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The effect of repeated cycles of selection on genetic variance, heritability, and response

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Summary. The genetic variance of a quantitative trait decreases under directional selection due to generation of linkage disequilibrium. After a few cycles of selection on individual phenotype, a limit is reached where there is no further reduction in the genetic variance. Bulmer's model is extended to an animal breeding situation where selection is on information on relatives rather than on the individual's own performance. Algebraic expressions are derived to predict the decrease in genetic variance and associated reductions in heritability and response in the limit. Consequences of the results are discussed in the context of breeding strategies.

Key words: Linkage disequilibrium – Selection – Genetic variance – Breeding strategies

Introduction

Bulmer (1971) has shown that if a quantitative trait is determined by an infinite number of unlinked loci, selection will cause a temporary change in genetic variance due to the generation of covariances between genotypic values of different loci. Under selection, genetic variance decreases until a limiting value is reached in only four or five generations. At this point, the reduction in variance due to selection on parents is compensated for by the regeneration of variance due to free recombination. If selection is then relaxed, initial genetic variance is regenerated quickly. Bulmer (1971) considered the effect of selection on genetic variance when the criterion for selection is the individual's own performance. In many livestock species the criterion is not always the phenotypic value of individual animals. Techniques for evaluation such as selection indices or Best Linear Unbiased Prediction (BLUP), which incorporate information on relatives, are widely used.

Fimland (1979) has considered the effect of selection on both genetic variance of traits and covariance between traits. A procedure is described here to extend the results of Bulmer (1971) to the situation where selection is on an index based on information on relatives, to obtain the value of genetic variance when its limit under selection is reached. Associated with the reduction in genetic variance is a decrease in heritability, which decreases accuracy and response to selection. Algebraic expressions to predict the value of these parameters in the limit can be derived using the procedure described here. Implications of the results will be discussed in the context of breeding strategies.

Genetic variance in the selected group of parents

Let us consider a model where the trait is influenced by an infinite number of additive and unlinked loci with no dominance or epistasis. Population size is assumed to be infinite. Selection is on individuals and is directional and by truncation. Let A and $\hat{A}$ be bivariate normal variables, where A is the additive genetic value and $\hat{A}$ its estimate by selection index methods. We assume that there are no departures from normality after selection (Bulmer 1980). Now we rank animals by their $\hat{A}$ and then select the top ranking individuals $\hat{A}_s$.

The regression equation of A on the selected individuals $\hat{A}_s$ is

$$E(A|\hat{A}_s) = \mu_A + \frac{\sigma_{A,\hat{A}_s}}{\sigma^2_{\hat{A}_s}} (\hat{A}_s - \mu_s)$$

with variance

$$\mathrm{Var}\,[E\,(A|\hat{A}_s)] = \frac{(\sigma_{A,\hat{A}})^2}{(\sigma^2_{\hat{A}})^2}\,\sigma^2_{\hat{A}_s}$$

where μ_A = overall mean of additive genetic values, μ_s = mean of additive genetic values of selected individuals, $\sigma^2_{\hat{A}}$ = variance of the estimated additive genetic values, and $\sigma_{A,\hat{A}}$ = covariance between true (A) and estimated ($\hat{A}$) additive-genetic values.

The conditional variance of A given $\hat{A}_s$ is

$$\mathrm{Var}\,(A|\hat{A}_s) = \sigma^2_A - \frac{(\sigma_{A,\hat{A}})^2}{\sigma^2_{\hat{A}}}$$

where σ^2_A = variance of true additive-genetic values.

