Theor Appl Genet (1985) 70: 123–127

Phenotypic response to selection for traits with direct and maternal components when generations overlap

J. P. Mueller* and J. W. James

School of Wool and Pastoral Sciences, University of New South Wales, Kensington 2033, Australia

Received September 19, 1984
Communicated by J. S. F. Barker

Summary. Prediction of response to selection for traits with direct and maternal components is described for discrete and overlapping generations. Expected phenotypic response is the sum of direct and maternal contributions, the latter having a genetic and an environmental component. With overlapping generations the selection differentials achieved on these components are added to respective updated vectors containing age-sex distributions with values of previous selection rounds. An example demonstrates that in the early stages, results may be considerably affected by environmental correlations between direct and maternal effects. The method could be helpful in interpreting phenotypic changes in a population selected for traits with maternal effects.

Key words: Selection – Maternal effects – Overlapping generations

Introduction

There are several reasons why accurate prediction of response in traits with direct and maternal components is not straightforward (see review by Willham 1980). Genetic gains in maternal effects are expressed one generation later than genetic gains in direct effects; expression of maternal effects is sex limited; and direct and maternal effects may be genetically and environmentally correlated. The asymptotic rate of response to selection for such traits was first given by Dickerson (1947) and is usually referred to as being proportional to "total additive heritability", defined as the regression of total (direct plus maternal) genotype on phenotype. If we wish to predict phenotypic response, the maternal ability of selected dams of the current generation must be considered, since it affects the next generation of progeny. With non-zero environmental correlation between direct and maternal effects it is not sufficient to consider genetic differentials only. With overlapping generations we also need a description of the flow of genes through the population in order to keep track of contributions made by individuals born at different stages of the program (Hill 1974). Aspects of the design and evaluation of selection programs involving maternal effects were discussed by Koch (1972); Hanrahan (1976); Van Vleck et al. (1977) and Koch et al. (1982). Little has been published on formal methods to describe selection response with maternal effects in a general fashion, although Van Vleck et al. (1977) presented a method for predicting phenotypic response when generations do not overlap (or are equal in both sexes) and where environmental correlations between direct and maternal effects were not taken into account.

Here we shall develop methods for predicting phenotypic changes in a population undergoing selection for a trait influenced ba maternal effects, allowing for overlapping generations and environmental correlations between direct and maternal effects.

Theory

The model

Our model is a version of the more general one presented by Willham (1963). The phenotypic value P of an individual is made up of direct (D) and maternal (M) contributions, each

---

* Present address: Instituto Nacional de Tecnologia Agropecuaria, San Carlos de Bariloche 8400, Argentina

of which has genetic (G) and environmental (E) components. Thus

$$P = G_D + E_D + G'_M + E'_M\,.$$

The prime denotes contributions from the dam of the individual, which are reflected in P. The genetic components in an individual's phenotype are $G_D + G'_M$, whereas its own genotypic value is $G_D + G_M$. The phenotypic variance is then

$$\sigma^2 = \sigma^2_{GD} + \sigma^2_{ED} + \sigma^2_{GM} + \sigma^2_{EM} + \mathrm{cov}\,(G_D, G_M)\,,$$

where σ^2 denotes variance, and $\mathrm{Cov}\,(G_D, G_M)$ denotes the covariance between G_D and G_M. It has been assumed that genetic and environmental effects are independent, and that the same is true for environmental effects on dam and offspring. However, the covariance between environmental effects on direct and maternal values of the one individual, $\mathrm{cov}\,(E_M, E_D)$, is not assumed to be zero. It will be assumed that all genetic effects are additive, and that variances and covariances are constant during the selection program.

