

Genetic response to selection on reindeer calf weights

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Abstract: Selection response was investigated after 11 years of selection in the herding district of Ruvhten Sijte in Sweden (63°N,12°E) by comparing the weights of calves owned by herders applying selection with the weights of calves owned by herders not applying selection. Three owner groups in Ruvhten Sijte have selected calves at the autumn slaughter every year since 1986 by retaining heavy calves. They own approximately 45% of the reindeer in Ruvhten Sijte. The other owners do not select on recorded weights, and all animals mix during the mating season. The recorded data on calf weights (1986 to 1997) consisted of 12 484 observations, with mean selection differentials of 2.9 kg and 4.6 kg for female and male calves, respectively (phenotypic standard deviation equal to 4.4 kg). The female generation interval was 6.4 years. In 1996 and 1997, autumn live weights of calves owned by herders applying selection ($n = 971$) were compared with the weights of calves owned by herders not applying selection ($n = 1125$). The observed difference was 0.67 kg (total mean = 42.6 kg), of which 0.32 kg was due to differences in dam age structure between the two types of herds, therefore the estimated difference in selection response was 0.35 kg. The realized heritability was 0.2. The potential response that would have been realized if the selected part of the herd had been isolated from gene flow was predicted to be 2.0 kg. In conclusion, the introduction of a selection programme applied by all owners in a herding district would result in an increase in calf weights of approximately 2 kg after two generations of selection.

Key words: gene flow, maternal effects, random mating, *Rangifer t. tarandus*, subpopulations.

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Introduction

Since 1986 a selection programme has been applied in the reindeer herding district of Ruvhten Sijte (formerly known as Tännäs Sameby) in Härjedalen, Sweden (63°N,12°E), where each year calves have been selected at the autumn slaughter by retaining heavy calves. Not all reindeer owners in Ruvhten Sijte apply the selection programme and the reindeer within the herding district mix during the rut. Further, sires are unknown, whereas the dams are identified in connection with the recording of the calves.

It is important to assess a selection programme to

evaluate the potential of improving the response. Due to large environmental variations between years, however, the selection response cannot be assessed from the recorded data within the selected part of the herd alone. Comparing the selected flocks with unselected ones, which share the same environmental conditions, can eliminate annual variations. Further, the realized selection response cannot be measured directly on the basis of phenotypic differences between the flocks subjected to selection and the ones not subjected to selection. The reason for this is the continuous mutual gene flow between selected and non-selected flocks. As a consequence,

the difference between flocks will be less pronounced than in the situation where selected and unselected animals are genetically unconnected.

Rönnegård & Danell (2001) developed the concept of *potential response* to evaluate such breeding programmes where matings cannot be controlled and the breeding strategies of intermingling owner flocks interact. The potential response, R_p , is the gain from selection that would have been realized if the reindeer in the selection programme had been isolated from gene flow. They showed that R_p could be predicted from the phenotypic differences between a flock subjected to selection and one not subjected to selection, without prior knowledge of the heritability. Furthermore, maternal genetic effects (Willham, 1963) were shown to influence the potential response.

Earlier published evaluations of reindeer breeding programmes have been limited to investigating effects of herd structure (sex ratio, age structure and weight distribution of adult females) without taking into account inherited effects (Lenvik, 1988; Lenvik, 1990), by making rough estimates of heritabilities in experimental herds (Varo, 1972), or by investigating how calf selection affects weights at older ages (Petersson & Danell, 1993). In these earlier investigations there were no comparisons between different breeding strategies.

The aim of this paper is twofold. The first objective is to estimate the difference in realized genetic response between calves in flocks where selection was applied versus flocks with no selection, all within the same herding district. The second and main objective is to predict R_p from the estimated difference in genetic response. This prediction shows the feasibility of selection based on calf weights of reindeer under field conditions.

