

MATERNAL EFFECTS AND SELECTION RESPONSE

Effets maternels et réponse à la sélection

Efectos maternos y respuesta a la selección

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Maternal influences are an important source of variation in mammalian species. While husbandry methods for farm species have tended to minimise or eliminate much of this source of variation in growth and development it is still of potential importance in beef and sheep populations. To the extent that this source of variation is genetically determined it should be taken into account in examining the efficiency of alternative livestock selection programmes. The presence of genetically determined maternal effects complicate the prediction of genetic gain. Some of these complications have been considered by DICKERSON (1947), WILLHAM (1963), VAN VLECK (1970), HANRAHAN and EISEN (1973, 1974) and EISEN *et al.* (1973). However, there has been little consideration given to how maternal genetic effects influence the relative efficiency of the common testing and selection procedures in animal breeding.

GENERAL MODEL

The model used assumes autosomal inheritance, additive gene action, no linkage and no inbreeding. The model follows that given by WILLHAM (1963) with phenotypic value given as $P = A_o + A_m^d + E$, where P = phenotypic deviation from the mean, A_o = additive direct genetic effect, A_m^d = additive maternal genetic effect, E = environmental effect peculiar to each individual. Variation due to maternal genetic effects is due to genetic differences between dams that are only expressed in the phenotype of their progeny. For example, milk yield of ewes is a maternal effect as far as the progeny phenotype for growth is concerned.

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The response to selection (R) is given by the regression of breeding value on the selection criterion (B) times the selection differential, symbolically $R = B \cdot S$ (COCHRAN, 1951). This fundamental definition will be used to examine the possible magnitude of bias in computing the accuracy of progeny testing if maternal effects are ignored when in fact they exist. The consequences of maternal genetic effects for the relative accuracy of progeny and performance test selection will be examined.

MATERNAL EFFECTS AND PROGENY TESTING

The accuracy of a progeny test is defined as the correlation (r) between breeding value and the mean of a progeny group (\bar{P}). Usually progeny testing is only practicable for male parents and hence only this case will be considered. It is assumed that the progeny group consists of half-sibs from unrelated mothers. Then, since the breeding value of an individual is $A'_o + A'_m$ (prime denotes parental generation) the accuracy of a progeny test is computed as

$$r = \text{Cov} (A'_o + A'_m, \bar{P}) / [\text{Var} (\bar{P}) \text{Var} (A'_o + A'_m)]^{1/2}$$

From the model given above for P and defining σ_o^2 , σ_m^2 and σ_{om} as the variance of direct genetic and maternal genetic effects and their covariance, respectively, then

$$r = \frac{\sigma_o^2 + \sigma_{om}}{\sigma_p (\sigma_o^2 + \sigma_m^2 + 2\sigma_{om})^{1/2}} \cdot 1/2 \left\{ \frac{n}{1 + (n-1)t} \right\}^{1/2}$$

where t = intraclass correlation of the progeny group and equals $1/4 h_o^2$ in the present case and σ_p^2 = phenotypic variance. However, in assessing the accuracy of progeny testing maternal effects are usually assumed (tacitly) absent and the accuracy is computed as

$$r^* = \frac{\sigma_o^2}{\sigma_o \sigma_p} \cdot 1/2 \left\{ \frac{n}{1 + (n-1)t} \right\}^{1/2}$$

Let $Q = r^* / r$

$$\begin{aligned} \text{Then } Q^2 &= \left\{ 1 + \frac{\sigma_m^2 + \sigma_{om}}{\sigma_o^2 + \sigma_{om}} \right\} \left\{ \frac{\sigma_o}{\sigma_o^2 + \sigma_{om}} \right\} \\ &= (1 + x)(1 + y). \end{aligned}$$

This expression will be examined for two distinct cases; (a) $\sigma_{om} < 0$, (b) $\sigma_{om} > 0$. In the first case $y < 0$. Then, if $\sigma_o^2 = \sigma_m^2$, $1 + x = 2$ and $Q = [2(1 + y)]^{1/2}$. Under these circumstances the accuracy of progeny testing is overestimated by more than 40 percent. If, however, $\sigma_{om} > 0$ then $y < 0$ and $2(1 + y) < 2$ and the overestimation of efficiency is reduced.

The more general consequences are best examined by computing the actual value of Q for a range of values of σ_o^2 , σ_m^2 and σ_{om} . This is most conveniently done in terms of the corresponding standardised measures h_o , h_m and r_{mo} . The results are presented in Table 1. It is clear from an examination of the values in Table 1

that substantial overestimation of the accuracy of progeny testing can occur. The magnitude of the error declines as the correlation between direct and maternal genetic effects changes from zero through positive values. When $r_{om} = 1$ the value of Q is unity unless unlikely scale effects are operating.

For the cases in Table 1 where r_{om} is negative substantial errors can be made

TABLE 1
VALUES OF Q FOR VARYING VALUES OF THE GENETIC PARAMETERS

h_o^2	h_m^2	r_{om}				
		-0.8	-0.5	0.0	-0.2	-0.5
0.1	0.1	3.16	2.00	1.41	1.29	1.15
	0.2	6.56	4.30	1.73	1.47	1.24
	0.3	2.88	11.24	2.00	1.43	1.17
0.2	0.1	1.40	1.38	1.22	1.14	1.10
	0.2	3.16	2.00	1.41	1.29	1.15
	0.3	35.88	2.91	1.58	1.39	1.20
0.3	0.1	1.19	1.22	1.15	1.19	1.13
	0.2	1.66	1.56	1.29	1.57	1.12
	0.3	3.16	21.00	1.41	1.29	1.15

in estimating the true accuracy. In fact for permissible values of the genetic parameters it is possible that genetic change will occur in the direction opposite to that intended unless maternal effects are taken into account.

