MEASURING THE HERITABILITY OF CHARACTERS OF HONEYBEES *

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Summary

Parent-offspring regression, intra-sire regression of offspring on dam, and sibling analysis, were examined for their usefulness in estimating heritabilities of characters of the honeybee (*Apis mellifera*). These examinations indicate the allowances required for sibling workers with a coefficient of relationship of 0·75, and provide an approach to evaluate the usefulness of selecting breeding queens on the basis of their response, although the aim is improvement of response in worker progeny. Consideration is given to the consequences of a character being an attribute of individual workers, of groups of workers, or of queens.

Introduction

Heritability (h^2) is a statistical tool used by geneticists interested in improving economically important characteristics. It serves to estimate the amount of additive genetic variance (V_A) associated with a character expressed by the individuals in a specific population. Estimates of the V_A predict success prior to embarking on a selection programme, and they are important in setting up reasonable selection indexes.

This paper examines three methods for estimating h^2, and evaluates their application to honeybee genetics. Falconer's book (1960) has been used as the source of information on methods applicable to organisms having a diploid-diploid system.

Major considerations relating to honeybees

Considerations resulting from castes

When estimating h^2 in the honeybee (*Apis* spp.) complications arise as a consequence of morphological, physiological and behavioural differences between castes. Many characteristics of interest (honey production, for example) are expressed only by non-reproductive workers. This precludes a straightforward use of methods for estimating h^2 based on parent-offspring comparisons.

Other characteristics, for example larval resistance to disease, are expressed in queens and drones as well as workers. However, the physiology of sex and of caste may influence the expression of these characteristics (see e.g. Rinderer & Rothenbuhler, 1969), and h^2 in a queen / daughter-queen structure may well be different from h^2 for the same characteristic in a queen / daughter-worker structure. Experimental data from selection experiments indicate that this is so for larval honeybee resistance to *Bacillus larvae* (Rinderer, unpublished), and for resistance of newly emerged adults to carbaryl insecticide (Tucker, personal communication). In such circumstances, selection programmes based exclusively on measurements of reproductives may not yield the desired improvements in workers.

Considerations resulting from the haploid-diploid system

A further complication arises from the genetic nature of drones. Since they produce an aggregate of genetically identical spermatozoa, worker-daughter progeny fathered by a

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* In co-operation with Louisiana Agricultural Experiment Station.

single drone have 75% of their alleles in common by descent. Also, since all the semen produced by a drone (or a group of drones) is routinely required to inseminate one queen, half-sibling families fathered by a single drone are, with present technology, unavailable. Thus, instrumental inseminations of queens produce families of workers where coefficients of relationship are 0·75 (single-drone inseminations) or a mixture of 0·75 and 0·25 (multiple-drone inseminations with drones from different queen sources), or a mixture of 0·75 and 0·50 (multiple-drone inseminations with drones from one queen source). The full-sibling relationship in diploid-diploid systems is 0.50, so it is inappropriate to apply to certain situations in the honeybee the genetic mathematics derived for diploid-diploid organisms.

Methods for calculating coefficients of relationships have been obtained by modifying formulae derived for organisms with two diploid sexes (Crow & Roberts, 1950) and by utilizing the concept of queen-to-queen matings for various breeding schemes in honeybees (Polhemus, Lush & Rothenbuhler, 1950). The concept of queen-to-queen mating views a drone as a gamete of his mother-queen; it has certain utility in evaluating mating schemes used to estimate h^2. It provides a rational basis for establishing half-sibling families of workers fathered by a queen designated as a drone-mother, and provides a similar framework for mating schemes designed to yield data for regression analysis.

Parent-offspring regression

Regression analysis of the scores of offspring, either on the scores of parents of one sex or on the midparent scores of a number of matings, is a straightforward method in general use for estimating h^2. Because of a low sampling variance, regression analysis has special value for estimating a low h^2 (Falconer, 1961).

Parent-offspring regression is especially useful for estimating h^2 for characteristics displayed by queens. The relationship of a daughter-queen to her maternal parent is the same as the daughter-mother relationship in diploid animals. Consequently, a regression of the scores of daughter-queens on the scores of their maternal parents is a valid estimate of $0·50h^2$ for random mating populations.

A regression of daughter-queen scores on midparent scores is also possible: the drone-producing queens are considered to be sire-queens, and their drones are considered to be sire gametes, following the example of Polhemus, Lush and Rothenbuhler (1950) who used this concept for calculating inbreeding coefficients. If mixed pooled semen from a large number of drones (over 20) from a sire queen is used for an insemination, the probability of sibling offspring queens with $r = 0·75$ is low (with 20 drones, only 1 of 20 pairs of siblings is expected to have a coefficient of relationship of 0·75), and the mating system can be interpreted as though it were diploid. The slope of the regression line of the scores of offspring queens on midparent scores (dams and sire-queens) gives a direct estimate of h^2 for queen characteristics such as quality and quantity of oviposition.