Selection differentials

Selection may be based on arbitrary indices I_m and I_f in males and females designed to improve overall genetic merit H, of which G_D and G_M for the trait of interest may be components. Genetic selection differentials for any trait are then given by the phenotypic selection differential for the index multiplied by the regression of breeding value for the trait on the index. If i denotes the standardised selection differential, the phenotypic selection differential is $i\,\sigma_I$, where σ stands for standard deviation. The regression is $\mathrm{Cov}\,(G, I)/\sigma^2_I$. Then the genetic selection differentials for direct effects in males and females are

$$g_{Dm} = \mathrm{Cov}\,(G_D, I_m)\; i_m/\sigma_{Im}$$

$$g_{Df} = \mathrm{Cov}\,(G_D, I_f)\; i_f/\sigma_{If}\,.$$

We pay special attention to selection based on the trait itself, such as weaning weight. For such traits

$$\begin{aligned}\mathrm{Cov}\,(G_D, P) &= \mathrm{Cov}\,(G_D, G_D) + \mathrm{Cov}\,(G_D, G'_M)\\ &= (h^2_D + r_G\, h_D\, h_M/2)\; \sigma^2_P\end{aligned}$$

where h^2_D and h^2_M are the fractions of σ^2_P due to variation in G_D and G_M respectively, and r_G is the genetic correlation between direct and maternal effects. Thus for selection on phenotype

$$g_{Dm} = (h^2_D + r_G\, h_D\, h_M/2)\; i_m\, \sigma_P$$

$$g_{Df} = (h^2_D + r_G\, h_D\, h_M/2)\; i_f\, \sigma_P\,.$$

In addition to transmitting genes for direct and maternal effects, selected females also contribute their own maternal ability $G_M + E_M$ to the phenotype of their progeny. To estimate this contribution, we need the covariance of maternal ability with the index:

$$\mathrm{Cov}\,(G_M + E_M, I_f) = \mathrm{Cov}\,(G_M, I_f) + \mathrm{Cov}\,(E_M, I_f)\,.$$

Thus this covariance has both genetic and environmental components. The genetic selection differential is

$$g_{Mf} = \mathrm{Cov}\,(G_M, I_f)\; i_f/\sigma_{If}\,,$$

while the environmental selection differential is

$$e_{Mf} = \mathrm{Cov}\,(E_M, I_f)\; i_f/\sigma_{If}\,.$$

Sires pass on to their progeny genes for both direct and maternal effects, the latter being expressed in the maternal ability of their daughters. The maternal genetic selection differential for sires is

$$g_{Mm} = \mathrm{Cov}\,(G_M, I_m)\; i_m/\sigma_{Im}\,.$$

For direct selection, differentials for maternal effects can be found as follows.

$$\begin{aligned}\mathrm{Cov}\,(G_M, P) &= \mathrm{Cov}\,(G_M, G_D) + \mathrm{Cov}\,(G_M, G'_M)\\ &= (r_G\, h_D\, h_M + h^2_M/2)\; \sigma^2_P\end{aligned}$$

$$\begin{aligned}\mathrm{Cov}\,(E_M, P) &= \mathrm{Cov}\,(E_M, E_D)\\ &= q_E\, \sigma^2_P\,.\end{aligned}$$

The corresponding differentials are:

$$g_{Mm} = (r_G\, h_D\, h_M + h^2_M/2)\; i_m\, \sigma_P$$

$$g_{Mf} = (r_G\, h_D\, h_M + h^2_M/2)\; i_f\, \sigma_P$$

$$e_{Mf} = q_E\, i_f\, \sigma_P\,.$$

Response with discrete generations

The total additive response (Dickerson 1947) would be given by

$$\begin{aligned}&(g_{Dm} + g_{Mm} + g_{Df} + g_{Mf})/2\\ &\quad = (h^2_D + 3\, r_G\, h_D\, h_M/2 + h^2_M/2)\; (i_m + i_f)\; \sigma_I/2\,.\end{aligned}$$

In a population with discrete generations, the first generation of selection would give a response as follows. The direct value of the progeny would be increased by $(g_{Dm} + g_{Df})/2$, while the maternal ability of their dams would be increased by $g_{Mf} + e_{Mf}$. Thus the phenotypic improvement in the progeny would be

$$(g_{Dm} + g_{Df})/2 + g_{Mf} + e_{Mf}\,,$$

and thus would differ from the total additive response by

$$e_{Mf} + (g_{Mf} - g_{Mm})/2\,.$$

After two generations of selection the gain in the direct component would be $(g_{Dm} + g_{Df})$, the gain in maternal effect from the first generation of selection would be $(g_{Mm} + g_{Mf})/2$ and the effect of selection of dams would be $g_{Mf} + e_{Mf}$, so the total response to two generations of selection would be

$$(g_{Dm} + g_{Df}) + (g_{Mm} + g_{Mf})/2 + g_{Mf} + e_{Mf}\,.$$

Then the change from first to second generation would be the total additive response, as would subsequent gains (Van Vleck et al. 1977).