Material and methods

Population structure and selection procedure

In 1980 three reindeer owners in the herding district of Ruvhten Sijte started using individual ear-tags on their reindeer. In this paper the reindeer belonging to these owners will be called Sel (for selected). The calves were ear-tagged and their identities were coupled with their mothers at the annual calf marking in July (as in Lenvik & Fjellheim, 1987), whereas sires are unknown. Since 1986 the owners have weighed the calves prior to the autumn slaughter (October – December), where they slaughter mainly calves, with only a low rate of adults being culled. Heavy calves were selected on the basis of recorded calf weights. The proportion of calves selected each year was within the range of 0.10 – 0.27 for males

and 0.29 – 0.52 for females. Selection was also based upon earlier production of the dam (i.e. calves from dams with many and heavy calves were selected), but no formally defined selection index was used. Accumulated information on a female's reproduction can only be used for older mothers and after several years of recording. Therefore, in this paper, calf selection is assumed to have been based solely on individual calf weights.

In 1996 and 1997, three other reindeer owners in Ruvhten Sijte weighed their calves. The reindeer belonging to these owners will be called Cont (for control). They had not selected calves based on weights but practised a more traditional slaughter, i.e. did not use scales and individual ear-tags, and they tended to slaughter equal proportions of females from all age classes. This difference in slaughter strategies was reflected in a larger proportion of slaughtered female reindeer other than calves.

During the snow-free season from May – October (between calving and calf slaughter), the Sel and Cont animals mix and utilise common grazing grounds (926 km²). The rut commences in late September, and the Sel and Cont animals mate without any influence from the owners. In winter the owners keep their reindeer separated. The animals were only occasionally supplementary fed when there was no access to lichens because of poor weather conditions, and none of the herders practised supplementary feeding prior to the calving period. The total number of animals retained (both calves and adults) after slaughter each winter, in the whole herding district of Ruvhten Sijte, varied between 4500 and 8000, and the Sel animals made up approximately 45% of the total herd.

Material

The data of the Sel animals, recorded between 1986 and 1997, consisted of 12 484 records including: calf weights, identities of the calf and its mother, the mother's age, date of recorded weight, sex and status (culled or selected). Mothers of unknown age were assumed to be born before the selection began in 1986.

Both Sel and Cont calves were weighed during four days in November 1996 and six days in November 1997. Calf weight, sex and date were recorded. The animals were weighed before the slaughter, and no difference in the recording was made between culled and retained animals. Before weighing, the reindeer were kept for up to two days in a large corral with access to snow and pasture. The date of recorded calf weight was treated as fixed class effects in the statistic analyses to account for possible weight loss while in corral. In the final analyses of

the difference between Sel and Cont, there was a total of 971 observations of autumn calf weights from Sel and a total of 1125 observations from Cont. Recorded data of calf weights from one owner ($n = 965$) were excluded from the final analyses due to indication of mistakes in the recording. In pre-analyses of calf weights the interaction between year and owner was found to be highly significant ($P = 0.0001$) with the data included, whereas the differences in calf weights between owners were consistent between years when the weight records from the flock were excluded ($P = 0.34$ for interaction term between year and owner). It was concluded that errors in the analyses would be minimized by deleting the data.

Description of the method to predict potential response

A detailed mathematical description of the concept of the potential response is given by Rönnegård & Danell (2001). Below we describe the principle of selection response and gene flow methodology, which the concept of potential response is based upon. Thereafter, we define our assumptions and give the formulae we used to calculate the potential response, along with a description of estimated parameters. Definitions of all parameters used throughout the paper are found in Table 1.

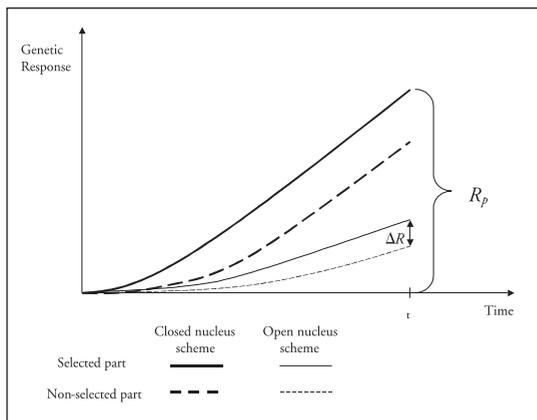


Fig. 1. Predicted development of selection response for a one-way (closed nucleus scheme) and two-way gene flow (open nucleus scheme) between a selected and a non-selected subpopulation. The response in the closed selected subpopulation represents the potential response (R_p). In the case of the open selection scheme, the upper of the two lines is the outlined development in Sel and the lower line corresponds to Cont. ΔR is the realized difference in genetic response between the selected and non-selected parts in year t .