Parent-offspring regression is also useful for estimating h^2 for characters held in common by queens and workers, for example resistance to disease or to insecticides. Following the methods already discussed, the scores of offspring workers and of offspring queens can be independently regressed on the scores of either one parent or the midparent. The regressions calculated for the different caste relationships (queen / daughter-worker or queen / daughter-queen) can then be compared. The comparison will give information on the usefulness of selecting breeding queens on the basis of their response, when desiring to improve response in the worker progeny. For some characters this approach to selection may be useful; this would be indicated if values of h^2 estimated from the two regressions are similar. For other characters the selection approach may be frustrated by environmental, dominance, or epistatic differences between castes; this would be indi-

cated by a low h^2 estimated for the queen / daughter-worker relationship and a relatively high h^2 estimated for the queen / daughter-queen relationship.

Intra-sire regression of offspring on dam

In the second mating structure, each of a number of males is normally mated to several females. Heritability is estimated from the average regression of progeny on dams calculated within sire groups. Regressions from each sire group are pooled in a weighted average. This method can also be used to estimate h^2 for characters of queens, or of queens and workers, if the semen from more than 20 drones produced by the drone-mothers (sires) is pooled and mixed prior to insemination of the dam. The mixing of pooled semen produces a family that is very similar to one of diploid full-siblings.

Sib analysis

Another common data source for estimating h^2 from a mating of a number of males, each to several females, is the set of phenotypic scores of siblings. The data, in the form of half-sib and full-sib families, are submitted to analysis of variance, and h^2 is estimated from the interpretation of the analysis (Falconer, 1961). However, before making such an analysis with honeybees, the character in question must be associated clearly with the appropriate caste. An analysis, based on the relationship of sibling queens, made on data from either their worker or their queen progeny is inappropriate because, between colonies, the families measured are families of cousins and not families of siblings. A colony cannot be treated as a single genetic identity: either the queens or the workers between colonies can be identified as siblings, but not both (unless inbreeding has been practised). For full-sibling mother queens $r = 0 \cdot 75$, but for their progeny (cousins) $r = 0 \cdot 188$. This difference between the values of r has considerable impact on an estimate of h^2. A mating structure with honeybees utilizing queens selected at random as dams, and drone-mother queens selected at random as sires, will yield a collection of full-sib and half-sib families of female progeny. The following approaches with such a mating system render sibling analysis quite useful for estimating h^2 in honeybees.

If a character is one which can be measured in individual workers or queens, a primary consideration is the relatedness of the siblings. With single-drone inseminations, the relatedness is $0 \cdot 75$ in families designated as full-sibs. Such a situation augments the correlation of full-sibs, and will tend to increase unduly the between-dam variance contribution. In this case, the sibling correlation $t = 0 \cdot 75h^2$, i.e. $h^2 = 4t/3$. However, further augmentation of the correlation between full-sibs can easily arise from the common sibling environment (reared in the same comb in the same colony). Thus, with single-drone inseminations, the sire component appears to be most useful for estimating h^2. Multiple-drone inseminations, performed by mixing pooled semen from a large number of drones (over 20) from each drone-mother (sire) would more closely approximate to the relationships in diploid-diploid systems, and would increase the usefulness of estimates of h^2 derived from the between-dam variance.

If the character of interest is a group behaviour pattern, then only multiple measures made with collections of the progeny of each queen can be used to estimate the response of the sibling population. Variance between test replicates can arise only from environmental influences, for all groups large enough to function socially would have essentially identical genetic constitutions. Thus for group characteristics full-sibling variance is not available in the analysis, and no estimate of h^2 can be made from between-dam variance. The analysis would be the same if only a single offspring were produced from each mating. With this analysis, the data are in the form of measures of half-sib families, and h^2 for the group behaviour is estimated from the between-sire component in the

analysis. For group behaviour patterns, the estimate of h^2 should not be influenced by the number of drones used to inseminate dams, since full-sibs cannot be evaluated.

Discussion

These three methods of estimating h^2 focus on the important considerations necessary for making valid estimates in honeybees. They show how accommodations can be made for the identical spermatozoa produced by a drone, and the consequent relationship of $0 \cdot 75$ for sibling sisters, either by simulating diploid-diploid systems by using mixed-sperm mating, or by dropping out inappropriate elements of analysis.

Emphasis is placed on properly attributing a character to individual workers, to groups of workers, or to queens. Such distinctions determine, in part, the appropriate method for measuring heritability. Assignation of a character to a queen or to her worker daughters becomes difficult when the character is dependent upon a number of bees and is thereby related to the rate of egg production. However, clear character description, and testing designed to measure the character in the most precise terms, may help to overcome this difficulty.

Acknowledgement

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