The genetic variance in the selected group is

$$\begin{aligned}\sigma^2_{A_s} &= \mathrm{Var}\,(A|\hat{A}_s) + \mathrm{Var}\,[E\,(A|\hat{A}_s)]\\ &= \sigma^2_A - \sigma^2_A\,r^2\left(1 - \frac{\sigma^2_{\hat{A}_s}}{\sigma^2_{\hat{A}}}\right)\\ &= \sigma^2_A\,(1 - k\,r^2)\end{aligned}$$

with

$$r = \frac{\sigma_{\hat{A},A}}{\sqrt{\sigma^2_{\hat{A}}\,\sigma^2_A}} \quad \text{and} \quad k = i\,(i - x)$$

where i and x are the selection intensity and normal deviate corresponding to the proportion selected, so that with truncation selection, $\sigma^2_{\hat{A}_s} = (1-k)\,\sigma^2_{\hat{A}}$. These results were first obtained by Cochran (1951).

With selection on phenotype, the accuracy of selection (r) is $\sqrt{h^2}$ and $\sigma^2_{A_s} = \sigma^2_A\,(1 - k\,h^2)$, which is well known (Bulmer 1971; Robertson 1977).

Genetic variance among offspring following selection

Gametic phase disequilibrium generated in selection of parents affects genetic variance among their progeny. With an infinite number of unlinked loci, the disequilibrium is halved in the progeny generation (Bulmer 1971) under random mating in the selected parents, so the total additive genetic variance among unselected progeny in generation 1 is

$$\sigma^2_{A_1} = [1 - (1/2)\,k\,r^2_0]\,\sigma^2_{A_0}$$

where $\sigma^2_{A_0}$ is the genetic variance in generation 0 and r_0 is the accuracy of selection in generation 0.

In later generations the genetic variance becomes

$$\sigma^2_{A_t} = [1 - (1/2)\,k\,r^2_{t-1}]\,\sigma^2_{A_{t-1}} + (1/2)\,(\sigma^2_{A_0} - \sigma^2_{A_{t-1}})$$

where t is the generation number.

The first term measures the new loss in variance attributable to disequilibrium, and the term $(1/2)\,(\sigma^2_{A_0} - \sigma^2_{A_{t-1}})$ measures the increase in genetic variance due to free recombination. After only a few cycles of selection, a limiting value for genetic variance is reached where the decrease in genetic variance due to generation of new disequilibrium is compensated for by the increase due to recombination. Genetic variance in the limit is

$$\sigma^2_{A_L} = [1 - (1/2)\,r^2_L\,k]\,\sigma^2_{A_L} + (1/2)\,(\sigma^2_{A_0} - \sigma^2_{A_L})$$

where $\sigma^2_{A_t} = \sigma^2_{A_{t-1}} = \sigma^2_{A_L}$ and r_L is the accuracy in the limit. After some algebraic manipulation this reduces to

$$\sigma^2_{A_L} = \frac{\sigma^2_{A_0}}{1 + k\,r^2_L} \tag{1}$$

Limiting values for genetic variance, heritability, and response under phenotypic selection

After repeated cycles of selection a limiting value for heritability is reached:

$$h^2_L = \frac{\sigma^2_{A_L}}{\sigma^2_{A_L} + \sigma^2_E}, \tag{2}$$

where σ^2_E is the environmental variance that is assumed constant from generation to generation.

After substituting the value of $\sigma^2_{A_L}$ from Eq. (1), the heritability in the limit becomes

$$h^2_L = \frac{\sigma^2_{A_0}}{\sigma^2_{A_0} + \sigma^2_E + k\,h^2_L\,\sigma^2_E} = \frac{h^2_0}{1 + (1 - h^2_0)\,k\,h^2_L} \tag{3}$$

where h^2_0 is heritability in generation 0, and $r_L = \sqrt{h^2_L}$. The only solution to Eq. (3) is

$$h^2_L = \frac{-1 + \sqrt{1 + 4\,h^2_0\,k\,(1 - h^2_0)}}{2\,k\,(1 - h^2_0)} \tag{4}$$

A similar expression, but for the disequilibrium in the limit, was previously given by Bulmer (1971). Solving for heritability has the advantage that value of heritability in the limit is independent of the value of genetic variance in the base population.

Figure 1 shows the values for heritability in the limit for different heritabilities in the base population prior to selection under three different selection intensities corresponding to selection of the top 1%, 20%, and 50% of the population. Values of h^2_L and h^2_0 are very similar if h^2_0 is either very high or low and when different selection intensities are compared differences between h^2_L and h^2_0 are very small.