R_p is the expected response from selection in a closed population. For discrete generations the potential response from one round of selection is $R_p = b^2 S$, where b^2 is the heritability and S is the selection differential (mean deviation of selected from total mean).

In a population consisting of a selected and a non-selected subpopulation the potential response will be reached when the selected subpopulation is closed from incoming gene flow (Fig. 1), whereas if the subpopulations mix the response will be reduced. In the latter case, the difference in response, ΔR , depends on b^2 and the selection differential in females, S_f , if the animals are randomly bred (see equation 2 in Rönnegård & Danell, 2001).

An important prerequisite of the method for calculating R_p , fulfilled in reindeer management, is that a dam and her offspring belong to the same selection regime (i.e. have the same owner). Furthermore, the assumption is made that males mate randomly between the two subpopulations and that the environmental conditions are similar for all animals.

The initial increase in selection response will not be as smooth as in Fig. 1 when there are overlapping generations. These irregularities were accounted for by modelling the gene flow from parents to offspring in terms of gene flow matrices (Hill, 1974), which are calculated from the age distribution of parents.

Rönnegård & Danell (2001) showed that ΔR is independent of the selection of males and the proportion of the total population being selected, and that R_p can be predicted from ΔR in two steps. The realized heritability, \hat{h}^2 , is calculated using an estimate of ΔR and the cumulated selection differentials in females (equation 20 in Rönnegård & Danell, 2001):

$$\hat{h}^2 = \frac{\Delta R}{\mathbf{v} \sum_{n=1}^t \mathbf{F}^n (S_f \ 0 \ \dots \ 0)'} \quad \text{eq. 1}$$

where S_f is the selection differential of females, \mathbf{F} is the matrix describing the gene flow from mother age classes to daughters in the selected subpopulation, and \mathbf{v} is a realisation vector that extracts the response in the cohort of year t . Given the realized heritability, the potential response is then estimated as a product of \hat{h}^2 and the cumulated selection differentials of both males and females in the selected subpopulation, assuming no gene flow from the non-selected subpopulation (from equation 16 in Rönnegård & Danell, 2001):

$$R_p(t) = \mathbf{v} \sum_{n=1}^t \mathbf{P}_A^n (S_m \ 0 \ \dots \ 0 | S_f \ 0 \ \dots \ 0) \hat{h}^2$$

eq. 2

where S_m is the selection differential of males, \mathbf{P}_A is the matrix describing the gene flow within a closed selected subpopulation and when raised to n years takes account of the accumulation of selection differentials. Note that \mathbf{F} describes one path of gene flow from mothers to daughters, whereas \mathbf{P}_A describes all four paths of gene flow from fathers and mothers to sons and daughters within the closed subpopulation.

The potential response was evaluated after 11 years of repeated selection ($t = 11$), i.e. in 1997. The observed difference in calf weights between Sel and Cont was used as an estimate of ΔR after adjusting for non-genetic effects caused by differences in dam age structures between the two subpopulations.

Selection differentials were calculated, separately for each sex and year, as the difference between the mean adjusted weight of selected calves and the mean adjusted weight of all calves in Sel. Calf weights were adjusted for date of recorded weight and the mother's age, using a linear model with calf weight as the dependent variable and with date and dam age as fixed class effects.

For the estimation of the elements in \mathbf{P}_A (eq. 2), the age distribution of Sel-sires was derived from the selection of male reindeer described by the owners of Sel, with male calves selected at the autumn slaughter, 80% of 1 1/2-year-males slaughtered and all 2 1/2-year-old males culled. Furthermore, equal reproductive success for males in age class 2 and 3 was assumed (i.e. males aged 1 1/2 and 2 1/2 at the rut), whereas the reproductive success of calves was assumed to be small and negligible.