When generations overlap, the pattern of response can be more complicated, and we now turn to consider how to deal with this.

Response with overlapping generations

As pointed out by Hill (1974), predictions with overlapping generations require a matrix rather than a scalar description because age distributions have to be considered at any one time. Let the direct and maternal genetic values at any one time t for j male and k female age groups be

$$u_t' = (\mathrm{u}_{\mathrm{m1t}}\,\mathrm{u}_{\mathrm{m2t}} \ldots \mathrm{u}_{\mathrm{mjt}}\,\mathrm{u}_{\mathrm{f1t}}\,\mathrm{u}_{\mathrm{f2t}} \ldots \mathrm{u}_{\mathrm{fkt}}) .$$

Thus u_{Dt} and u_{Mt} contain mean breeding values for direct and maternal contributions by age-sex groups. If initially $(\mathrm{t}=0)$ all age-sex groups have the same breeding value and we wish to express response as deviation from initial values u_0 is a vector of zeros. Suppose selection takes place on individuals born at $\mathrm{t}=0$ so that we have vectors d with the genetic selection differentials of 1 time unit old individuals:

$$d_{\mathrm{D}}' = (\mathrm{g}_{\mathrm{Dm}}\,0 \ldots 0\,\mathrm{g}_{\mathrm{Df}}\,0 \ldots 0)$$

$$d_{\mathrm{M}}' = (\mathrm{g}_{\mathrm{Mm}}\,0 \ldots 0\,\mathrm{g}_{\mathrm{Mf}}\,0 \ldots 0) .$$

The distribution of breeding values (u's) at t = 1 for either direct or maternal genetic contribution is

$$u_1 = P\,u_0 + d ,$$

where P is a "gene flow" matrix (Hill 1974) which updates previous breeding values. With a second round of selection on individuals born at time t = 1:

$$u_2 = P\,(P\,u_0 + d) + d .$$

Indeed after t rounds of selection

$$u_t = P^t\,u_0 + (I + P + \ldots + P^{t-1})\,d$$

where I is an identity matrix. If we are interested in the fluctuations of breeding values after one round of selection, then, at time t

$$u_t = P^t\,u_0 + P^{t-1}\,d .$$

We may now describe the general form of the P-matrix by denoting first with $\mathrm{p}_{\mathrm{1m}}, \mathrm{p}_{\mathrm{2m}} \ldots \mathrm{p}_{\mathrm{jm}}$ the proportion of genes contributed by $1, 2 \ldots \mathrm{j}$ time units old males to the next progeny crop, and similarly p_{1f}, $\mathrm{p}_{\mathrm{2f}} \ldots \mathrm{p}_{\mathrm{kf}}$ the proportion of genes contributed by female age groups to the next progeny. The proportion of genes from males, as well as from females must add to 0.5. Then, P is a square matrix of size j + k with the first row of each sex exhibiting the proportion of genes contributed by age-sex groups, the remaining rows allowing for ageing.

$$P = \begin{bmatrix} \mathrm{p}_{\mathrm{1m}} & \mathrm{p}_{\mathrm{2m}} & \cdots & \mathrm{p}_{\mathrm{j-1m}} & \mathrm{p}_{\mathrm{jm}} & \mathrm{p}_{\mathrm{1f}} & \mathrm{p}_{\mathrm{2f}} & \cdots & \mathrm{p}_{\mathrm{k-1f}} & \mathrm{p}_{\mathrm{kf}} \\ 1 & 0 & \ldots & 0 & 0 & 0 & 0 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & 1 & 0 & 0 & 0 & \ldots & 0 & 0 \\ \mathrm{p}_{\mathrm{1m}} & \mathrm{p}_{\mathrm{2m}} & \cdots & \mathrm{p}_{\mathrm{j-1m}} & \mathrm{p}_{\mathrm{jm}} & \mathrm{p}_{\mathrm{1f}} & \mathrm{p}_{\mathrm{2f}} & \cdots & \mathrm{p}_{\mathrm{k-1f}} & \mathrm{p}_{\mathrm{kf}} \\ 0 & 0 & \ldots & 0 & 0 & 1 & 0 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & 0 & 0 & 0 & 0 & \ldots & 1 & 0 \end{bmatrix}$$

