

# CAUSES OF DISAGREEMENT BETWEEN ESTIMATED AND REALISED GENETIC PARAMETERS

H. JORJANI

DEPARTMENT OF ANIMAL BREEDING AND GENETICS  
SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

## SUMMARY

Problems associated with prediction of response are discussed. It is concluded that the technical problems in evaluating the standardised selection differential as a result of the reduction in variance due to inbreeding and correlation of family members and their effects on order statistics, as well as positive and negative assortative mating contributed to the disagreement between predicted and realised selection response.

## INTRODUCTION

Quantitative geneticists, as well as animal or plant breeders are interested in predicting the selection results. In other words they want to know how much genetic progress, if any, will be achieved by practicing a certain kind of selection. Unfortunately the most of the quantitative genetics theory is of descriptive nature rather than predictive. To solve this geneticists have looked at the response to selection from the viewpoint of regression of offspring on mid-parents,  $R = b_{0\bar{P}} S$ ,  $S$  being mean of the selected parents or the selection differential, and  $R$  is mean of the offspring produced by this selected group of parents. Since  $b_{0\bar{P}}$  is in fact equal to the heritability,  $h^2$ , although a range of difficulties arise from this, geneticists have conveniently replaced  $b_{0\bar{P}}$  by  $h^2$ . These difficulties, however will not be discussed here in any details.

On the other hand the mean of the selected parents,  $S$ , not only could be decided on before selection, or at least its expected value predicted, but also if expressed in deviations from parental generation it can provide a useful means of comparison. Standardisation of  $S$  and non-random mating of selected parents are what this paper intends to discuss. Some old and some new results are considered and their practical implications mentioned. By doing this I hope to shed more light on the problem of disagreement between estimated and realised genetic parameters.

## ASSORTATIVE MATING

Contrary to what is implied by  $R = b_{0\bar{P}} S$ , selection is not practiced among random mated individuals of the parental generation, but selected individuals of the parental generation are used in matings to produce the next generation, and this with respect to the whole population is positive assortative mating (first level of assortative mating). This problem and its conse-

quences were discussed by Falconer(1989). In this section the results of positive and negative assortative mating of selected individuals as compared to the random mating among them, which in anyway is positive assortative mating with respect to the whole population, is considered (second level of assortative mating).

It is well known that positive assortative mating enhances the response to selection as compared to random mating. McBride and Robertson(1963) tested the effectiveness of positive assortative mating in individual and index selection lines of *D.melanogaster* and concluded that in all of their comparisons, positive assortative mating gave a greater selection response. DeLange (1974) found that positive and negative assortative mating gave the highest and the lowest selection response, respectively, while random mating gave intermediate results over a range of heritabilities, intensities of selection and different genetic models. More recently Smith and Hammond (1987) approved and extended the results of Baker (1973) and concluded that depending on the selection method, intensity of selection and heritability in the parental and offspring generations, positive assortative mating is able to increase the response to selection up to 21%. However, in reported selection experiments one often finds either ignoring assortative mating and its effects or a failure to mention the careful recording of matings.

Now let us see what are the circumstances which causes unwanted or rather unnoticed assortative mating. Firstly, in selection experiments, as well as breeding projects number of parents is so small which makes them subject to the rules of small populations. In this respect it means that if we have enough replication of selection lines, not all of them show random mating and in certain proportion of them positive assortative mating and in certain proportion of them negative assortative mating would have occurred, and this in turn causes either an increased or decreased selection response as compared with predicted response.

Secondly, since the best individuals are more likely to come from the same families, prevention of full-sib and half-sib matings in order to avoid inbreeding can also lead to negative assortative mating and hence the reduction of selection response below the expected value.

#### SELECTION DIFFERENTIAL

As the last step in order to predict the response to selection, the selection differential is standardised by dividing it by phenotypic standard deviation, i.e.  $i = S/\sigma_p$ , and therefore  $R = ih^2\sigma_p$ . Since under assumption of normality of phenotypic values, the height of the ordinate at the point of truncation divided by the proportion selected is equal to standardised selection differential,  $i = z/p$ , tables of deviations of ranked data are used to find

the relevant quantities.