In equations 1 and 2 it is assumed that the only genetic effect influencing calf weight is inherited directly from the sire and dam (direct genetic effects). However, a mother's ability to take care of and nourish a calf affects the calf's weight, which is a phenotypic expression of a maternal genetic effect if the ability of the mother is a trait with genetic inheritance. The extent to which maternal genetic effects influence the potential response is estimated from the maternal-direct effects ratio, $K = \sigma_{MP} / \sigma_{DP}$, where σ_{MP} is the covariance between maternal genetic effects and the selected phenotype, and σ_{DP} is the covariance between the direct genetic effects and the selected phenotype. The incorporation of K into eq. 1 and eq. 2 is given in equation 31 of Rönnegård & Danell (2001). For $K = 0$, i.e. no maternal genetic

effects, eq. 1 and eq. 2 are obtained. The potential response was calculated for $K = 0.15$, corresponding to unpublished estimates of direct and maternal heritabilities of pre-slaughter calf weights in reindeer ($b^2 = 0.35$, $b_m^2 = 0.15$, $r_{am} = -0.10$ (Appel & Danell, unpubl.)).

Table 1. Definitions of parameters.

Parameter	Definition
R_p	Potential selection response
$\Delta R, \Delta R_{obs}$	Genetic and observed difference in calf weights between Sel and Cont
S, S_f, S_m	Average, female and male selection differentials, resp.
b^2, b_m^2	Direct and maternal heritability
r_{am}	Correlation between direct and maternal genetic effects
\hat{h}^2	Realized direct heritability
K	Maternal-direct effects ratio
\mathbf{F}	Gene flow matrix from mothers to daughters
\mathbf{P}_A	Gene flow matrix within a closed selected subpopulation
\mathbf{v}	Realisation vector of the response for a given cohort
t	Number of years of selection
Δ_{Age}	Difference in mean calf weights caused by different dam age structures in Sel and Cont
\mathbf{L}	Leslie matrix
k	Age class
f_k	Fecundity of females in age class k (including survival of calves the first year)
$c_r(k)$	Calving rate of females in age class k
$P_{k,k+1}$	Survival of females from age class n to age class $k+1$
p, p_0	Adult and calf survival, resp.
s_a, s_c	Proportion of adults and calves slaughtered, resp.

Observed difference in calf weights between Sel and Cont

In the estimation of the difference between Sel and Cont calf weights, ΔR_{obs} , a linear model was used with calf weight as the dependent variable and the following independent fixed class effects: group (Sel or Cont), year of recorded weight, date of recorded weight, and calf sex. In a preliminary analysis there was no interaction found between group and year ($P = 0.87$); thus, the difference between the two groups was concluded to be the same in 1996 and 1997.

Statistical analyses were performed using SAS software (SAS, 1999).

Accounting for non-genetic effects in ΔR_{obs}

Calf weight is influenced by the mother's age (Rönnegård *et al.*, 2002), hence, mean calf weight depends on the age structure of the dams. Further, the owners of Sel and Cont apply different slaughter strategies and dam age structures may therefore differ (Lenvik, 1990). Consequently, there may be a difference in mean calf weights caused by different dam age structures in Sel and Cont. Let this difference be denoted by Δ_{Age} . This is a non-genetic effect that needs to be accounted for in order to obtain an unbiased estimate of the genetic difference in selection response between Sel and Cont. The difference in selection response between the Sel and Cont was calculated as: $\Delta R = \Delta R_{obs} - \Delta_{Age}$.

Estimated Δ_{Age}

Δ_{Age} was estimated from equilibrium age structures of females using a Leslie-matrix model (e.g. Caswell, 2001), with the Leslie-matrix defined as:

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & \cdots & \cdots & f_{11} \\ P_{1,2} & 0 & \cdots & \cdots & 0 \\ 0 & P_{2,3} & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & P_{10,11} & 0 \end{pmatrix}$$

where f_k is the fecundity of females in age class k and $P_{k,k+1}$ is the survival of females from age class k to $k+1$.

