

Gene flow and potential selection response in age-structured subpopulations having a common male pool

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Abstract

*In extensive pastoral systems, where mating cannot be controlled, the breeding strategies of intermingling owner flocks interact. We present a method to evaluate a breeding programme in extensive reindeer (*Rangifer tarandus*) management which can also be applied to other pastoral production systems. Our main objective was to evaluate the method by applying sensitivity analyses. The method included a gene flow model with maternal effects. The potential response R_p was defined as the response that could be achieved in a closed nucleus with a given selection procedure. The value of R_p was derived from the gene flow from dams to daughters, selection differentials, and the realized difference between subpopulations. We studied a population structure having two subpopulations, only one of which had been subjected to selection. Random mating between subpopulations and a common male pool were assumed. A reference case was defined using reindeer data from the literature. After 9 years of continued selection among progeny the estimate of R_p was 7.0 times higher than the realized subpopulation difference. We analysed deviations of R_p from the reference case caused by different female age structures between subpopulations. We also analysed the sensitivity of maternal effects. The method proved insensitive to differences in female age structure between subpopulations but was sensitive to the relative contribution of maternal effects to progeny performance.*

Keywords: genetic gain, maternal effects, projections, randombred populations, reindeer.

Introduction

In extensive animal production systems, common grazing grounds are often used. It is difficult to evaluate the gain from selection in such a system if animals mix during the rutting period and not all flock owners apply the same type of selection. In such cases, the sires are unknown as they are from a common male pool, whereas dams can be identified in connection with the recording of young animals. In cases where selection strategies differ between flocks, the population on a common grazing area consists of subpopulations between which the males migrate. The breeding system of such a population will be characterized by nucleus groups that are closed with respect to females but open with respect to the male breeding population. An example of such a system is Fenno-Scandinavian reindeer management. Other examples include different extensive pastoral production systems, especially in developing countries, where the selection systems

are based on incomplete mating control and common grazing grounds are used (Khombe, 1998).

It is important to assess a selection programme with intermingling herds under pastoral conditions so that the possibilities of improving the programme can be evaluated. Due to large annual environmental variations, the selection programme cannot be assessed from recorded data within the selected flock alone. However, annual variations can be eliminated by comparing the selected flock with an unselected owner-flock sharing the same environmental conditions. The selection is still difficult to assess because the realized response cannot be measured directly on the basis of phenotypic differences between a flock subjected to selection and one not subjected to selection. The reason for this is that some progeny from selected dams will have unselected sires, and *vice versa*. Therefore, the difference between owner-flocks will be less pronounced than in the situation where selected and unselected animals are kept separate.

Hill (1974) developed an age-structured gene flow model to evaluate the selection response in populations with overlapping generations. An alternative method was developed by McClintock and Cunningham (1974) to study the genetic impact of individual animals introduced into an age-structured population. Their method is a computational technique rather than a tool for mathematical analysis. Furthermore, optimum selection strategies in nucleus breeding programmes with overlapping generations have been thoroughly investigated (Hopkins and James, 1978). We do not study optimum selection strategies in our paper but our population structure is a special case of nucleus breeding. Thus, conclusions from nucleus breeding in age-structured populations may be applied to our model. Bijma and Woolliams (1999) developed a method to study selection in age-structured populations. Their main objective was to predict genetic contributions. They also studied genetic gain from continued selection and elucidated assumptions made in Hill's (1974) model.

Here we develop a model, which includes Hill's (1974) model, population subdivision, unknown identity of sires, and maternal effects. The main objective was to evaluate a method to estimate the potential selection response based on realized subpopulation differences. The potential selection response is that which would be achieved in a selected subpopulation if it were a closed nucleus. In the **Method** section, our approach, including a gene flow model is presented and exemplified with demographic data borrowed from the literature. In the **Results** section the method is evaluated by carrying out sensitivity analyses on the demographic data.

Method

Population structure

In the model presented there are two intermingling herds, A and B. Initially no selection had been practised in either herd. The herds mix during the mating season and random mating between herds is assumed. The two herds are therefore initially part of a homogeneous base population. Beginning at $t = 0$, selection is practised on newborn of both sexes in herd A before their first mating season.

Henceforth, herds A and B are called subpopulations A and B, respectively. The mixing of males during the mating season may then be described as male migration between subpopulations. The two subpopulations have a common male pool, as random mating between subpopulations is assumed. Genes are thereby transferred between subpopulations by the sires. Consequently, the gain

from selection will be counteracted in subpopulation A, whereas subpopulation B will benefit from selection even though it is unselected.

The sires are not identified, whereas dams are identified in connection with the recording of young animals. The newborn in subpopulation A belong to dams of subpopulation A, while those in subpopulation B belong to dams of subpopulation B.

Definition of potential response

We use the realized subpopulation difference to estimate the expected gain from selection in subpopulation A if A had been isolated from gene flow. We shall refer to this expected gain as the *potential response*, $R_p(t)$, where t is the investigated period since selection began.

For phenotypic selection, the realized subpopulation difference is measured by recording phenotypic means in subpopulation A *versus* subpopulation B. It is assumed that the subpopulations share common environmental effects. From the realized subpopulation difference, a realized heritability is estimated with which the potential response is calculated.

Assuming the infinitesimal model (Fisher, 1918) the method is first illustrated for phenotypic selection and discrete generations. Using Hill's gene flow model (Hill, 1974) we show that an equivalent method can be applied over several rounds of selection among progeny in a population with overlapping generations, provided that the female age structures in subpopulations A and B are identical. In a later section we show that the method can also be applied in cases where maternal effects are included.

Potential response to phenotypic selection with discrete generations

The response to selection in a population with discrete generations is expressed by:

$$R = \frac{1}{2}(S_f + S_m)h^2 \quad (1)$$

where S_f and S_m are the selection differentials on females and males, respectively, and h^2 is the heritability. The gain from selecting males in subpopulation A is distributed equally between subpopulations, on the assumption of a common male pool. Consequently, the heritability can be estimated from the realized subpopulation difference, ΔR_p . For one round of selection the expected difference between the response in subpopulation A, R_A , and the response in subpopulation B, R_B , is:

$$\begin{aligned} \Delta R_1 &= R_A - R_B \\ &= [\frac{1}{2}(S_f + p \cdot S_m)h^2] - [\frac{1}{2}(p \cdot S_m)h^2] \\ &= \frac{1}{2}S_f h^2 \\ \Rightarrow \hat{h}^2 &= \frac{2\Delta R_1}{S_f} \end{aligned} \quad (2)$$

where p is the proportion of sires belonging to subpopulation A, and \hat{h}^2 is the realized heritability. The realized heritability depends not only on the true heritability, but also on the accuracy of the selection procedure. From (1) and the realized heritability in (2), together with the selection differential of males, S_m , the potential response $R_p(t)$ is deduced:

$$\begin{aligned} R_p(1) &= \frac{1}{2}(S_f + S_m) \hat{h}^2 \\ &= \frac{S_f + S_m}{S_f} \Delta R_1 \end{aligned} \quad (3)$$

Both selection differentials, S_m and S_f , are estimated for progeny within subpopulation A.

