	0
	12 :	1	0
	14 :	0	1
	15 :	0	1
	18 :	1	0
	27 :	1	0
Total number of feedings		118	65
Gm syrup hoarded/feeding		0.07114	0.06965
Number of feedings/hoarder		4.72	5.00

(1) Three bees died before the start of the observations on day 6.

The variance components for the mothers, daughters and samples were estimated by equating the expected mean squares and the mean squares for both untransformed and square root transformed data (Table 2). Using formulae 1 and 2, the heritability of hoarding behavior, based upon individual phenotypic differences, was estimated to be 0.188 ± 0.029 and 0.185 ± 0.029 for the untransformed and transformed data, respectively.

TABL. 2. — *Analysis of variance of hoarding behavior for the honey bee*

Source	Degrees of Freedom	Mean Square Hoarding (1) (gm/bee/day $\times 10^{-6}$)	Mean Square Hoarding (2) (square root gm/bee/day $\times 10^{-5}$)	Expected Mean Square
Mothers	13	7 395	2 861	$\sigma_s^2 + k_2 \sigma_D^2 + k_3 \sigma_M^2$
Daughters/mothers	86	3 283	1 231	$\sigma_s^2 + k_1 \sigma_D^2$
Samples/daughters/mothers	404	501.0	190.2	σ_s^2

$k_1 = 5.0053$, $k_2 = 5.2630$, $k_3 = 5.8275$

(1) $\hat{\sigma}_s^2 = 501.0$, $\hat{\sigma}_c^2 = 20\,\hat{\sigma}_s^2 = 10\,020$

$\hat{\sigma}_D^2 = 555.8$, $\hat{\sigma}_M^2 = 110.8$

$\hat{h}_D^2 = 0.188 \pm 0.029$

(2) $\hat{\sigma}_s^2 = 190.2$, $\hat{\sigma}_c^2 = 20$, $\hat{\sigma}_s^2 = 3\,804$

$\hat{\sigma}_D^2 = 207.9$, $\hat{\sigma}_M^2 = 44.00$

$\hat{h}_D^2 = 0.185 \pm 0.029$

DISCUSSION AND CONCLUSION

The heritability of worker hoarding behavior was estimated to be 0.187 ± 0.029. Therefore, hoarding behavior measured in test cages is influenced by the genotype of the queen and can be improved through selection. This heritability estimate may be biased upwards because of the half-sib family analysis used. The numerator of formula 1 includes maternal effects such as egg weight or a common hive environment. Nevertheless, this investigation still generates a valid estimate of the parameter. If the maternal and non-additive genetic effects are small, then this estimate can be used to predict genetic gain in a selection program to improve hoarding behavior. The progress for increased honey production during selection to improve hoarding behavior is dependent upon the magnitude of the genetic correlation between hoarding behavior and honey production. Presently, there is no estimate of this parameter in any population.

The distribution of results from these 504 cages was skewed. Most of the skewness was removed by performing a square-root transformation on the data, but it had little effect on the final estimate of the heritability. RINDERER and SYLVESTER (1978) examined the distribution of results of a different test of hoarding behavior for 38 colonies. The conclusions of MILNE (1980) indicate that their measure of hoarding behavior is not correlated with honey production in that locale. RINDERER and SYLVESTER have not demonstrated that their measure of hoarding behavior is correlated with honey production, and they did not report any skewness, such as noted here.

COLLINS *et al.* (1984) estimated the heritability of yet another hoarding behavior test. They took hoarding behavior to be the gm syrup removed per bee on days 2, 3 or 4. MILNE (1980) has shown that the syrup removal behavior on these days would not be correlated with honey production in that locale. COLLINS *et al.* have not reported that the measure of hoarding behavior they employ is related to honey production in any location. Nonetheless, the heritability estimate of hoarding behavior from this study can be compared with the estimate for syrup removal by COLLINS *et al.* Their estimate was obtained from single-drone matings of inbred European and Africanized lines, a much different population than that used in this study. Their estimates ranged from 0.20 to 0.86 and, in general, appeared to decrease from day 2 to day 4. The estimate of hoarding behavior heritability produced in this study, 0.187 ± 0.029, is not inconsistent with their results.

The results from the observations of hoarding behavior are intriguing. It appears that cage 1 hoarded more sugar syrup because it had more bees hoarding, rather than larger or more feedings by the hoarding bees. Not all 50 workers in the cage, even though the same age, engage in hoarding behavior. The number of bees hoarding sugar syrup from the vial on days 7-9 might be variable, rather than constant, in cages. Cage 1 had more bees hoarding, but these bees had an average number of feedings per hoarder and an average amount of syrup hoarded per feeding equal to cage 2. One possible interpretation of these data is that in these cages there is a division of labor such that only a few bees hoard syrup. Observations of hoarding behavior by caged workers in the future will undoubtedly reveal more interesting conclusions.