As an example of the use of this Table genetic parameters reported by HANRAHAN and EISEN (1973) for 6-week body weights in mice will be used. The following estimates were reported:

$$h_o^2 = 0.29, h_m^2 = 0.32, r_{om} = -0.39.$$

The nearest values in the table would be

$$h_o^2 = 0.3, h_m^2 = 0.3 \text{ and } r_{om} = -0.5.$$

The tabular Q -value is 2.00 and the actual value for Q is 1.93.

PERFORMANCE AND PROGENY TEST SELECTION

The genetic gain from selection on P is

$$R_d = (h_o^2 + 1/2 h_m^2 + 3/2 r_{om} h_o h_m) \bar{i}_d \sigma_p$$

and the corresponding genetic gain from progeny test selection may be written as

$$R_p = 1/2 (h_o^2 + r_{om} h_o h_m) [n / (1 + (n-1)t)]^{1/2} \bar{i}_p \sigma_p$$

The ratio R_p/R_d equals

$$1/2 \left\{ \frac{h_o^2 + r_{om} h_o h_m}{h_o^2 + 1/2 h_m^2 + 3/2 r_{om} h_o h_m} \right\} \left\{ \frac{n}{1 + (n-1)t} \right\}^{1/2} \frac{\bar{i}_p}{\bar{i}_d}$$

equals $K I$ where $I = \bar{i}_p/\bar{i}_d$ and the value of K is therefore defined. Values of K for a range of values of the genetic parameters and for two different values of ($n = 20, 50$) are given in Table 2. To use this table in assessing the impact of maternal effects on the ratio R_p/R_d some assumption must be made about the likely value of $I = \bar{i}_p/\bar{i}_d$. If $\bar{i}_p = \bar{i}_d$ the values in the table equal R_p/R_d . Usually \bar{i}_p will be less than \bar{i}_d . A reasonable assumption might be that if a progeny testing facility allows a selection intensity of 25% then a performance test would allow a selection intensity of 5%. In this case $\bar{i}_p/\bar{i}_d = 0.5$. Consequently, the values in Table 2 must be divided by two to give the appropriate ratio for

TABLE 2

VALUES FOR K WITH DIFFERENT VALUES OF h_o^2, h_m^2, r_{om} AND n

h_o^2	h_m^2	r_{om}				
		-0.5	-0.2	0.0	0.2	0.5
$n = 20$						
0.1	0.1	1.23	1.23	1.23	1.23	1.23
	0.2	0.57	0.84	0.92	0.97	1.03
	0.3	0.21	0.61	0.74	0.82	0.90
0.2	0.1	1.44	1.32	1.28	1.25	1.22
	0.3	0.75	0.87	0.91	0.94	0.97
$n = 50$						
0.1	0.1	1.57	1.57	1.57	1.57	1.57
	0.2	0.73	1.07	1.18	1.24	1.31
	0.3	0.26	0.78	0.94	1.05	1.15
0.2	0.1	1.71	1.57	1.52	1.48	1.44
	0.3	0.89	1.04	1.08	1.12	1.15

the rate of genetic gains. While the values in this table show the expected increase in relative value of progeny testing as n is increased most the values of K are close to or less than unity. When allowance is made for likely differences in selection intensity it is clear that progeny testing is likely to be very inefficient relative to performance testing given the assumed genetic model.

INDEX SELECTION

The appropriate weighting to give to individual and progeny records in a selection index depend on whether maternal effects are present and on the corresponding parameters. The economic weightings for maternal and direct genetic effects must also be considered.

It is evident that the results presented here have implications for livestock selection programmes in situations where the young depend to a large extent on the mother for early postnatal nutrition. In such situations the designing of a selection programme based on genetic parameters estimated from the usual half-sib covariances may be very inefficient. Thus, if livestock production systems which currently employ the dam as the postnatal food source for the offspring are to be served by efficient selection programmes, more effort should be expended in exploring the genetic relationships between direct and maternal genetic effects.

RESUME

Les effets maternels sont une source de variations importante chez la plupart des mammifères. Si cette variation a une composante génétique, les schémas de sélection supposant qu'il n'existe pas d'effets génétiques maternels peuvent ne pas être efficaces. On examine l'impact des effets maternels sur l'exactitude relative des examens de la progéniture. Les exactitudes relatives de la sélection des tests de la progéniture et des performances sont examinées, ainsi que les poids appropriés dans un index de sélection consistant en renseignements sur les examens de performances et de progéniture. On constate que les manques d'efficacité dus à l'ignorance des effets génétiques maternels réels peuvent être très importants.

RESUMEN

Los resultados maternos son un importante origen de variación en la mayoría de las especies de mamíferos. Si esta variación tiene un componente genético, entonces el esquema de selección derivado de la suposición de que no existan efectos genéticos maternos puede no ser eficaz. El impacto de los resultados maternos sobre la exactitud relativa de la prueba de la progenie es examinado en el trabajo. La exactitud relativa a las pruebas de progenie y de selección son examinadas también, así como su efecto sobre el índice de selección obtenido a base de ambos. La ineficiencia derivada de la ignorancia de los efectos genéticos maternos reales puede ser muy grande.

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