Cumulative response to phenotypic selection with discrete generations

The asymptotic value of ΔR from continued selection is (James, 1977):

$$\Delta R_\infty = h^2 S_f \quad (4)$$

This assumes that the proportion of offspring in subpopulation A having sires from subpopulation A is the same after as before selection. Males in subpopulation A are selected and their offspring will therefore have a selective advantage (Bijma and Woolliams, 1999).

Let p be the proportion of offspring in subpopulation A from sires in subpopulation A before selection, while p_s is the proportion of offspring in subpopulation A from sires in subpopulation A after selection. Assuming normal distributions of offspring phenotype within parental subgroups, then with equal female and male selection differentials (see **Appendix B**):

$$\Delta R_\infty = h^2 \bar{S} \cdot \frac{1}{1 - (p_s - p)} \quad (5)$$

where \bar{S} is the weighted mean selection differential for animals in subpopulation A from sires in A and sires in B (Hopkins and James, 1979).

If S_f in (4) is the realized difference between the phenotypic mean of the selected offspring and of all offspring, then $S_f = \bar{S}$ and the bias of estimating the realized heritability from (4) will be:

$$\frac{\hat{h}^2}{h^2} = \frac{1}{1 - (p_s - p)} \quad (6)$$

This does not take into account that descendants from a selected sire will have a selective advantage several generations later (Bijma and Woolliams, 1999).

For continued selection it is also assumed that the genetic variance is static such that the heritability remains constant over several rounds of selection.

Gene flow and maternal effects

Gene flow matrix of subpopulations A and B including age-structure

The gene flow matrix \mathbf{P} for subpopulations A and B with a common male pool has a dimension of $2(n + m) \times 2(n + m)$ where n and m are maximum female and male ages (Figure 1). The matrix is divided into blocks corresponding to subpopulations and sub-blocks corresponding to sex. The parameter a_k is the proportion of genes passing from females aged k in subpopulation A to progeny in subpopulation A, and similarly b_k is the proportion of genes from females within subpopulation B. The proportions of genes passing from males aged k in subpopulation A to progeny in subpopulations A and B are expressed by p_k and $p'_{k'}$ respectively. Similarly q_k and $q'_{k'}$ are the proportions of genes from males in subpopulation B passing to their progeny. Under random mating between subpopulations $p_k = p'_{k'}$ and $q_k = q'_{k'}$ assuming no effect of selective advantage on sires (see above).

Let α_k be the proportion of sires aged k within subpopulation A, such that:

$$p_k = p \alpha_k \quad (7)$$

where p is the proportion of sires in subpopulation A, and $1-p$ is consequently the proportion of sires in subpopulation B.

Cumulative response according to conventional gene flow theory. For direct additive effects the cumulative response to selection over t years is calculated as (Hill, 1974):

$$\mathbf{P}_t = \sum_{k=1}^t \mathbf{P}^k \mathbf{s} \quad (8)$$

$$\mathbf{v}_\Delta = (\frac{1}{2} 0 \cdots 0 \mid \frac{1}{2} 0 \cdots 0 \mid -\frac{1}{2} 0 \cdots 0 \mid -\frac{1}{2} 0 \cdots 0) \quad (14)$$

where \mathbf{v}_Δ is of length $2(n + m)$.

From (13), \hat{h}^2 is:

$$\hat{h}^2 = \frac{\Delta R_t}{\mathbf{v}_\Delta \Sigma \mathbf{P}^k (S_m 0 \cdots 0 \mid S_f 0 \cdots 0 \mid \mathbf{0}' \mathbf{0})'} \quad (15).$$

The potential response $R_p(t)$ is calculated from the realized heritability by assuming that subpopulations A and B are not connected. Therefore, the submatrix of \mathbf{P} describing the gene flow within subpopulation A, \mathbf{P}_A (dimension $(n + m) \times (n + m)$), is used. \mathbf{P}_A is identical to the top left quarter of \mathbf{P} in Figure 1, except that the elements p_k are replaced by α_k which is the proportion of sires aged k within subpopulation A in (7). The potential response is then:

$$R_p(t) = \mathbf{v} \Sigma \mathbf{P}_A^k \mathbf{s} \quad (16)$$

$$= \mathbf{v} \Sigma \mathbf{P}_A^k (S_m 0 \cdots 0 \mid S_f 0 \cdots 0)' \hat{h}^2.$$

The size of the realization vector \mathbf{v} agrees with \mathbf{P}_A , and the first element of \mathbf{v} is 1, while all other elements are zeros.

Simplified model with direct effects

The difference in response between subpopulations is due to the selection of female progeny in subpopulation A alone, as for the discrete case. Moreover, the turn-over time of genes is the same in both female subpopulations, provided that the female age structures are identical. Therefore, the realized subpopulation difference, ΔR_t , can be calculated from the gene flow from dams to daughters within subpopulation A (described by matrix \mathbf{F}). Equation (13) can thereby be simplified as follows (see **Appendix A**):

$$\Delta R_t = \mathbf{v} \Sigma \mathbf{F}^k \mathbf{s} \quad (17).$$

The gene flow matrix \mathbf{F} is the bottom right submatrix in \mathbf{P}_A :

$$\mathbf{F} = \begin{pmatrix} a_1 & a_2 & \cdots & a_n \\ 1 & & & \\ & 1 & & \\ & & \ddots & \\ & & & 1 & 0 \end{pmatrix} \quad (18)$$

where n is the maximum female age, and the dimension of \mathbf{F} is $n \times n$. The realization vector is $\mathbf{v} = (1, 0 \dots 0)$ of length n . The selection vector \mathbf{s} for selection among progeny is expressed by:

$$\mathbf{s} = S_f h^2 (1 0 \cdots 0)' \quad (19).$$

If \mathbf{F} , S_f and ΔR_t are known, the realized heritability can be computed from (19) and (17) by solving for h^2 :

$$\hat{h}^2 = \frac{\Delta R_t}{\mathbf{v} \Sigma \mathbf{F}^k S_f (1 0 \cdots 0)'} \quad (20).$$

The next step is to estimate the potential response, $R_p(t)$, from \hat{h}^2 . The additional information needed to calculate the potential response from (16) is the submatrix \mathbf{P}_A and the male selection differential, S_m .

Simplified model with direct and maternal effects

Using the same arguments as those used for direct additive genes, the method can be extended to include maternal effects. This is achieved by estimating the ratio σ_{DP}/σ_p^2 , in (11), from the realized subpopulation difference, ΔR .

