

Breeding schemes in reindeer husbandry

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Abstract: The objective of the paper was to investigate annual genetic gain from selection (ΔG), and the influence of selection on the inbreeding effective population size (N_e), for different possible breeding schemes within a reindeer herding district. The breeding schemes were analysed for different proportions of the population within a herding district included in the selection programme. Two different breeding schemes were analysed: an open nucleus scheme where males mix and mate between owner flocks, and a closed nucleus scheme where the males in non-selected owner flocks are culled to maximise ΔG in the whole population. The theory of expected long-term genetic contributions was used and maternal effects were included in the analyses. Realistic parameter values were used for the population, modelled with 5000 reindeer in the population and a sex ratio of 14 adult females per male. The standard deviation of calf weights was 4.1 kg. Four different situations were explored and the results showed: 1. When the population was randomly culled, N_e equalled 2400. 2. When the whole population was selected on calf weights, N_e equalled 1700 and the total annual genetic gain (direct + maternal) in calf weight was 0.42 kg. 3. For the open nucleus scheme, ΔG increased monotonically from 0 to 0.42 kg as the proportion of the population included in the selection programme increased from 0 to 1.0, and N_e decreased correspondingly from 2400 to 1700. 4. In the closed nucleus scheme the lowest value of N_e was 1300. For a given proportion of the population included in the selection programme, the difference in ΔG between a closed nucleus scheme and an open one was up to 0.13 kg. We conclude that for mass selection based on calf weights in herding districts with 2000 animals or more, there are no risks of inbreeding effects caused by selection.

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

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Introduction

Modern reindeer husbandry in Fennoscandia is developing towards slaughtering fewer adult males and more calves, reducing the proportion of adult males in the herd. This has opened up the opportunity of creating a selection differential among the calves kept and culled in a breeding scheme, particularly among the male calves. Development of calf selection will raise challenges for reindeer husbandry, many of which are not normally encountered in conven-

tional breeding schemes in developed countries. For example, the animals within a herding district are randomly mixed so that mating is not controlled and sires of calves are not known.

Within each reindeer herding district there are several owners with independent economic enterprises, and the decision to take part in a selection programme is made by each individual owner. Owners may be reluctant to take part in a selection programme because of the extra work and the initial

investment required for weighing and recording apparatus. Thus, when not all the owners apply the selection programme, a herding district will consist of selected and non-selected flocks that are randomly mixed.

In the selection programme developed in the pioneering Swedish herding community of Ruvhten Sijte, an *open nucleus* breeding scheme has been applied with gene flow between the selected and non-selected flocks (Rönnegård & Danell, 2003). A possibility in future selection programmes would be to select breeding males only in the selected flocks and cull all male calves in the non-selected flocks, and thereby achieve a *closed nucleus* scheme with gene flow from the selected to the non-selected flock. Such a scheme is expected to increase the genetic gain both for the selected and non-selected flocks, but it may also involve a risk because of increased rates of inbreeding (ΔF).

In the short term, high rates of inbreeding will increase the rate of change of gene frequencies for alleles associated with diseases and decreased fitness (due to increased homozygosity of recessive genetic defects). With lower rates, changes due to genetic drift are slower, giving more time for natural selection or more chance for husbandry actions to ameliorate the changes. In the long term there needs to be a large enough genetic variation within populations so that a population can develop and survive in a variable environment; genetic variation is also essential if a genetic gain from selection is to be maintained.

Deterministic predictions of ΔF for reindeer populations need to tackle several problems, such as overlapping generations, selection, gene flow between and within mixing subpopulations and inheritance models, including maternal effects. Methods of estimating ΔF in populations with overlapping generations, and where there is no selection, were developed by Hill (1972; 1979). Wray & Thompson (1990) and Woolliams *et al.* (1999) developed the concept of long-term genetic contributions to predict rates of inbreeding in selected populations. These methods were further developed by Rönnegård & Woolliams (2003) for situations where the trait under selection is influenced by a maternal effect.

The rate of inbreeding per generation is inversely proportional to the effective population size ($\Delta F = 1/(2N_e)$). This was a concept developed by Wright (1931), which gives good intuitive understanding of the risks of selection. The suggested minimum N_e needed to avoid inbreeding depression in the short term is 50, and the minimum N_e needed to uphold a viable population in the long term with sustainable genetic variation is 500 (Franklin, 1980; Mace & Lande, 1991).