All of these assume a large normally distributed population of uncorrelated individuals. Burrows (1972) gives approximate formula for observations coming from a finite group of individuals. Hill (1976) has considered the effect of correlation of family members on order statistics demonstrating a reduction in  $i$  as result of this correlation. He also extended Burrows' (1972) result to cover the correlation of family members and has discussed its genetic implication on different selection methods. Burrows (1975) further examined the variance of standardised selection differential,  $i$ , and average selection response.

In addition to what has already been said there is one point which needs more attention. In the account of the effect of correlation of family members on the order statistics given above the effects of inbreeding on order statistics was ignored. Inbreeding causes the within family genetic variance to be reduced by a factor of  $1-F$  (Foulley and Chevalet, 1981). This in combination with the reduction of between family genetic variance because of selection (Bulmer, 1971) causes total variation and hence standardised selection differential,  $i$ , to be reduced more than that predicted by Hill (1976, 1977).

#### DISCUSSION

In the comparisons made by Sheridan (1988) among 198 selection lines the estimated heritability overestimated the realised heritability in 57% and underestimated it in 38% of all comparisons. Causes of this enormous amount of disagreement could be demonstrated as follows.

first of all the problem of disagreement between estimated and realised selection response, as was briefly mentioned in the introduction, arises from unjustified replacement of  $b_{OP}$  by any estimate of  $h^2$ . The regression of offspring on mid-parent is equal to heritability only under a certain set of assumptions. Violation of any of these assumptions leads to introduction of an element of bias into the estimate of the heritability. These assumptions have been listed and briefly discussed by Sheridan (1988). Some more important points relevant to present paper have been discussed by Bulmer (1985) and Robertson (1977). Proper discussion of this subject is beyond the scope of this paper and needs an independent consideration on its own right, however, only one point will be mentioned here. In addition to the Bulmer effect, negative assortative mating practiced in order to avoid inbreeding is able to reduce the additive genetic variation by producing a negative correlation between breeding values of mating individuals. For the purpose of present paper it suffices to say that the usage of improper  $h^2$  causes under/over estimation of the realised response.

The second cause of disagreement arises from small number of selected individuals and their assortative mating, which could cause under/over estimation of realised response. If complete mating record is kept and the response is adjusted for assortative mating or possible effects of inbreeding depression, there will be less discrepancy between the estimated and realised response.

Thirdly, the effects of family members correlation and inbreeding on order statistics causes overestimation of realised response through ignoring the reduction of total variance and standardised selection differential, i.

By under/over estimation of selection response all of genetic parameters dependent on selection response will be accordingly affected.

What has been done here is the mere pointing to a range of possible causes of disagreement between estimated and realised genetic parameters and all of this has been based on some theoretical deductions and some presumably ignored practically important points. The next logical step is to formulate the problem and then to quantify the contribution of each cause. The main aim of this paper is to remind the real practical importance of some rather established results. If different authors were paying more attention to the results obtained by Sen and Robertson(1964) on the subject of number and size of replications in genetic experiments and its effects on variances of genetic parameters, as well as those results obtained by Burrows(1972,75), Bulmer(1971,85) and Hill(1976,77), Sheridan(1988) might have not found the realised heritability being exactly predicted in only 5% of 198 selection lines examined.

#### REFERENCES

- BAKER, R.J. 1973. Heredity 31:231-238  
BULMER, M.G. 1971. American Naturalist 105:201-211  
BULMER, M.G. 1985. The Math. Thoer. of Quant. Genet. Oxford U.P.  
BURROWS, P.M. 1972. Biometrics 28:1091-1100  
BURROWS, P.M. 1975. Biometrics 31:125-133  
DeLANGE, A.O. 1974. 1 World Congr. Genet. Appl. Livest. Prod. 3:421-25  
FALCONER, D.S. 1989. Introd. to Quant. Genet. Logman  
FOULLEY, J.L. CHEVALET, C. 1981. Ann. Genet. Sel. Anim. 13:189-196  
HILL, W.G. 1976. Biometrics 32:889-902  
HILL, W.G. 1977. Biometrics 33:703-712  
McBRIDE, G., ROBERTSON, A. 1963. Genet. Res. 4:356-369  
ROBERTSON, A. 1977. Z. Tierzucht. Zuchgbiol. 94:131-135  
SEN, B.K., ROBERTSON, A. 1964. Genetics 50:199-209  
SHERIDAN, A.K. 1988. Anim. Breed. Abs. 56:877-889  
SMITH, S.P., HAMMOND, K. 1987. Genet. sel. Evol. 19:189-196