The expected difference in response between subpopulations A and B is deduced from (10):

$$\Delta R_t = \mathbf{v}_{M\Delta} \Sigma_{k=1}^t \mathbf{P}^{k-1} \mathbf{s}_M + \mathbf{v}_\Delta \Sigma_{k=1}^t \mathbf{P}^k \mathbf{s} \quad (21).$$

Vector \mathbf{v}_Δ is defined in (14), and selection vectors \mathbf{s} and \mathbf{s}_M are the same as in (11) and (12). The realization vector for the difference in maternal effects between A and B is:

$$\mathbf{v}_{M\Delta} = (\mathbf{0} \mid 2a_1 \ 2a_2 \cdots 2a_n \mid \mathbf{0}' \mid -2b_1, -2b_2 \cdots -2b_n) \quad (22)$$

where a_k and b_k are the female gene flow elements in \mathbf{P} . The realization vector expresses the proportional contribution of dams in different age classes to progeny as in (10).

With regard to direct effects, the gene flow from dams to daughters alone affects the expected subpopulation difference (see (14)). A similar simplification can be applied in cases where maternal effects are included. On the assumption that female

age structures in A and B are alike, (21) is simplified (see **Appendix A**) to:

$$\Delta R_t = \mathbf{v}_M \sum_{k=1}^t \mathbf{F}^{k-1} \mathbf{s}_M + \mathbf{v} \sum_{k=1}^t \mathbf{F}^k \mathbf{s} \quad (23)$$

where

$$\mathbf{s}_M = \frac{\sigma_{MP}}{\sigma_p^2} (S_f 0 \cdots 0)'$$

$$\mathbf{s} = \frac{\sigma_{DP}}{\sigma_p^2} (S_f 0 \cdots 0)'$$

$$\mathbf{v}_M = (2a_1 \ 2a_2 \ \cdots \ 2a_n)$$

$$\mathbf{v} = (1 \ 0 \ \cdots \ 0).$$

To calculate the potential response, the relationship between the vectors of direct and maternal effects must be fixed by an *a priori* known *maternal-direct effects ratio*:

$$K = \frac{\sigma_{MP}}{\sigma_{DP}} \quad (24)$$

where σ_{DP} and σ_{MP} are defined in (11) and (12).

We then get:

$$\mathbf{s}_M = K \mathbf{s} \quad (25)$$

For phenotypic selection, the maternal-direct effects ratio K can be calculated from the estimates of the direct additive genetic variance σ_D^2 , the maternal additive genetic variance σ_M^2 , and the direct-maternal genetic covariance σ_{DM} (Willham, 1972):

$$K = \frac{\sigma_{DM} + \frac{1}{2}\sigma_M^2}{\sigma_D^2 + \frac{1}{2}\sigma_{DM}} \quad (26)$$

If the maternal-direct effects ratio K is known, the elements of \mathbf{s} and \mathbf{s}_M can be estimated by solving for the ratio σ_{DP}/σ_p^2 in (23).

$$\begin{aligned} \Delta R_t &= \mathbf{v}_M \sum \mathbf{F}^{k-1} (K \mathbf{s}) + \mathbf{v} \sum \mathbf{F}^k \mathbf{s} \\ &= \frac{\sigma_{DP}}{\sigma_p^2} [\mathbf{v}_M \sum_{k=1}^t \mathbf{F}^{k-1} (K i_f \mathbf{x}) + \mathbf{v} \sum_{k=1}^t \mathbf{F}^k (i_f \mathbf{x})] \end{aligned} \quad (27)$$

where $\mathbf{x} = (1 \ 0 \ \cdots \ 0)$.

Let $\theta = \sigma_{DP}/\sigma_p^2$. Rearranging (27) will then result in:

$$\hat{\theta} = \frac{\Delta R_t}{\mathbf{v}_M \sum \mathbf{F}^{k-1} (K i_f \mathbf{x}) + \mathbf{v} \sum \mathbf{F}^k (i_f \mathbf{x})} \quad (28)$$

With no maternal effects, $\hat{\theta}$ is equal to the realized heritability. Thus $\hat{\theta}$ is calculated in a way similar to that used to calculate \hat{h}^2 in (20). By combining (11) with the value of $\hat{\theta}$ (28), the direct selection vector can be calculated as:

$$\mathbf{s} = \hat{\theta} (S_m \ 0 \ \cdots \ 0 \ ; \ S_f 0 \ \cdots \ 0)' \quad (29)$$

The maternal selection vector is calculated from (25) and (26).

The potential response, $R_p(t)$, is calculated using (10) and the same reasoning as for (16):

$$R_p(t) = \mathbf{v}_M \sum_{k=1}^t \mathbf{P}_A^{k-1} \mathbf{s}_M + \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k \mathbf{s} \quad (30)$$

where \mathbf{P}_A and \mathbf{v} are defined in (16), and $\mathbf{v}_M = 2(\mathbf{0} \ ; \ a_1 \ a_2 \ \cdots \ a_n)$.

A simple example illustrating the method is given in **Appendix C**.

Sensitivity analyses

The sensitivity of the potential response to small changes in parameter K is analysed using an expression derived from (28) and (30):

$$R_p(t) = \frac{[Kc_1(t) + c_2(t)] + \frac{S_m}{S_f} [Kc_3(t) + c_4(t)]}{2K + 1} \Delta R \quad (31)$$

where c_1 , c_2 , c_3 and c_4 are constants calculated for each t from the gene flow matrix \mathbf{P} (see **Appendix D**). The sensitivity value for K is then obtained by differentiating (31).

Data for sensitivity analyses

The elements of \mathbf{P} can be calculated from a population structure and age-specific reproduction (Charlesworth, 1994). Here we study a general example of phenotypic selection on juvenile body weight, for example of reindeer.

By letting $\Delta R_t = 1.0$ kg for all years t the measure of R_p is equivalent to the ratio $R_p/\Delta R_t$ for every ΔR_t

(see (31)). Thus the sensitivity analysis is performed on the relative potential response $R_p/\Delta R_t$.

Population parameters

The method was applied to simplified population parameters corresponding approximately to those used by Petersson and Danell (1992) on reindeer. Maximum ages were set to 9 years for females and 7 years for males. The age-specific female reproduction was then {0, 0.25, 0.46, 0.56, 0.64, 0.72, 0.80, 0.86, 0.86} for ages 1 to 9 years, respectively. The annual rate of natural mortality was assumed to be 0.07 for both sexes and all ages.

Slaughter strategies

Two sustainable but different slaughter strategies (A and B), which lead asymptotically to constant population size, were considered. Strategy A involves calf slaughter almost exclusively, whereas in strategy B, equal proportions of each age class are slaughtered. It was assumed that strategy A was practised in subpopulation A and strategy B in subpopulation B. The latter strategy resembles a traditional slaughter strategy in a pastoral system, whereas strategy A resembles a slaughter strategy in which slaughter decisions are based on recorded data. In strategy A, 43% of the female calves but none of the adult females, were culled each year. Seventy-six percent of the male calves were culled, 80% of the male yearlings were slaughtered randomly and all 2-year-old males were slaughtered. In strategy B, 9.5%

of the animals in each age class were slaughtered every year.