The objective of the paper is to investigate the predicted gain from selection, and the influence of selection on N_e , for open and closed nucleus breeding schemes. A realistic population structure is modelled with a high production of calves and skewed mating ratio, to obtain the upper limit of genetic gain and conservative predictions of N_e .

Methods

Population structure

A population model is developed that attempts to model all reindeer within a herding district with flocks that are either subject to selection or will make selection progress only as a result of mixing with the selected flocks. This division is determined in practice by the different ownerships of the animals. The selected and non-selected parts of the herd will be referred to as subpopulations. Four different cases were investigated (described in detail below). The models reflect the general situation in reindeer husbandry with a randomly bred population, where the ownership of a calf is defined by the ownership of the dam rearing the calf, and where sires are not identified.

The population consisted of 5000 animals in the winter herd (*i.e.* after slaughter and prior to calving), which corresponds to a small to medium-sized reindeer district in Sweden (Statistics Sweden, 1999). Furthermore, the population was assumed to be closed, with no immigration. The parameters used in the analyses are summarised in Table 1. There are overlapping generations with maximum female and male age being 11 and 3 years, respectively. The age classes are defined so that the number of individuals in each age class is assumed to be taken from a pre-calving census. The age of first breeding was 2 years for both females and males. Mass selection on calf weight was assumed to be practised in late autumn after the rut. Thus, mating occurs before slaughter so that culled 1½-year-old males may have offspring in age class two. The average number of adult females mated by an adult male was 14, which resembles reindeer districts where the proportion of adult females is large enough to enable a large annual calf production yet there are enough males to ensure that all females have the opportunity of being mated.

Male reproductive success and female fecundity within age classes were assumed to be independent of phenotype but to differ between ages. Furthermore, natural mortality was assumed to be the same in both sexes, and both slaughter and natural mortality of breeding adults were assumed to occur independent of phenotype.

Females

The population consisted of 4100 adult females aged 2 to 11 years at calving. The age-specific fecundity (f_k) reaches a maximum of 0.73 at the age of 6 years (Table 1). There are 2800 calves born each year. The parameters used to calculate the age structure in this paper (Table 1) were the same as in Rönnegård & Danell (2003), with a calf slaughter strategy. The female age structure assumes a constant population size at equilibrium, calf mortality in the first winter equal to 13%, annual natural mortality in adults equal to 2.5% independent of age, 5% annual slaughter of adult females aged 1 to 10 years, and 50% slaughter of female calves (*i.e.* 700 female calves retained).

Males

Equal reproductive success was assumed for 1½- and 2½-year-old males, *i.e.* males in age class 2 and 3, respectively. No calf reproduction was assumed. Further, 80% of male calves were slaughtered (*i.e.* 280 male calves retained), and 80% of 1½-year-old males and all 2½-year-old males were culled. Thus, the total number of adult males (*i.e.* in age classes 2 and 3) is 292. The sex ratio of adults is therefore 14:1, since the number of adult females is 4100.

Cases investigated

The cases were chosen to build the complexity of the model stage by stage, and to separate out the impact of the factors studied. For each case, N_e and the annual genetic gain (ΔG) was predicted.

Case 1:

Single randomly culled population

In this case, culling in the whole population is practised and it is independent of calf weight.

Case 2:

Single population where calves are selected on weight

It is assumed that all calves with weights above a certain sex-specific limit are selected each year (*i.e.* truncated mass selection).

Case 3:

Two randomly mixed subpopulations, of which one is selected (open nucleus)

The simulated herding district consists of selected and non-selected flocks that are randomly mixed. Furthermore, the sex and age distributions are the same in both subpopulations. The owners that do not apply the selection are assumed to cull calves inde-

pendent of weight, as in Case 1. The proportion of the population included in the selection programme was a variable studied within this case.

Case 4:

Two subpopulations, of which one is selected, and where the male calves in the randomly selected subpopulation are culled to maximise ΔG (closed nucleus)

In this case the male calves born by non-selected dams are culled, and the number of males in the population is constant (280 male calves retained). For small proportions of the population included in the selection programme, a large part of the male calves in the selection programme have to be retained. However, when the proportion of male calves that have to be retained becomes larger than a crucial proportion, the genetic gain will be greater if male calves are selected at random from the non-selected part of the herd rather than selecting calves with extremely low weights from the selected part. According to Smith (1969), this crucial proportion is reached when the truncation point of selection is below the mean of calf weights in the non-selected part of the herd. The difference in genetic level between the selected and non-selected parts was therefore calculated. The crucial proportion, where it would be better to retain calves from the non-selected part of the herd, was estimated from the difference in genetic level.