In order to consider current generation environmental selection differential we may define a vector u_{Kt}, which at any time t contains the e_{Mf} value in the appropriate female age groups. Let

$$d_{\mathrm{K}}' = (0\,0 \ldots 0\,\mathrm{e}_{\mathrm{Mf}}\,0 \ldots 0) ,$$

and define a matrix F with zeros everywhere except for the 1's corresponding to ageing in females. It is convenient for the dimensions of these matrices to be compatible with the previous, but with zeros in the blocks corresponding to males. Then,

$$u_{\mathrm{K1}} = F\,u_{\mathrm{K0}} + d_{\mathrm{K}} ,$$

and after t rounds of selection:

$$u_{\mathrm{Kt}} = F^t\,u_{\mathrm{K0}} + (I + F \ldots + F^{t-1})\,d_{\mathrm{K}} .$$

In a previously unselected population, u_{K0} would be a zero vector.

We are now in a position to calculate response to selection. The response in progeny born at time t will be $s'\,u_{\mathrm{Dt}}$ for direct genetic effects, where s' is

$$s' = (\mathrm{p}_{\mathrm{1m}}\,\mathrm{p}_{\mathrm{2m}} \ldots \mathrm{p}_{\mathrm{jm}}\,\mathrm{p}_{\mathrm{1f}}\,\mathrm{p}_{\mathrm{2f}} \ldots \mathrm{p}_{\mathrm{kf}}) .$$

Response in maternal effects is $p'\,(u_{\mathrm{Mt}} + u_{\mathrm{Kt}})$, where p' is

$$p' = (0\,0 \ldots 0\,2\mathrm{p}_{\mathrm{1f}}\,2\mathrm{p}_{\mathrm{2f}} \ldots 2\mathrm{p}_{\mathrm{kf}}) .$$

On summing the two components we get the total response at time t

$$\mathrm{R}_t = s'\,u_{\mathrm{Dt}} + p'\,(u_{\mathrm{Mt}} + u_{\mathrm{Kt}}) .$$

If only one cycle of selection is applied, all selected females are lost from the population at time $\mathrm{t} = \mathrm{k} + 1$ and u_{Kt} is zero thereafter. In a continued program, u_{Kt} at this time would have all terms equal to e_{Mf}. In either case, all subsequent fluctuations reflect genetic changes only.

Example

For illustration we take an example in pig breeding also used by Hill (1974). Consider a herd in which boars are mated once and sows twice, having first offspring at 12 months of age (or 2 time units). Both female age groups contribute equally to the progeny crop and selection intensity among progeny of first and second parity sows is the same. Then

$$s' = (0 \quad 0.5 \quad 0 \quad 0.25 \quad 0.25)\,, \quad p' = (0 \quad 0 \quad 0 \quad 0.5 \quad 0.5)$$

$$P = \begin{bmatrix} 0 & 0.5 & 0 & 0.25 & 0.25 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0.25 & 0.25 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}, \quad F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}.$$

One out of 40 males and one out of eight females are selected before first mating on body weight gain per day. Phenotypic standard deviation for this trait is 70 g/day. The phenotypic selection differentials are

$$i_m \sigma_P = (2.34)\ (70\ \text{g/day}) = 163.8\ \text{g/day}$$

$$i_f \sigma_P = (1.65)\ (70\ \text{g/day}) = 115.5\ \text{g/day}\,.$$

In the original example, growth rate was assumed to be a direct additive trait with heritability 0.3. Suppose we suspect maternal effects to be important and take estimates for h_D^2, h_M^2 and r_G from the literature. For instance, Hohenboken and Brinks (1971) calculated for weaning weight in cattle $h_D^2 = 0.23-0.27$, $h_M^2 = 0.34-0.40$ and $r_G = -0.28$ yielding a total heritability $h_T^2 = h_D^2 + h_M^2/2 + 3\,r_G\, h_D\, h_M/2 = 0.28-0.33$. Assuming a similar pattern would apply in pigs, we will assume four our example $h_D^2 = 0.2$, $h_M^2 = 0.4$ and $r_G = -0.236$, so that $h_T^2 = 0.3$, the same as in the original example. The required regressions are