Substituting h^2_L from Eq. (1) gives genetic variance in the limit as

$$\sigma^2_{A_L} = \frac{2\,\sigma^2_{A_0}\,(1 - h^2_0)}{1 - 2\,h^2_0 + \sqrt{1 + 4\,h^2_0\,k\,(1 - h^2_0)}}$$

Associated with the changes in genetic variance and heritability are changes in response to selection. To estimate those changes independent of the value of genetic

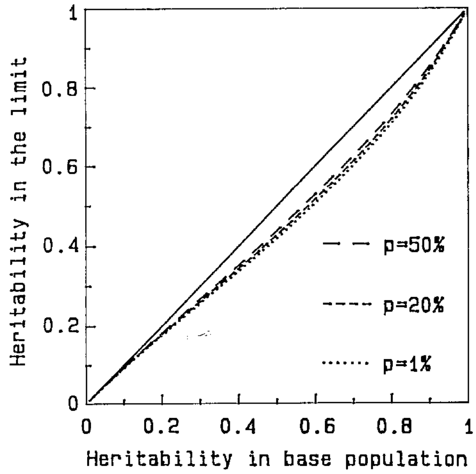

Fig. 1. Changes under phenotypic selection in heritability in the limit, along with heritability in the base population for selection intensities corresponding to varying proportions selected (1%, 20%, and 50%). The diagonal represents the case when heritability in the limit is equal to heritability in the base population

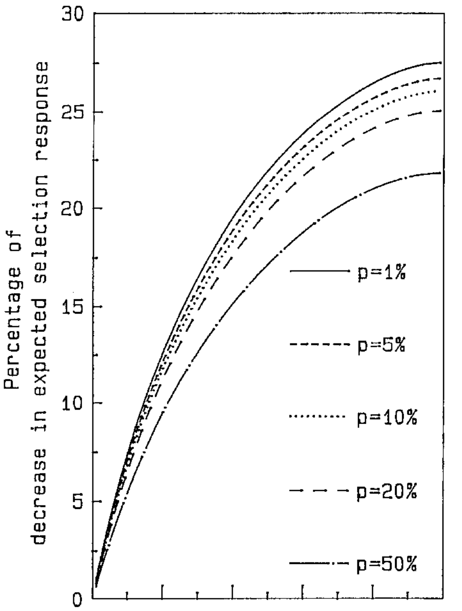

Fig. 2. Changes under phenotypic selection in the percentage of decrease of the response in the limit, along with heritability in the base population for selection intensities corresponding to varying proportions selected (1%, 5%, 10%, 20%, and 50%)

variance, we will consider the percentage of decrease in the response in the limit, R_L, with respect to that obtained in the first generation of selection, R_1:

$$E = 1-(R_L/R_1) = 1-\frac{i\,h_L\,\sigma_{A_L}}{i\,h_0\,\sigma_{A_0}} = 1-\sqrt{\frac{h_L^2}{h_0^2\,(1+k\,h_L^2)}}$$

The percentage decrease in response for different selection intensities and for different heritabilities in the base population is shown in Fig. 2. As heritability in the base population increases, so does the percentage decrease in response. The effect of selection intensity on the percentage decrease in response is closely related to heritability in the base population. The effect of selection intensity on decrease in response increases with heritability.

Limiting values for genetic variance, heritability and response under index selection

Obtaining the value of heritability in the limit can also be straightforward when the selection criterion is not performance of the individual. In this case, values of accuracy obtained by selection index theory are substituted in Eq. (1), $\sigma_{A_L}^2$ is also substituted in the standard formula of heritability in Eq. (2), and then a solution is obtained for h_L^2. Values of genetic variance, accuracy, and percentage of decrease in response in the limit can be obtained by substituting the resulting value of h_L^2 into the corresponding formula.