In Case 3 and 4, ΔG and N_e were predicted for different proportions of the population included in the selection programme.

Genetic Model

Inheritance of calf weight

A maternal effects model (Willham, 1963) was assumed where the weight, P_i , of an individual calf i is affected by the breeding value for the direct effect of the calf, A_i , an environmental influence of the dam, $P_{i,maternal}$, and residual effects E_i :

$$P_i = A_i + P_{i,maternal} + E_i$$

The maternal effect $P_{i,maternal}$, is a partly inherited trait with breeding value M_d for dam d , and with an environmental (non-inherited) part C_d :

$$P_{i,maternal} = M_d + C_d$$

Breeding values are the average inherited effect of the genes affecting calf weight (*e.g.* Falconer & Mackay, 1996). These are inherited additively so that an individual's breeding value is the sum of half the dam's breeding value plus half the sire's breeding value plus a Mendelian sampling term due to the segregation of loci:

$$A_i = \frac{1}{2}A_d + \frac{1}{2}A_s + a_i \text{ and } M_i = \frac{1}{2}M_d + \frac{1}{2}M_s + m_i,$$

where a_i and m_i are the Mendelian sampling terms of the direct and maternal effects, respectively. The variances of direct and maternal breeding values are denoted by $V(A)$ and $V(M)$, and their covariance by $\text{Cov}(A, M)$. Furthermore, $V(P)$ and $V(C)$ denote the phenotypic variance of the trait and the variance of the environmental part of the maternal effect, respectively. An infinitesimal genetic model with additive effects was assumed (Fisher, 1918), with the heritability of direct and maternal effects defined as

$$h_A^2 = V(A)/V(P) \text{ and } h_M^2 = V(M)/V(P), \text{ respectively.}$$

The genetic correlation between direct and maternal effects is $r_{AM} = \text{Cov}(A, M) / \sqrt{V(A)V(M)}$, and the proportion of the phenotypic variance accounted by the environmental part of the maternal effects is given by $c^2 = V(C)/V(P)$.

Unpublished heritability estimates (Appel & Danell, unpubl.) of autumn calf weights from recorded data from between 1986 and 1997 in the herding district of Ruvhten Sijte in Sweden were used. The estimates rounded to the first decimal were:

$$h_A^2 = 0.4, h_M^2 = 0.1, r_{AM} = -0.1 \text{ and } c^2 = 0.1.$$

The phenotypic standard deviation estimated in the same analysis was 4.1 kg. The phenotypic response from selection in a closed population is proportional to b_w^2 (known as 'Willham heritability'; Willham, 1972), which with these parameters equals 0.42 (since $b_w^2 = b_A^2 + \frac{3}{2}r_{AM}b_A b_M + \frac{1}{2}b_M^2$).

Gene flow

In this paper the gene flow in a population was investigated by using the theory of expected long-term genetic contributions (Woolliams *et al.*, 1999). A major advantage of the theory, compared to conventional selection theory (*e.g.* Falconer & Mackay, 1996), is that both ΔG and ΔF can be predicted simultaneously. In Rönnegård & Woolliams (2003), predictions were evaluated for maternal effects as defined above, and a thorough description of the theory is given there.

The gene flow of an individual i to a cohort far into the future depends on the category that the individual belongs to, where a category is defined by the individual's age, sex and subpopulation membership. Furthermore, in a selected population the gene flow is also influenced by the breeding values of an individual and the environmental influence it has on the offspring, *i.e.* A_i , M_i and C_i . These are referred to as the *selective advantages* (Woolliams *et al.*, 1999). The expected long-term genetic contribution from

an individual in category q , $\mu_{i(q)}$, is expressed as a linear relationship of the selective advantages:

$$\mu_{i(q)} = \alpha_q + \beta_q \mathbf{s}_{i(q)} \quad [1]$$

where α_q is the average contribution from category q , $\mathbf{s}_{i(q)}$ is the vector of selective advantages $[A_i \ M_i \ C_i]$, and β_q gives the influence that the selective advantages of individual i in category q have on the gene flow.