The asymptotic age distributions of retained female stocks are shown in Figure 2. The female generation intervals were 5.86 and 5.38 years for subpopulations A and B, respectively. Asymptotically, 83% of the males in subpopulation A were 1-year-olds, and the rest 2-year-olds. The number of males in subpopulation B decreased asymptotically by 16% between subsequent ages.

Male reproductive models

A male reproductive model had to be assumed in order to make calculations of the elements in **P** based on the asymptotic age distribution. Two extreme alternatives were studied so as to include a wide range of possible values of male reproductive success. In the *non-competitive* alternative all males were equally successful at reproducing. In the *hierarchical* alternative, males were most successful at a full-grown age of 4 years. In the latter alternative, approximate values of relative reproductive success were taken from Hirotsani (1994) {1 : 2 : 3 : 4 : 4 : 4 : 4} for male aged 1 to 7 years, respectively. Thus, a 7-year-old male had four times more offspring than a 1-year-old male.

Based on these two models and the asymptotic age distribution, the elements of the matrix **P** were calculated (Table 1).

Selection intensities

Since equation (31) includes a ratio of female and male selection differentials, it is sufficient to know

Table 1 Elements of the gene flow matrix **P** derived for two different models of relative male reproductive success (Alt. 1 = non-competitive alternative, Alt. 2 = hierarchical alternative)

Age	Subpopulation A		Subpopulation B			
	Females†	Males‡	Females§	Males		
	Alt. 1	Alt. 2	Alt. 1	Alt. 2		
1	0.000	0.417	0.357	0.000	0.114	0.041
2	0.033	0.083	0.143	0.047	0.096	0.069
3	0.056			0.073	0.080	0.087
4	0.063			0.075	0.067	0.097
5	0.067			0.071	0.056	0.081
6	0.070			0.067	0.047	0.068
7	0.072			0.063	0.040	0.057
8	0.072			0.057		
9	0.067			0.047		

† Elements a_k of **P**.

‡ α_k of equation (7).

§ Elements b_k of **P**.

|| The parameters β_{ki} , where $q_k = (1 - p)\beta_{ki}$; p is defined in (7) and q_k are elements of **P**.

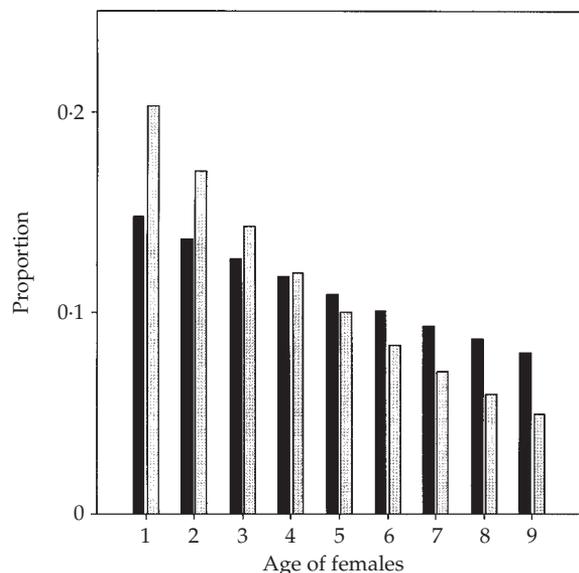


Figure 2 Age distribution of females in subpopulation A (■, calf slaughter) and subpopulation B (▨, equal proportions slaughtered from each age class).

the selection intensities, when truncated selection is applied, if the phenotypic variance is assumed to be the same in both sexes.

In subpopulation A, truncated phenotypic calf selection and slaughter strategy A were assumed. This implies that the female intensity of selection i_f was 0.69, as 57% of the female calves were retained. The male intensity of selection i_m was 1.3 as 24% of the male calves were retained in subpopulation A, while the older age classes were culled non-selectively. In subpopulation B, slaughter strategy B and no selection were assumed. There was no selective culling in B.

Maternal effects during phenotypic selection

The maternal-direct effects ratio, K , was calculated from (26) on the assumption of phenotypic selection. A value of $K = 0.15$ corresponds approximately to unpublished heritability estimates on reindeer (L. Appel and Ö. Danell, in preparation). An extreme range for K was calculated from the heritability estimates reviewed by Mohiuddin (1993). The interval $\{-0.15 < K < 1.0\}$ included 86% of the estimates of the heritability of cattle weaning weight.

For comparison, a reference case was defined

In the reference case the female age structure of subpopulation B was assumed to equal that of subpopulation A. The non-competitive male model and no maternal effects were assumed. Furthermore, the ratio of male to female selection intensities i_m/i_f was 1.88 (1.3/0.69).

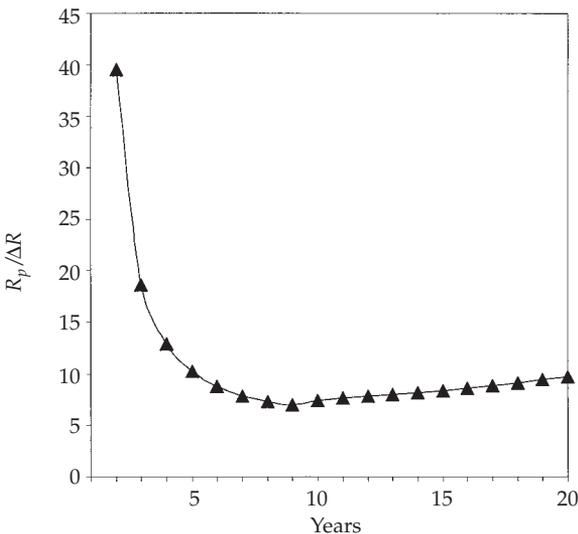


Figure 3 Relative potential response ($R_p/\Delta R$) over 20 years of continued selection. Reference case assumed.

Results

Bias in realized heritability due to selective advantage of sires

Assuming equal numbers of sires in subpopulations A and B ($p = 0.5$), a selection differential of $S = 1.0$ and a heritability of $h^2 = 0.4$, the realized heritability was calculated to be 1.05 times ($h^2 = 0.42$) the true heritability, using equation (6). The proportion of offspring in subpopulation A from sires in subpopulation A after selection (p_s) was 0.55. The bias decreases for very small (or large) p , being smaller at lower heritabilities and selection differentials.

Relative potential response for the reference case

In Figure 3 the relative potential response, $R_p/\Delta R$, is shown for the reference case, calculated using equation (16) over 20 years of continued selection. The value of the relative potential response was defined first in year 2, when the first selected females reproduce. In the early years of selection, the relative potential response was extremely high because the effect of selection on males was large, whereas females became fully reproductively mature at older ages. The relative potential response, as shown in Figure 3, did not change much from years 6 to 20 (minimum of 7.0 in year 9 and maximum of 9.8 in year 20). Asymptotically the gain from selecting females reaches a plateau, and $R_p/\Delta R$ increases at a constant rate.