We now consider a more complicated situation where sires are selected on the average of records on p daughters, each with one record, and dams are selected on the average of n records each. We will consider the simplest of cases, where number of daughters per sire and records per dam are the same for any sire or dam, i.e., all animals of the same sex are evaluated with equal accuracy. The same generation interval is assumed in both sexes. It is convenient to decompose the value of repeatability in the limit into two components.

$$\mathrm{rep}_L = \frac{\sigma_{A_L}^2+\sigma_{PE}^2}{\sigma_{A_L}^2+\sigma_{PE}^2+\sigma_{TE}^2} = h_L^2\,(1-w)+w$$

where σ_{PE}^2 = permanent environmental variance, σ_{TE}^2 = temporary environmental variance and

$$w = \frac{\sigma_{PE}^2}{\sigma_{PE}^2+\sigma_{TE}^2}$$

The genetic variance in the limit is

$$\sigma_{A_L}^2 = \frac{\sigma_{A_0}^2}{1+(1/2)\,(k_s\,r_{S_L}^2+k_d\,r_{D_L}^2)}, \tag{5}$$

where k_s and k_d are the values of k previously defined for sires and dams, respectively.

Accuracy in the limit for sires and dams is

$$r_{S_L} = \sqrt{\frac{p\,h_L^2}{4+(p-1)\,h_L^2}} \tag{6}$$

$$r_{D_L} = \sqrt{\frac{n\,h_L^2}{1+(n-1)\,\mathrm{rep}_L}}. \tag{7}$$

Heritability in the limit is

$$h_L^2 = \frac{h_0^2}{1+(1/2)\,(1-h_0^2)\left[\dfrac{\alpha\, h_L^4+\beta\, h_L^2}{\gamma\, h_L^4+\delta\, h_L^2+\varepsilon}\right]}, \tag{8}$$

where

$$\alpha = [k_s\, p\,(n-1)\,(1-w)] + [k_d\, n\,(p-1)]$$
$$\beta = k_s\, p + [k_s\, p\,(n-1)\, w] + [4\, n\, k_d]$$
$$\gamma = (p-1)\,(n-1)\,(1-w)$$
$$\delta = [4\,(n-1)\,(1-w)] + [p-1] + [(p-1)\,(n-1)\, w]$$
$$\varepsilon = 4 + 4(n-1)\, w\,.$$

This equation has a solution between 0 and 1 which is

$$h_L^2 = \frac{[(q\cos\phi)-b]}{a}$$

where

$$\phi = (1/3)\arccos\,(-4\,G/q^3]$$
$$q = 2\sqrt{b^2-a\,c}$$
$$G = a^2\, d - 3\,a\,b\,c + 2\,b^3$$
$$a = [2\gamma + (1-h_0^2)\,\alpha]$$
$$b = (1/3)\,[2\,\delta + (1-h_0^2)\,\beta - 2\,\gamma\, h_0^2]$$
$$c = (2/3)\,[\varepsilon - \delta\, h_0^2]$$
$$d = -2\,h_0^2\,\varepsilon\,.$$

Values for heritability in the limit for different sets of parameters in Eq. (8) were obtained to show the relative influence of heritability in the base population, selection intensity, and accuracy. Three heritabilities, 0.10, 0.30, and 0.60, in the base population were considered, as were two different selection intensities corresponding to selection in the top 50% in each sex, and the top 3% and 10% in males and females, respectively. Figures 3 and 4 show the changes in heritability in the limit along with the number of daughters in sire evaluations, when dams are evaluated on the performance of one (Fig. 3) and five (Fig. 4) records. The parameter w was set to 1/3 (repeatability = 0.40 for $h^2 = 0.10$). Both selection intensity and accuracy produce changes in heritability in the limit, but the magnitude of such changes depends on the original heritability in the base population. Increased heritability and increased accuracy both reduce heritability in the limit. Differences between heritabilities in the base population and at the limit increase as heritability in the base population increases.