Parameters used to calculate the elements of the Leslie-matrix were: age-specific calving rates, $c_r(k)$, with estimates obtained from Rönnegård *et al.* (2002) as $0.32 + 0.15k - 0.012k^2$; natural survival of calves, p_0 , equal to 0.87; natural survival of adults, p , equal to 0.97 (Rönnegård & Forslund, unpubl.); proportion of female calves slaughtered, s_c ; and proportion of adult females slaughtered, s_a , with s_a equal to 0.05 in Sel (Rönnegård & Forslund, unpubl.).

The elements of \mathbf{L} were calculated, assuming a pre-breeding census of parameters, with $f_1 = 0$ (i.e. no 1-year-old female parents), $f_k = c_r(k) p_0 (1-s_c)$ for $k = 2$ to 11, and $P_{k,k+1} = p(1-s_a)$ for $k = 1$ to 10, where the proportion of calves and adults slaughtered, s_c and s_a respectively, varied between Sel and Cont. The proportion of calves slaughtered, s_c , in Sel and Cont was calculated by constraining the dominant eigen-

value of the Leslie-matrix to be 1.0, i.e. for constant population size at equilibrium. Further, the proportion of adults slaughtered in Cont was calculated by constraining s_a to be equal to s_c ; thus females were assumed to be slaughtered proportionally from all age classes in Cont. These constraints correspond to $s_c = 0.16$ and $s_a = 0.16$ in Cont, and $s_c = 0.50$ in Sel.

The female age structures of Sel and Cont were then given by the eigenvector of \mathbf{L} for the parameter values given below. The age distribution of mothers (Fig. 2) was calculated from the female age structure weighted by the age-specific calving rates ($c_r(k)$) $\cdot \Delta_{Age}$ was then calculated for the equilibrium age structure of mothers in Fig. 2 and with calf weight (y) as a function of the mother's age (k) taken from Rönnegård *et al.* (2002):

$$y = (0.0210 + 0.0857k^{-1} - 0.00015k + 0.000025k^2)^{-1}$$

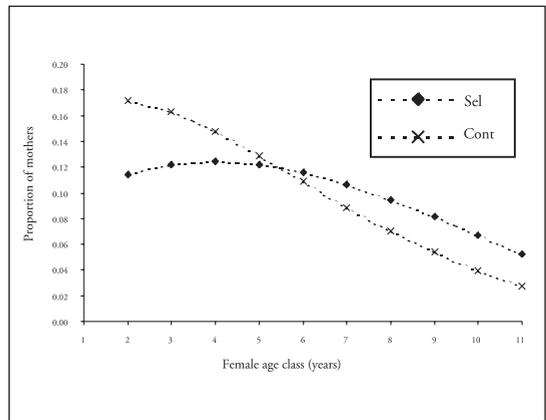


Fig. 2. Equilibrium age distributions of mothers in Sel and Cont.

Results

The results from the analyses of calf weights in Sel and Cont are summarized in Table 2. The mean calf weight was 42.6 kg and the observed difference between Sel and Cont calves, ΔR_{obs} , equalled 0.67 kg.

The difference in mean calf weights due to differences in dam age structure, Δ_{Age} , was 0.32 kg. Thus, the difference in selection response between Sel and Cont calves, ΔR , became 0.35 kg.

Mean selection differentials between 1986 and 1997 were 2.9 kg and 4.6 kg for female and male calves, respectively (Fig. 3), and the common phenotypic standard deviation was 4.4 kg. The proportion of selected female calves having mothers that were selected as calves based on weights increased as the years of selection proceeded (Fig. 4). The average age of the Sel dams in 1996 and 1997 was 6.4 years.

Table 2. Summary of analyses of calf weights in Sel and Cont. A linear model was used with calf weight (kg) as a dependent variable and the following independent fixed effects: group (either Sel or Cont), year of recorded weight, date of recorded weight, and calf sex ($R^2 = 0.11$). The estimated difference in group-effect is the value of ΔR_{obs} referred to in the text.