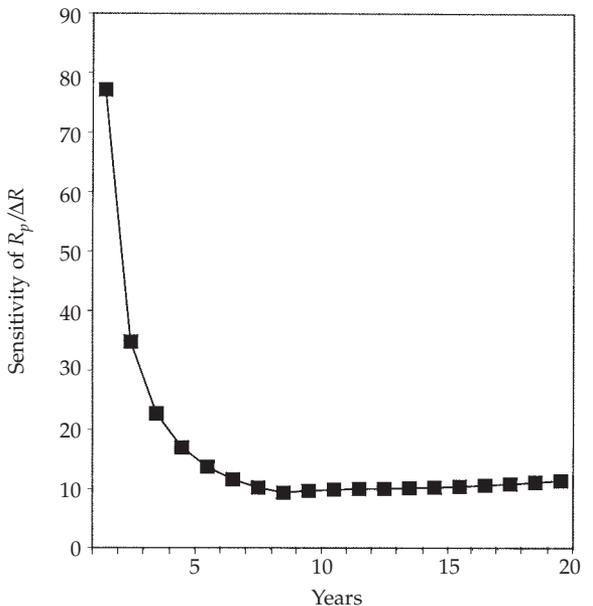


Figure 4 Sensitivity (partial derivative) of the relative potential response for the maternal-direct effects ratio K is calculated by differentiating (31) with $K=0$.

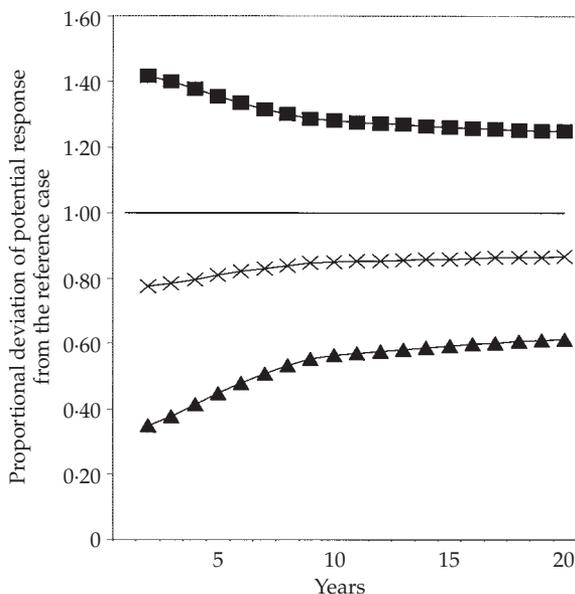


Figure 5 Proportional deviation of $R_p/\Delta R$ from the reference case (K is the maternal-direct effects ratio defined in the text; —■— $K = -0.15$; —×— $K = 0.15$; —▲— $K = 1.0$).

Sensitivity analyses

Maternal-direct effects ratio. The sensitivity of K was calculated for values of K close to zero (Figure 4). Since the relative potential response is a non-linear

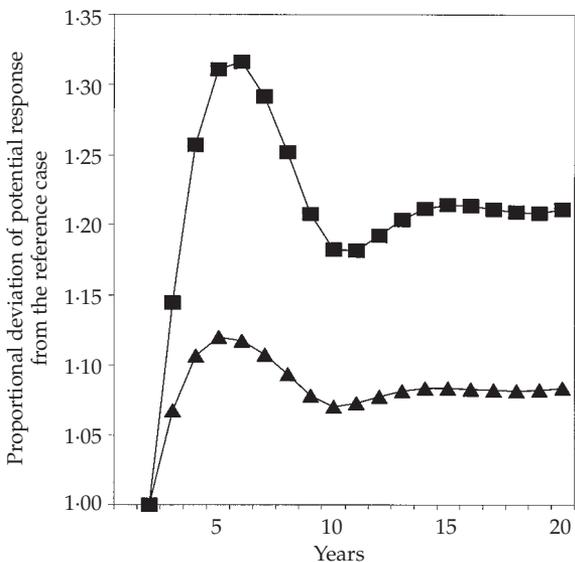


Figure 6 Proportional deviation of $R_p/\Delta R$ from the reference case due to differences in female age structure between subpopulations A and B (p is the proportion of males in subpopulation A); —■— $p = 0$; —▲— $p = 0.5$.

function of K in (31), the sensitivity of the maternal-direct effects ratio varies with K . The deviation in the potential response from the reference case is shown in Figure 5 for $K = 0.15, -0.15$, and 1.0 .

Different female subpopulation age structures. Differences in female age structure between subpopulations affect the potential response to a varying extent, depending on the proportion of males in subpopulations A and B. The effect of female age structure was studied using equation (12) and the age structures in Figure 2. When all males are in subpopulation A, differences in female age structure do not affect the potential response. The relative effects of different age structures are shown in Figure 6 for two different scenarios: (i) when there are equal numbers of reproductive males in the two subpopulations, and (ii) when all males are in subpopulation B.

Hierarchical male model. When a hierarchical male reproductive model was assumed, the relative deviation of R_p from the reference case was in the range 2.2 to 3.0% between years 6 and 20.

Discussion

Populations under pastoral conditions are subject to large annual environmental variations. The method presented eliminates annual variations by comparing a selected subpopulation with an unselected subpopulation. The method was based on the assumptions that males mate randomly, that the female age structures in selected and unselected subpopulations were equal, and that selective advantage due to origin of sires could be ignored. On these assumptions the realized subpopulation difference was caused by selecting females and the subsequent gene flow from dams to daughters. The potential response, R_p , could thereby be estimated on the basis of realized subpopulation difference, ΔR . The main advantage of these assumptions was that only information on the selected subpopulation had to be known.

The realized heritability is expected to exceed the true heritability due to the selective advantage of offspring from selected sires. This effect was shown to be small, although the proportions of offspring from selected sires before and after selection differed. Although equation (6) did not take into account that genetic contributions of ancestors to future generations can differ from contributions to selected offspring, the effect on potential response should still be negligible (Bijma and Woolliams, 1999).

Furthermore, Hill's model assumes moderate or low genetic selection differentials when calculating gain

from continued selection (Bijma and Woolliams, 1999). The selection intensities for females and males were $i_f = 0.69$ and $i_m = 1.3$ in the example used for sensitivity analysis. With moderate heritability ($h^2 < 0.4$) the genetic selection differentials were lower than those used in the example by Bijma and Woolliams (2000). They concluded that conventional gene flow theory yields an accurate prediction of genetic gain, even though conventional gene flow theory gives poor predictions of genetic contributions.

Lower values of selection differentials may be expected from field data under pastoral conditions for three main reasons. Firstly, an unpredictable variation in mortality from year to year makes it necessary to select larger proportions. Secondly, accurate adjustment factors are seldom available, which reduces the accuracy of the selection procedure. Thirdly, it may be difficult to gather all the newborn animals together at the same time for selection assessment, which inhibits use of maximum selection intensities.