Values of accuracy in the limit for sires and dams can be obtained substituting the previously obtained value of h_L^2 in Eqs. (6) and (7), respectively. Genetic variance in the limit can be obtained substituting Eqs. (6) and (7) in

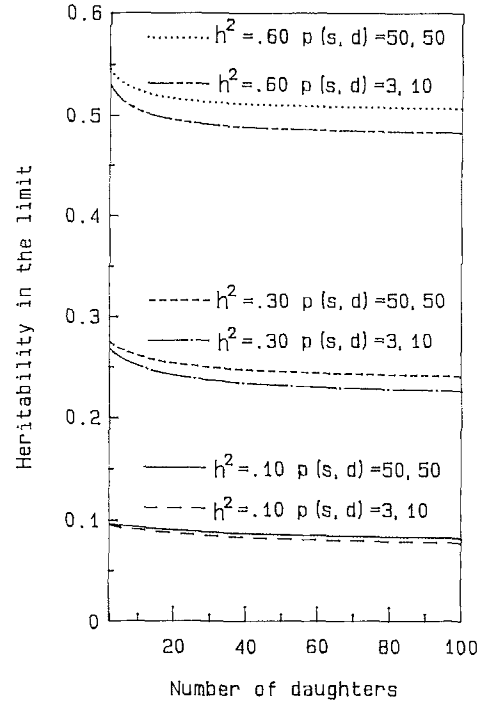

Fig. 3. Changes in heritability in the limit with number of daughters used in sire evaluation for three different heritabilities in the base population (0.10, 0.30, and 0.60) and two different selection intensities: $p\,(s, d) = 50, 50$ (50% of each sex); $p\,(s, d) = 3, 10$ (3% in sires and 10% in dams). Dams selected on one record

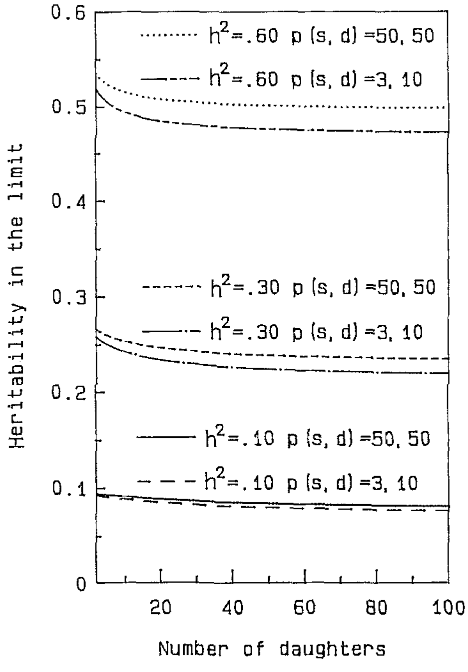

Fig. 4. Changes in heritability in the limit with number of daughters used in sire evaluation for three different heritabilities in the base population (0.10, 0.30, and 0.60) and two different selection intensities: $p\,(s, d) = 50, 50$ (50% of each sex); $p\,(s, d) = 3, 10$ (3% in sires and 10% in dams). Dams selected on average of five records. The parameter w was set to 1/3

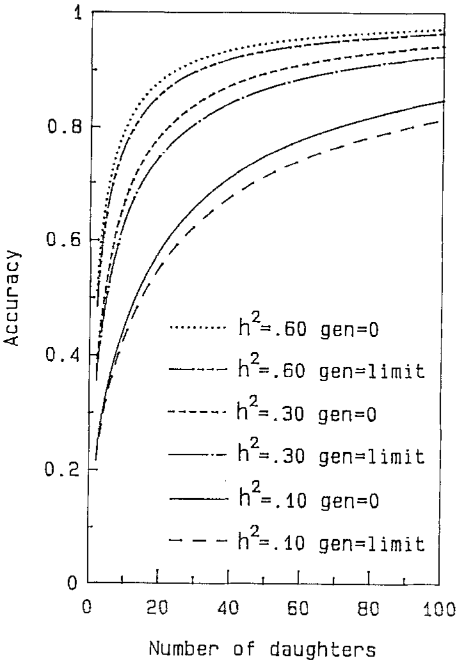

Fig. 5. Accuracies of evaluating sires in generation 0 and limit corresponding to number of daughters used in the evaluation for three different heritabilities in the base population (0.10, 0.30, and 0.60). Selection intensity corresponds to selection of the top 3% and 10% for sires and dams, respectively. Dams selected on one record