$$h_D^2 + r_G\, h_D\, h_M/2 = 0.1666$$

$$r_G\, h_D\, h_M + h_M^2/2 = 0.1332\,.$$

Therefore:

$$d_D' = (27.3 \quad 0 \quad 19.2 \quad 0 \quad 0) \qquad d_M' = (21.8 \quad 0 \quad 15.4 \quad 0 \quad 0)\,.$$

We will consider three estimates of environmental covariances:

$$q_E = 0.35 \quad d_K' = (0 \quad 0 \quad 40 \quad 0 \quad 0)$$

$$q_E = 0.00 \quad d_K' = (0 \quad 0 \quad 0 \quad 0 \quad 0)$$

$$q_E = -0.35 \quad d_K' = (0 \quad 0 \quad -40 \quad 0 \quad 0)\,.$$

Results for a single round of selection are shown in Table 1. The asymptotic phenotypic change is that expected for genetic change:

$$(2.34 + 1.65)\ (0.3)\ (70)/(2 + 2.5) = 18.6\,.$$

In the early stages of the program and until selected sows disappear from the herd the effect of q_E can be important.

In a continued selection program, responses from previous selection rounds are added to give the cumulative response shown in Fig. 1. Assuming $q_E = 0.0$ when it is -0.35, results in overestimation of phenotypic response by 52% at $t = 5$ and 23% at $t = 10$ in this case.

The parameters used in this example are arbitrary and give inconsistent heritability estimates from paternal half sib (HS) or dam offspring (DO) covariances. For the above parameters:

$$h_{HS}^2 = 4\ \text{Cov}\ (\text{HS})/\sigma_P^2 = h_D^2 = 0.2$$

$$h_{DO}^2 = 2\ \text{Cov}\ (\text{DO})/\sigma_P^2 = h_D^2 + 5\, r_G\, h_D\, h_M/2 + 2\, q_E + h_M^2$$
$$= 1.13\ (q_E = 0.35),\ 0.43\ (q_E = 0.0) \quad \text{or}$$
$$-0.26\ (q_E = -0.35)\,.$$

Table 1. Expected response at time of birth in successive time units after one round of selection on pigs born at time $t = 0$, assuming different environmental covariances (q_E) between direct and maternal effects. Parameters and age structure are given in the text. Pigs growth rate in g/day

Time	Direct effects	Direct and maternal effects		
		$q_E = -0.35$	$q_E = 0.0$	$q_E = 0.35$
1	0	0	0	0
2	33.8	6.1	26.2	46.2
3	8.8	−7.5	12.5	32.5
4	25.3		21.2	
5	15.0		17.5	
6	21.2		19.0	
7	17.6		18.5	
8	19.6		18.7	
9	18.5		18.6	
10	19.1		18.6	

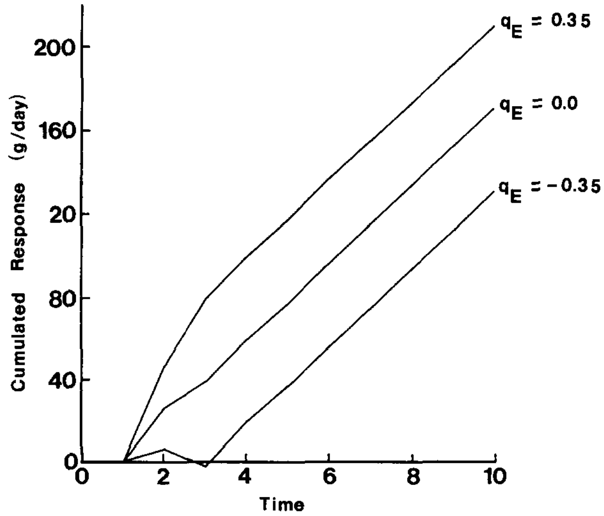

Fig. 1. Expected cumulative response to selection on growth rate in pigs assuming different environmental covariances (q_E) between direct and maternal efffects. Assumptions are given in the text