The potential response will be realized only if the response can be extrapolated with constant genetic gain, i.e. without approaching any selection limit. It is conceivable that the environmental conditions will restrict the response in pastoral production systems if the requirements of the animals increases due to genetic change.

The relative potential response changed considerably with the lapse of time during the early stages of the selection programme (Figure 3). Therefore, an empirical measure of the realized subpopulation difference, ΔR_t , and thereby R_p , would not be meaningful before at least one female generation interval had elapsed, i.e. after the sixth year of selection in this example. As the realized subpopulation difference is caused solely by selecting females and the subsequent gene flow from dams to daughters, the subpopulation difference is probably small as well, and can only be measured with reasonable accuracy after several years of selection.

An appealing property of the proposed method is that maternal effects can be studied generally through a single parameter, K (maternal-direct effects ratio). This makes the method applicable to a wide range of animal production systems, but the maternal *v.* direct contribution to the selection criterion has to be known *a priori*. One problem is that the potential response appears to be sensitive to small changes in K (Figure 4). However, even though

a wide range of K values were used, the potential response was limited (Figure 5).

The relative potential response was unaffected by changes in mating success related to advancing male age, one reason for this being that males were culled at early ages in the selected subpopulation. Early culling is often a preferred strategy in breeding programmes, as it increases the gain from selection.

Although equal female age structures was a principal assumption of the simplified model when testing the method, the results differed little between the two extreme slaughter strategies (Figure 6). Although the age structures differed considerably between subpopulations, this result was expected (Figure 2) because a common male pool was assumed.

The conclusion of the sensitivity analysis is that prior knowledge of expected maternal genetic (co)variance estimates is required. Nevertheless, the method can be applied even though the female age structures differ between subpopulations and the mating success for different male ages is unknown. In an intended application of the method to Fennoscandinavian reindeer management, the realized subpopulation difference ΔR_t will be measured as the subpopulation difference in mean calf-weights in one year ($t > 6$ years) after adjustment for non-genetic effects, e.g. calf sex ratio and dam age structure. Given female and male selection differentials, reasonable values of the gene flow elements of selected females, and an approximate age structure of the selected males, the potential response may be calculated with a precision determined mainly by the accuracy of the maternal-direct effects ratio K .

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Appendix A

Male paths of gene flow can be ignored when female age structures are alike in the two subpopulations: direct and maternal effects

Here we show, assuming Hill's (1974) model, that equation (21) including all gene flow in the total population ('full model')

$$\Delta R_t = \mathbf{v}_{M\Delta} \sum_{k=1}^t \mathbf{F}^{k-1} \mathbf{s}_M + \mathbf{v}_\Delta \sum_{k=1}^t \mathbf{F}^k \mathbf{s}$$

and (23) including only gene flow of dams to daughters in the selected subpopulation ('simplified model')

$$\Delta R_t = \mathbf{v}_M \sum_{k=1}^t \mathbf{F}^{k-1} \mathbf{s}_M + \mathbf{v} \sum_{k=1}^t \mathbf{F}^k \mathbf{s}$$

are equivalent, when random mating between subpopulations and equal female age structures is assumed.

The response in progeny from 1 year of selection, r_t , is calculated from (10):

$$r_t = \mathbf{v}_M \mathbf{P}^{t-1} \mathbf{s}_M + \mathbf{v} \mathbf{P}^t \mathbf{s}$$

where \mathbf{P} is the gene flow matrix in Figure 1, and \mathbf{v}_M and \mathbf{v} are realization vectors as defined in (10). From (11) and (12) we have:

$$\mathbf{s} = \frac{\sigma_{DP}}{\sigma_P^2} (S_m \ 0 \ \dots \ 0 \mid S_f \ 0 \ \dots \ 0 \mid 0 \ 0 \ 0)'$$

$$\mathbf{s}_M = \frac{\sigma_{MP}}{\sigma_P^2} (S_m \ 0 \ \dots \ 0 \mid S_f \ 0 \ \dots \ 0 \mid 0 \ 0 \ 0)'$$

From here on, \mathbf{s}_t and $\mathbf{s}_{M,t}$ are help variables, which split the response r_t into direct and maternal components:

$$\mathbf{s}_t = \mathbf{P}' \mathbf{s} \text{ and } \mathbf{s}_{M,t} = \mathbf{P}' \mathbf{s}_M$$

then:

$$\mathbf{s}_{t+1} = \mathbf{P} \mathbf{s}_t \text{ and } \mathbf{s}_{M,t+1} = \mathbf{P} \mathbf{s}_{M,t}$$

$$\Leftrightarrow r_t = \mathbf{v}_M \mathbf{s}_{M,t-1} + \mathbf{v} \mathbf{s}_t$$

Let the elements x_t^* , x_t , y_t^* , y_t be the responses to selection in the first age class of males in subpopulation A, females in subpopulation A, males in subpopulation B, and females in subpopulation B, respectively. Similarly the gain from maternal additive genes is expressed by $x_{M,t}^*$, $x_{M,t}$, $y_{M,t}^*$, $y_{M,t}$. Then the elements of \mathbf{s}_t and $\mathbf{s}_{M,t}$ can be written as:

$$\mathbf{s}_t = (x_t^* \ \dots \ x_{t-m+1}^* \mid x_t \ \dots \ x_{t-n+1} \mid y_t^* \ \dots \ y_{t-m+1}^* \mid y_t \ \dots \ y_{t-n+1})'$$

$$\mathbf{s}_{M,t} = (x_{M,t}^* \ \dots \ x_{M,t-m+1}^* \mid x_{M,t} \ \dots \ x_{M,t-n+1} \mid y_{M,t}^* \ \dots \ y_{M,t-m+1}^* \mid y_{M,t} \ \dots \ y_{M,t-n+1})'$$

A1 Full model with gene flow matrix \mathbf{P}

Gene flow and selection of both males and females is used to deduce an expression of ΔR_t . Let:

$$z_t = x_t - y_t$$

$$z_{M,t} = x_{M,t} - y_{M,t}$$

$$\Delta r_t = \mathbf{v}_{M\Delta} \mathbf{s}_{M,t-1} + \mathbf{v}_\Delta \mathbf{s}_t$$

where Δr_t is the total difference in progeny response between subpopulations. The vectors $\mathbf{v}_{M\Delta}$ and \mathbf{v}_Δ are realization vectors extracting population differences in maternal and direct response (as defined in equations (14) and (22)). Furthermore, let \mathbf{p}_1 be the first row in the matrix \mathbf{P} , and \mathbf{p}_{n+m+1} row number $n+m+1$ (i.e. the row under the middle partitioning line in Figure 1). then:

$$\begin{aligned} & \mathbf{s}_{t+1} = \mathbf{P} \mathbf{s}_t \\ & = (\mathbf{p}_1 \mathbf{s}_t \ x_t^* \ \dots \ x_{t-m}^* \mid \mathbf{p}_1 \mathbf{s}_t \ x_t \ \dots \ x_{t-n} \mid \mathbf{p}_{n+m+1} \mathbf{s}_t \ y_t^* \ \dots \ y_{t-m}^* \mid \mathbf{p}_{n+m+1} \mathbf{s}_t \ y_t \ \dots \ y_{t-n}) \end{aligned}$$

and

$$\begin{aligned}
 \mathbf{s}_{M,t+1} &= \mathbf{P}\mathbf{s}_{M,t} \\
 &= (\mathbf{p}_1 \mathbf{s}_{M,t} x_{M,t}^* \cdots x_{M,t-m}^* | \mathbf{p}_1 \mathbf{s}_{M,t} x_{M,t} \cdots x_{M,t-n} | \mathbf{p}_{n+m+1} \mathbf{s}_{M,t} \\
 &\quad y_{M,t}^* \cdots y_{M,t-m}^* | \mathbf{p}_{n+m+1} \mathbf{s}_{M,t} y_{M,t} \cdots y_{M,t-n})
 \end{aligned}$$