Effect	Estimate	P
Intercept	40.3	
Group difference	0.67 ^a	0.0003
Year difference	1.02 ^b	0.04
Date	-	<0.0001 ^c
Sex difference	2.23 ^d	<0.0001

^a Sel calves heavier than Cont, S.E. = 0.18.

^b Calf weights were higher in 1996.

^c Type III test.

^d Males heavier than females.

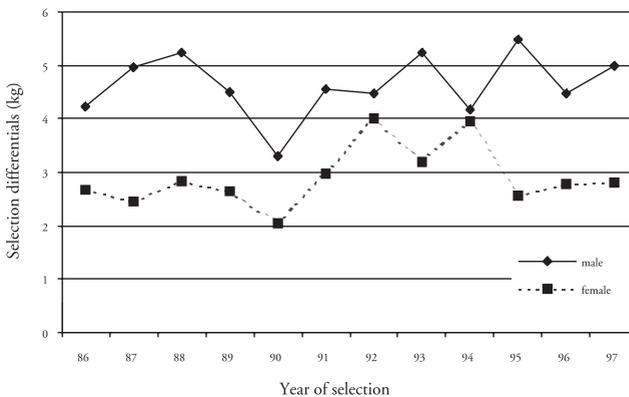


Fig. 3. Observed male and female selection differentials 1986 to 1997 (phenotypic standard deviation equal to 4.4 kg).

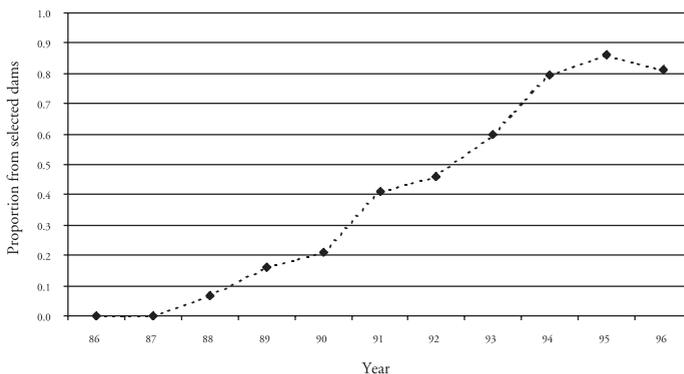


Fig. 4. Proportion of selected female calves having mothers that were selected on weight as calves from 1986 to 1996.

From the results above, the potential response, R_p , was predicted to be 2.0 kg after 11 years of repeated selection, which corresponds to an annual genetic gain of 0.4% of the phenotypic mean. Furthermore, this potential response corresponds to a realized heritability of 0.2 in eq. 2 where maternal effects are ignored.

Discussion

For published results from selection programmes on sheep, the annual improvement of lamb weights is within the range of 0.05 – 2.0 % of the mean (Guy *et al.*, 1986; Näsholm, 1999; YapiGnaore *et al.*, 1997) with most values being less than 1%. For cattle the annual improvement of calf weights and weight gain is within 0.1 – 0.6% of the mean (Crump *et al.*, 1997; HaileMariam & Philipson, 1996; Stålhammar, 1997; Sullivan *et al.*, 1999). We thereby conclude that the potential selection response estimated in our study was low to moderate

compared to what could be expected in selection programmes with other domestic species.

Important factors that influence the annual genetic gain are generation interval, genetic variation, accuracy of selection and selection intensity. The generation interval of female reindeer (6.4 years) is high compared to comparable domestic species and puts a restraint on the potential response. The realized heritability of 0.2 suggests that the genetic variation in reindeer calf weights are on the same level as for similar traits in other domestic species, even though it is lower than other heritability estimates in reindeer. (Varo, 1972) reported a heritability in reindeer calf weights of 0.6, and Appel & Danell (unpubl.) estimated a heritability of 0.4. The accuracy of selection in the studied herd was limited in that no formally defined selection index was used and not all calves in the