Thus, the dam offspring heritability would take values outside the 0 to 1 range with $q_E = \pm 0.35$. However, even if both h^2_{HS} and h^2_{DO} were measured in the population and were equal so that we would not suspect maternal effects, one could still make errors in response predictions because of compensating values of r_G, h^2_M and q_E. For example, suppose $h^2_{HS} = h^2_{DO} = h^2_D = 0.3$ and $r_G = -0.471$, $q_E = -0.05$ and $h^2_M = 0.6$. That gives the same expected response as before ($h^2_T = 0.3$) with deviations in the first four progeny crops ($t = 2$ to 5) of 33%, 24%, 20% and 12%.

Discussion

The proposed prediction method describes phenotypic response to selection as the sum of direct and material contributions, the latter having a genetic and an environmental component. The selection differentials achieved on these components are added to respective updated vectors containing age-sex distributions with values of previous selection rounds. The procedure is an extension of the discrete generation model described by Van Vleck et al. (1977). In their equation, response to selection in a continued program at time t is given by the sum of t times the genetic response in direct effects, $t-1$ times the genetic response in maternal effects and the maternal genetic selection differential for selected females, the latter accounting for the current generation maternal ability. This differs from our approach in that we use the phenotypic selection differential to account for maternal ability in the current generation, and this amounts to taking consideration of environmental covariance between direct and maternal effects. In one set of examples, describing early response to selection in Van Vleck et al. (1977), q_E is equal to -0.35. This would introduce an appreciable reduction in expected responses using our method.

In general, response prediction errors due to q_E will take the sign of the difference between assumed and true q_E. The shorter the evaluation period of a program, the larger the effects of non-zero q_E, because with increasing time genetic contributions become relatively more important compared to current generation effects. It follows that the shorter the female generation interval, and the higher the female selection intensity, the higher is the weight on possible environmental covariances. Consequently, estimates of realised heritability from long term selection experiments can be poor predictors of short term response.

If the evidence indicating negative covariances (Koch 1972) reflects the true situation we would expect responses to selection to be initially very slow. Although several studies have shown slow and even negative response to weaning weight selection (see the review by Barlow 1978) it is not always clear which components restricted response. The response equations derived in this paper could help to explain why initial phenotypic changes in a population selected for traits with maternal influences sometimes do not agree with expectations from genetic changes, and may be useful in the interpretation of experiments involving such traits.

Acknowledgement. J. P. M. is gratefully for the support received from the Instituto Nacional de Tecnologia Agropecuaria, INTA (Argentina).

References

Barlow R (1978) Biological ramifications of selection for preweaning growth in cattle. A review. Anim Breed (Abstr) 46:469–494

Dickerson GE (1947) Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. Res Bull Iowa Agric Exp Stn 354:489–524

Hanrahan JP (1976) Maternal effects and selection response with an application to sheep data. Anim Prod 22:359–369

Hill WG (1974) Prediction and evaluation of response to selection with overlapping generations. Anim Prod 18: 117–139

Hohenboken WD, Brinks JS (1971) Relationships between direct and maternal effects on growth in Herefords. 2. Partitioning of covariance between relatives. J Anim Sci 32:26–34

Koch RM (1972) The role of maternal effects in animal breeding. 4. Maternal effects in beef cattle. J Anim Sci 35:1316–1323

Koch RM, Gregory KE, Cundiff LV (1982) Critical analysis of selection methods and experiments in beef cattle and consequences upon selection programs applied. Proc 2nd World Congr Genet applied to livestock production, vol 5. Ed Garsi, Madrid, pp 514–526

Van Vleck LD, St Louis D, Miller JI (1977) Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal genetic effects. J Anim Sci 44:360–367

Wilham RL (1963) The covariance between relatives for characters composed of components contributed by related individuals. Biometrics 19:18–27

Willham RL (1980) Problems in estimating maternal effects. Livest Prod Sci 7:405–418