Because $\mathbf{v}_{M\Delta} = 2(\mathbf{p}_1 - \mathbf{p}_{n+m+1})$ in equation (22) and $a_k = b_k$ for all ages when equal female age structures of subpopulation A and B are assumed (a_k and b_k are elements of \mathbf{P} as defined in Figure 1), we can develop a set of three recursion formulae:

$$\begin{cases}
 z_{t+1} = x_{t+1} - y_{t+1} = \mathbf{p}_1 \mathbf{s}_t - \mathbf{p}_{n+m+1} \mathbf{s}_t = \sum_{k=1}^n (a_k x_{t-k+1} - b_k y_{t-k+1}) \\
 \quad = \sum_{k=1}^n a_k z_{t-k+1} \\
 z_{M,t+1} = x_{M,t+1} - y_{M,t+1} = \mathbf{p}_1 \mathbf{s}_{M,t} - \mathbf{p}_{n+m+1} \mathbf{s}_{M,t} = \sum_{k=1}^n [a_k x_{M,t-k+1} - b_k y_{M,t-k+1}] \\
 \quad = \sum_{k=1}^n a_k z_{M,t-k+1} \\
 \Delta r_{t+1} = \mathbf{v}_{M\Delta} \mathbf{s}_{M,t} + \mathbf{v}_{\Delta} \mathbf{s}_{t+1} = 2 \sum_{k=1}^n [a_k x_{M,t-k+1} - b_k y_{M,t-k+1}] + z_{t+1} = 2 \sum_{k=1}^n a_k z_{M,t-k+1} + z_{t+1} \\
 \quad = 2z_{M,t+1} + z_{t+1}
 \end{cases}$$

A2 Simplified model with gene flow matrix F

In the simplified model the matrix \mathbf{F} is used instead of \mathbf{P} , and only the female parts of the selection vectors are used (length n).

$$\mathbf{F} = \begin{pmatrix} a_1 & a_2 & \cdots & a_n \\ 1 & & & \\ & 1 & & \\ & & \ddots & \\ & & & 1 & 0 \end{pmatrix}$$

Using the same definition as above we obtain:

$$\begin{aligned}
 \mathbf{s}_{t+1} &= \mathbf{F}\mathbf{s}_t \\
 \mathbf{s}_{M,t+1} &= \mathbf{F}\mathbf{s}_{M,t}
 \end{aligned}$$

When x_t , $x_{M,t}$ and r_t are defined as above, with only female gene flow included, then: $\mathbf{s}_{t+1} = (\mathbf{f}_1 \mathbf{s}_t x_t x_{t-1} \cdots x_{t-n})$ and $\mathbf{s}_{M,t+1} = (\mathbf{f}_1 \mathbf{s}_{M,t} x_{M,t} x_{M,t-1} \cdots x_{M,t-n})$, where the row vector \mathbf{f}_1 is the first row of \mathbf{F} . Because $\mathbf{v}_M = 2\mathbf{f}_1$, we obtain the following set of recursion formulae:

$$\begin{cases}
 x_{t+1} = \sum_{k=1}^n a_k x_{t-k+1} \\
 x_{M,t+1} = \sum_{k=1}^n a_k x_{M,t-k+1} \\
 r_{t+1} = \mathbf{v}_M \mathbf{s}_{M,t} + \mathbf{v}_s \mathbf{s}_{t+1} = 2 \sum_{k=1}^n a_k x_{M,t-k+1} + x_{t+1} \\
 \quad = 2x_{M,t+1} + x_{t+1}
 \end{cases}$$

A3 Initial selection vectors

The initial selection vectors are identical because:

$$\begin{aligned}
 x_0 &= z_0 \\
 x_{M,0} &= z_{M,0}
 \end{aligned}$$

As the system of recursion formulae is the same in **A1** as in **A2**, and because the initial values are equal (**A3**), it follows that Δr_t (in **A1**) and r_t (in **A2**) are equal for all t . Thus the full and simplified models are equivalent.

Appendix B

The realized heritability is expected to exceed the true heritability. Subpopulations A and B with discrete generations

As a simplification, the selection differentials are assumed to be the same in both sexes, i.e. $S_m = S_f$. Normal distributions of offspring phenotype within parental subgroups, with equal variance, is also assumed. The proportion of offspring in subpopulation A from sires in subpopulation A before and after selection are p and p_s , respectively.

Newborn in subpopulation A from sires in A and sires in B are called subgroup A and B, respectively. The mean difference between subpopulations at time T is ΔR_T . Therefore, the difference before selection between the subgroup A mean, μ_A , and the subgroup B mean, μ_B , is:

$$\mu_A - \mu_B = \frac{1}{2} \Delta R_T$$

The weighted mean selection differential for selected animals in subgroups A and B combined, \bar{S} , is:

$$\bar{S} = p_s S_A + (1 - p_s) S_B$$

where S_A and S_B are the selection differentials for subgroups A and B, respectively. Let π_A and π_B be the proportions selected within subgroups A and B, respectively. Then:

$$p_s = \frac{p\pi_A}{p\pi_A + (1-p)\pi_B}$$

Let the elements p_{ij} of the matrix \mathbf{P} be the proportion contributed by subpopulation i to subpopulation j after selection, where $i, j = A$ or B . Matrix \mathbf{P} is equivalent to that of Hopkins and James (1979), which is an extension of Hill's (1974) model, taking selection into account in matrix \mathbf{P} . Let the selection vector \mathbf{s} include genetic selection differentials of subpopulations A and B. Furthermore, realization vector \mathbf{v}_{Δ} is the difference of the total contribution to subpopulation A and B, before selection. The realized subpopulation difference, ΔR_T , after T years of selection is then:

$$\begin{aligned}
 \Delta R_T &= \mathbf{v}_{\Delta} \sum_{k=0}^{T-1} \mathbf{P}^k \mathbf{s} \\
 &= \left(\frac{1}{2} \quad -\frac{1}{2} \right) \sum_{k=0}^{T-1} \mathbf{P}^k \begin{pmatrix} h^2 \bar{S} \\ 0 \end{pmatrix}
 \end{aligned}$$

where:

$$\mathbf{P} = \begin{pmatrix} \frac{1}{2} + \frac{p_s}{2} & \frac{1-p_s}{2} \\ \frac{p}{2} & \frac{1}{2} + \frac{(1-p)}{2} \end{pmatrix}$$

Diagonalization of \mathbf{P} gives:

$$\mathbf{P} = \mathbf{E}_v \mathbf{D} \mathbf{E}_v^{-1}$$

where \mathbf{E}_v is a matrix of eigenvectors of \mathbf{P} , corresponding to eigenvalues of \mathbf{P} on the diagonal of \mathbf{D} :

$$\mathbf{E}_v = \begin{pmatrix} 1 & 1 \\ 1 & -p_s \end{pmatrix} \quad \mathbf{D} = \begin{pmatrix} 1 & 0 \\ 0 & \lambda \end{pmatrix}$$

and $\lambda = (1 + p_s - p)/2$.