selected part of the herd, for practical reasons, could be gathered for evaluation at the same time. On the other hand, additional information on a dam's earlier production was used to make selection decisions at calf slaughter, and since we made the assumption in the analyses that individual calf weight was the only information used, the realized heritability might have been slightly overestimated. This could have been analysed further using the recorded data, but the effect is likely to be small since the information on a dam's earlier production becomes substantially accumulated only after several years of recording. Further, the proportion of females needed to be retained to keep a stable population limits the selection intensity of females. In reindeer, females have at most one calf per year and because of yearly fluctuations in survival a greater proportion of calves need to be retained than in other less extensive production systems. Considering these limitations, the potential response was high in the studied reindeer herd and the prospective of selection in reindeer breeding in the short term is as good as in other species and production systems.

Theoretically environmental limits to selection response could be expected in reindeer breeding, because of the small degree of control by the herders of the environment and the food intake, which may limit the selection in the long term. Our calculations of the potential response did not consider such environmental limits. Furthermore, the Ruvhten Sijte herding district is one of the most southern in Sweden and not a typical herding district of the whole Fenno-Scandinavian region. Ruvhten Sijte has good winter pastures but a limited summer grazing area, whereas most herding districts in Fenno-Scandinavia have in general good summer pastures and winter pastures of poorer quality. Thus, extrapolation of results to other herding districts should not be made without due consideration. One hypothetical limitation is that long-term selection based purely on weights may create nutritionally more demanding animals, which suffer more in poor winter conditions. Further, Ropstad *et al.* (1991) have shown that heavy female calves may reproduce prematurely as 1-year-olds and that their development in weight is thereafter retarded. However, such side effects of selection have not been shown in Ruvhten Sijte and should not seriously influence our estimates.

The prediction of potential response from the difference in selection response between Sel and Cont assumed random mating by males between the two parts of the herd. The Sel and Cont animals mix freely throughout the snow-free season and there are no geographical barriers between the two parts of the

herd. Consequently, non-random mating between Sel and Cont is not likely unless the animals mate assortatively. The results from a recent study of mating success in an experimental reindeer herd indicated no correlation between the dominance status of sires and dams (Røed *et al.*, 2002), i.e. heavy males do not tend to mate with heavy females, nor do light males tend to mate with light females. Hence, these results support our assumption of random mating between Sel and Cont. Røed *et al.* (2002) also reported that all females prefer to mate with heavy males, but such behaviour does not influence the potential response as long as the females behave equally in Sel and Cont, since the male influence cancels out in the model used in estimating the potential response (Rönnegård & Danell, 2001).

This paper deals with direct response from selection in calf weights, but indirect benefits of applying the selection programme are not only reflected in calf weights. Retaining heavy calves by selection implies that the physical capacity of animals is improved as the calves grow and become adults (Pettersson & Danell, 1993). Improving the condition of the females in a herd may also increase calving rates (Rönnegård *et al.*, 2002), which may be of more economic advantage to the owners than an increase in calf weights alone. This is empirically observed by the herders in Ruvhten Sijte (Edvin Rensberg, reindeer herder in Tännäs, pers. comm.)

A considerable improvement of the dam age structure can be obtained within one generation interval after the introduction of an individual recording system that makes it possible to detect the age of females. The improved dam age structure is achieved by steering the culling of females to older age classes, and there will be a quick increase in calf weights due to the improved condition of the females (Lenvik, 1990). However, the gain in calf weights due to optimised dam age structure will not continue to increase, whereas repeated selection in a closed population will accumulate genetic gain for as long as the selection is applied.

In this paper we have argued that the full potential of selection in a reindeer herd could be obtained in a closed nucleus breeding scheme (the case of one-way gene flow in Fig. 1). The design of a closed nucleus might be achieved by culling all male calves in the non-selected part of herd, thereby isolating the animals in the selected part of the herd from gene flow. Aspects of designing such breeding schemes in reindeer breeding will be addressed in a future article.

The essential result of our present investigation is that we can expect that the introduction of a selection programme with a closed nucleus system into

another herding district, with similar environmental conditions, would result in an increase in calf weights of approximately 2 kg after two generations of selection.

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