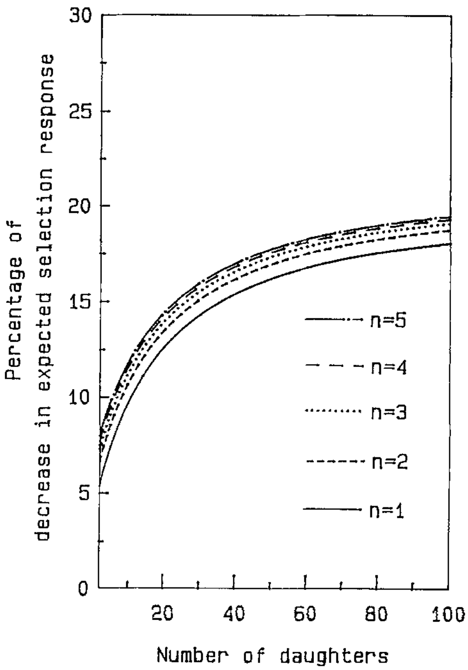

Fig. 6. Percentage decrease in response to selection at the limit corresponding to number of daughters used in sire evaluation for proportions selected of 3% and 10% for sires and dams, respectively. Dams selected on $n=1$ to $n=5$ records. Heritability in base population is 0.10

Eq. (5). Figure 5 shows values of accuracy in the limit for varying numbers of daughters per sire when dams were selected for their performance on one record. Selection intensity corresponded to selection of the top 3% and 10% for sires and dams, respectively. Heritabilities in the base population were 0.10, 0.30, and 0.60. Due to linkage disequilibrium, genetic variance decreases and so does heritability. As a consequence, accuracy in the progeny test also decreases in comparison with the base population.

Due to the changes in genetic variability, heritability, and accuracy, genetic progress is also affected. To measure the magnitude of such changes we use the percentage of decrease in the response due to disequilibrium in the limit.

$$E = 1 - [R_L/R_1]$$

$$= 1 - \frac{r_{S_L} i_S + r_{D_L} i_D}{(r_{S_0} i_S + r_{D_0} i_D)\sqrt{1 + (1/2)\,(k_s r_{S_L}^2 + k_d r_{D_L}^2)}},$$

where i_S and i_D are selection intensities for sires and dams, respectively, r_{S_L} is accuracy for sires in the limit, r_{D_L} is accuracy for dams in the limit, r_{S_0} is accuracy for sires in generation 0, and r_{D_0} is accuracy for dams in generation 0. Other terms were defined previously.

Values of the percentage decrease in response in the limit in relation to number of daughters in the sire evaluation are shown in Figs. 6–8 for heritabilities of 0.10, 0.30, and 0.60, respectively. Proportion selected was 3% and 10% for sires and dams, respectively. The number of records used in dam evaluation ranged from one to five. The value of w was set to 1/3. The proportional decrease in response increases as accuracy of sire and dam evaluation increases. As heritability in the base population increases, so does percentage decrease in response for any given level of accuracy, based on the number of daughters of sires or dam records.