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RÉSUMÉ

ESTIMATION DE L'HÉRITABILITÉ DU COMPORTEMENT D'AMASSEMENT (« HOARDING ») CHEZ L'ABEILLE

MILNE (1980) a montré que le comportement d'amassement est une caractéristique importante du point de vue économique. Les colonies, dont les ouvrières en cages prélèvent plus de sirop de sucre dans un récipient et en stockent plus dans le rayon, produisent plus de miel. Cette étude a été menée afin d'estimer l'héritabilité du comportement d'amassement d'après la covariance de groupes de fratries. On a déterminé le comportement d'amassement chez la descendance ouvrière de 100 reines fécondées librement, filles de 14 reines mères. On a défini le comportement d'amassement par le nombre de grammes de sirop (g) prélevé/abeille/jour durant les 7^e, 8^e et 9^e jours après la mise en cage. Chaque cage comportait 50 ouvrières fraîchement écloses, un morceau de rayon, des récipients avec de l'eau et du sirop. Suite à une analyse de variance, l'héritabilité a été calculée d'après les formules mises au point par MILNE et FRIARS (1984).

La distribution des résultats des tests de comportement d'amassement réalisés sur 504 cages est déplacée vers la droite et une transformation de la racine carrée supprime presque totalement ce déplacement. On a obtenu 0,187 ± 0,029 comme estimation de l'héritabilité. Cette estimation montre que le comportement d'amassement est influencé par le génotype de la reine et peut être augmenté par sélection. Si les autres effets sont faibles, on peut utiliser cette estimation pour prédire le progrès génétique au cours de la sélection destinée à améliorer le comportement d'amassement. La corrélation génétique entre comportement d'amassement et production de miel, paramètre inconnu à l'heure actuelle, est nécessaire pour prédire le progrès génétique dans la production de miel lors de cette sélection. COLLINS *et al.* (1984) ont également estimé l'héritabilité d'une autre mesure du comportement d'amassement et ont trouvé qu'elle se situait dans la fourchette de 0,20 à 0,86.

ZUSAMMENFASSUNG

EINE SCHÄTZUNG DER HERITABILITÄT DES EINLAGERUNGSVERHALTENS DER HONIGBIENE

MILNE (1980) zeigte, daß das Einlagerungsverhalten (« hoarding behaviour ») eine ökonomisch wichtige Eigenschaft der Honigbiene ist. Kolonien, deren Arbeiterinnen mehr Zuckersirup aus dem Glas abnehmen und in Waben einlagern, produzieren mehr Honig. Die vorliegende Arbeit macht den Versuch einer Heritabilitätsschätzung des Einlagerungsverhaltens durch die Kovarianz von Nachkommengruppen. Das Einlagerungsverhalten wurde bei den weiblichen Nachkommen (Arbeiterinnen) von 100 freifliegenden (standbegatteten) Königinnen gemessen, die Töchter von 14 Königinnenmüttern waren. Das Einlagerungsverhalten wurde folgendermaßen definiert : Die in Gramm gemessene Menge des pro Biene und pro Tag abgenommenen Zuckersirups, festgestellt am 7-9 Tag einschließlich, an Käfigen mit 50 frischgeschlüpften Arbeiterinnen, einem Stück Wabe und Gefäßen mit Zuckersirup und Wasser. Nach der Varianzanalyse wurde die Heritabilität nach den von MILNE und FRIARS (1984) entwickelten Formeln berechnet.

Die Verteilung der Ergebnisse des 504 Käfige umfassenden Tests zum Einlagerungsverhalten war rechtsschief, die Schiefe konnte aber durch Wurzel-Transformation größtenteils behoben werden. Es wurde eine Heritabilitäts-Schätzung von 0,187 ± 0,029 errechnet. Diese Schätzung weist darauf hin, daß das Einlagerungsverhalten vom Genotyp der Königin beeinflußt wird und durch Selektion vermehrt werden kann. Wenn andere Effekte klein gehalten werden, kann diese Schätzung dazu benutzt werden, den Selektionserfolg zur Steigerung des Einlagerungsverhaltens vorauszuberechnen. Die genetische Korrelation zwischen dem Einlagerungsverhalten und der Honigproduktion, ein noch unbekannter Parameter, wäre notwendig, um den genetischen Fortschritt in der Honigproduktion während dieser Selektion voraussagen zu können. Die Heritabilitätsschätzung von 0,187 ± 0,029 ist nicht unvereinbar mit bereits veröffentlichten Schätzungen anderer Messungen des Einlagerungsverhalten.

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