The sum of \mathbf{P}^k is the sum of a geometric series, thus:

$$\Delta R_T = \left(\frac{1}{2} - \frac{1}{2}\right) \mathbf{E}_v \begin{pmatrix} T & 0 \\ 0 & \frac{1-\lambda^k}{1-\lambda} \end{pmatrix} \mathbf{E}_v^{-1} \begin{pmatrix} h^2 \bar{S} \\ 0 \end{pmatrix}$$

The asymptotic value of ΔR_T is (since $\lambda < 1$):

$$\Delta R_\infty = h^2 \bar{S} \frac{1}{1 - (p_s - p)}$$

Thus, estimating the realized heritability from:

$$\hat{h}^2 = \frac{\Delta R_\infty}{S_f}$$

with $S_f = \bar{S}$ leads to an overestimate such that:

$$\frac{\hat{h}^2}{h^2} = \frac{1}{1 - (p_s - p)}$$

The proportion p_s and the asymptotic difference ΔR_∞ are calculated iteratively, given p , h^2 and \bar{S} .

Appendix C

A simple example

In subpopulation A, 50% of the offspring have dams aged 2 years and the rest of the dams are 3-year-olds. All sires are 2-year-olds. Female and male progeny are selected for weight each year with selection differentials of 1.0 and 2.0, respectively. A difference of 0.3 kg, before selection, was observed between progeny in subpopulations A and B, after 10 years of continued selection. Nothing is known about subpopulation B in earlier years except that selection had not been practised.

We therefore have:

$$\begin{aligned} S_f &= 1.0 \text{ kg} \\ S_m &= 2.0 \text{ kg} \\ \Delta R &= 0.3 \text{ kg} \\ t &= 10 \text{ years} \end{aligned}$$

$$\mathbf{P} = \begin{pmatrix} 0 & 0.5p & 0 & 0.25 & 0.25 \\ 1 & 0 & 0 & 0 & 0 \\ \hline 0 & 0.5p & 0 & 0.25 & 0.25 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} ?$$

where p is the proportion of progeny in subpopulation A with sires from A (unknown).

Thus the gene flow matrix within subpopulation A, if A had been isolated, is expressed by:

$$\mathbf{P}_A = \begin{pmatrix} 0 & 0.5 & 0 & 0.25 & 0.25 \\ 1 & 0 & 0 & 0 & 0 \\ \hline 0 & 0.5 & 0 & 0.25 & 0.25 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

with female submatrix:

$$\mathbf{F} = \begin{pmatrix} 0 & 0.25 & 0.25 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

Then via the realized heritability the potential response is calculated as:

$$\hat{h}^2 = \frac{\Delta R_T}{\mathbf{v} \sum_{k=1}^t \mathbf{F}^k \mathbf{S}_f \mathbf{x}'} = \frac{\Delta R_{10}}{(1 \ 0 \ 0) \sum_{k=1}^{10} \mathbf{F}^k \mathbf{S}_f (1 \ 0 \ 0)'} = 0.33$$

$$R_p(10) = \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k (S_m \ 0 \dots 0 | S_f \ 0 \dots 0)' h^2 = (1 \ 0 \ 0 \ 0 \ 0) \sum_{k=1}^{10} \mathbf{P}_A^k (2.0 \ 0 | 1.0 \ 0 \ 0)' \times 0.33 = 2.1 \text{ kg}$$

Appendix D

The parameters c_1 , c_2 , c_3 , and c_4 in equation (31) are derived From the potential response (equation (30)):

$$R_p(t) = \mathbf{v}_M \sum_{k=1}^t \mathbf{P}_A^{k-1} \mathbf{s}_M + \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k \mathbf{s}$$

and the estimate of $\hat{\theta} = \sigma_{DP} / \sigma_P^2$ (equation (28)):

$$\hat{\theta} = \frac{\Delta R_t}{\mathbf{v}_M \sum \mathbf{F}^{k-1} (K \mathbf{S}_f \mathbf{x}) + \mathbf{v} \sum \mathbf{F}^k (\mathbf{S}_f \mathbf{x})}$$

we get:

$$R_p(t) = \frac{\mathbf{v}_M \sum_{k=1}^t \mathbf{P}_A^{k-1} (S_m \ 0 \dots 0 | S_f \ 0 \dots 0) + \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k (S_m \ 0 \dots 0 | S_f \ 0 \dots 0)}{\mathbf{v}_M \sum \mathbf{F}^{k-1} (1 \ 0 \dots 0) K \mathbf{S}_f + \mathbf{v} \sum \mathbf{F}^k (1 \ 0 \dots 0) \mathbf{S}_f} \Delta R$$

The selection vectors (containing S_f and S_m) can be partitioned into male and female vectors, because only additive effects are considered. Therefore, the sums of cumulative response can be divided into male and female parts, and we obtain (equation (31)):

$$R_p(t) = \frac{[K c_1(t) + c_2(t)] + \frac{S_m}{S_f} [K c_3(t) + c_4(t)]}{2K + 1} \Delta R$$

where:

$$c_1 = \mathbf{v}_M \sum_{k=1}^t \mathbf{P}_A^{k-1} (0 \ 0 \ \dots \ 0 \ ; \ 1 \ 0 \ \dots \ 0)' / S_1$$

$$c_2 = \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k (0 \ 0 \ \dots \ 0 \ ; \ 1 \ 0 \ \dots \ 0)' / S_1$$

$$c_3 = \mathbf{v}_M \sum_{k=1}^t \mathbf{P}_A^{k-1} (1 \ 0 \ \dots \ 0 \ ; \ 0 \ 0 \ \dots \ 0)' / S_1$$

$$c_4 = \mathbf{v} \sum_{k=1}^t \mathbf{P}_A^k (1 \ 0 \ \dots \ 0 \ ; \ 0 \ 0 \ \dots \ 0)' / S_1$$

and

$$S_1 = \mathbf{v} \sum_{k=1}^t \mathbf{F}^k (1 \ 0 \ \dots \ 0)'.$$