Implications in breeding strategies

The conventional equation for prediction of response (Falconer 1981) is appropriate for only one generation of selection. When different schemes of selection are to be compared, goals are to maximize long-term progress and, as has been shown here, the predictions using the standard equation (Falconer 1981) are biased upwards. Magnitude of the bias depends on heritability, accuracy, and selection intensity in each scheme. As animals are selected more accurately and with greater intensity, bias in predic-

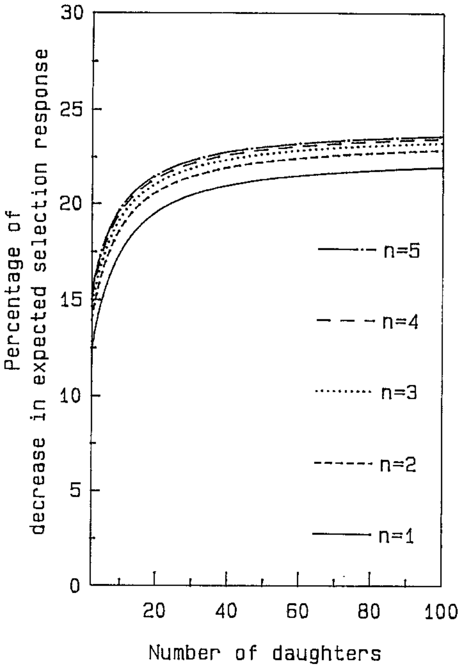

Fig. 7. Percentage decrease in response to selection at the limit corresponding to number of daughters used in sire evaluation for proportions selected of 3% and 10% for sires and dams, respectively. Dams selected on $n = 1$ to $n = 5$ records. Heritability in base population is 0.30

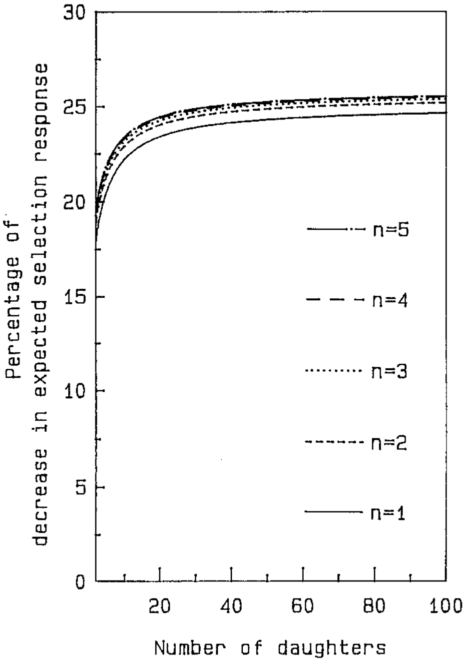

Fig. 8. Percentage decrease in response to selection at the limit corresponding to number of daughters used in sire evaluation for proportions selected of 3% and 10% for sires and dams, respectively. Dams selected on $n = 1$ to $n = 5$ records. Heritability in base population is 0.60

tion of response increases. Nicholas and Smith (1983) have proposed the use of MOET (Multiple Ovulation and Embryo Transfer) to increase the rate of response in dairy cattle. In the juvenile scheme, response is increased through shortening the generation interval, although accuracy of selection is decreased relative to the progeny test. When this scheme is compared with traditional breeding schemes in dairy cattle, the relative advantages will be larger than predicted, because animals are less accurately evaluated and, therefore, changes in genetic variability and response due to linkage disequilibrium will be less important. Meyer and Smith (1990) came to the same conclusion through a simulation study. They showed the decrease in genetic variability and response, after repeated cycles of selection due to generation of linkage disequilibrium in a large dairy cattle population. Possible applications of Restriction Fragment Length Polymorphism (RFLP) in animal improvement have been discussed recently (Soller and Beckmann 1982; Smith and Simpson 1986). Increased accuracy would permit increases in response to selection, but of a smaller magnitude than predictions when animals are already accurately evaluated. This technique could, however, shorten generation intervals. It seems more appropriate in the comparison of different breeding strategies to use the procedure described here to predict response in the limit rather than in the first generation.

The causes of disparity between theoretical genetic progress and that which has actually been attained in dairy cattle have been discussed recently (Van Vleck 1986). With current selection intensities and levels of accuracy in the evaluations, the theoretical estimates of progress in milk yield are overestimated by more than 20% in later generations with respect to first generation of selection. Therefore, other causes affecting response such as selection on secondary traits may not have been such important impediments to response in milk production as has been suggested.

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