The generation interval, L , is defined as the period of time for the population to renew itself (Woolliams *et al.*, 1999) and is equal to the reciprocal of the total sum of expected contributions:

$$L = 1 / \sum_q n_q \alpha_q,$$

where n_q is the number of individuals in category q . A persistent genetic gain is achieved by continuously selecting animals with superior Mendelian sampling terms, and where these animals contribute genes to future cohorts. The genetic gain (in the long-term) is therefore given by the expected long-term contribution of Mendelian sampling terms:

$$\Delta G = \sum_q n_q E(r_{i(q)} \mathbf{g}_{i(q)}),$$

where the annual direct and maternal genetic gains are the first two elements in the vector ΔG , and $\mathbf{g}_{i(q)}$ is the corresponding vector of Mendelian sampling terms, $[a_i \ m_i]$. In the present paper, the genetic gain (ΔG) is defined as the sum of annual direct and maternal genetic gains.

The predicted annual rate of inbreeding per year (ΔF_y) is equal to half the sum of squared lifetime μ_i for a single cohort of animals (Appendix A), and N_e for a generation was calculated from the generation interval and the predicted annual rate of inbreeding per year as: $N_e = 1/(2\Delta F_y L)$.

Poisson variance of family size was assumed for male and female parents. For male parents this is motivated by the investigation of Røed *et al.* (2002), whereas for female parents the variance in family size is slightly smaller than that predicted from a Poisson variance, since a dam has a maximum of one calf per year. This may result in an over-prediction of ΔF_y , but the bias was found to be less than 3% according to simulations made in a separate analysis (using eq. [A1] in Appendix A and the method described in Bijma & Woolliams (2000) to calculate the deviation caused by non-Poisson variance of family size).

Model extension

The model of expected long-term genetic contributions (Woolliams *et al.*, 1999; Bijma & Woolliams, 1999; 2000; Bijma *et al.*, 2000; Woolliams & Bijma,

2000; Rönnegård & Woolliams, 2003) was extended in the present paper to include: i) randomly mixed subpopulations, ii) phenotypic selection of calves and random culling of adults, and iii) age-specific fecundity.

The model was extended to include subpopulations in a straightforward manner by defining categories by age, sex and subpopulation membership. Thus, for a population with two subpopulations and n age classes of each sex, the total number of categories will be $4n$. The categories were ordered in a vector with the first n categories corresponding to the age classes of males in the first subpopulation, followed by the n age classes of females in the first subpopulation, and thereafter the corresponding categories of the second subpopulation.

Calf selection was incorporated by giving the number of calves born each year, the selection intensity of calves and the number of individuals within each category. Furthermore, culling of adults was assumed to be independent of selective advantages, so that individuals in category q were assumed to be a random subset of the selected calves within the same subpopulation and sex as q . This is different from earlier work on expected contributions, where parent selection was assumed and no random culling was included.

Age-specific fecundity was accounted for in the calculations of the elements in Hill's gene flow matrix (Hill, 1974), which is used as a starting point for the calculation of gene flow within the selected populations in the procedure of Woolliams *et al.* (1999). Consequently the age-specific fecundities were accounted for in the calculations of all parameters based on the gene flow, such as ΔF , ΔG and the generation interval L .

Results

Case 1:

Single randomly culled population

For a herding district, with population structure as defined in the method chapter, where all owners apply random culling the predicted genetic gain is zero. The generation interval was equal to 4.02 years, with the mean age of sires being 2.16 years and the mean age of dams being 5.88 years. ΔF_y equalled $0.52 \cdot 10^{-3}$, which is equivalent to $N_e = 2400$. A conventional estimate of effective population size (Wright,

1931; Hill, 1972) is $N_e = 4LMF/(M+F)$, where M and F are the number of male and female breeders, respectively, entering the population each year. This formula gives $N_e = 2700$ for the investigated population with $M = 244$ and $F = 565$. However, this estimate does not account for the delay in maturation and differences in survival between the sexes (Nunney, 1993).

Case 2:

Single population, where calves are selected on weight

For a herding district where all owners apply calf selection the annual genetic gain was $\Delta G = 0.42$ kg (direct genetic gain = 0.39 kg, maternal genetic gain = 0.03 kg). The annual rates of inbreeding increased due to selection ($\Delta F_y = 0.78 \cdot 10^{-3}$), and $N_e (= 1700)$ decreased compared to the previous case even though the generation interval decreased slightly ($L = 3.69$ years). L was reduced due to selection because the genetic progress will cause the genetic level of the young animals to be higher than that of the older ones and the selected offspring will thereby have younger parents. Average long-term genetic contributions (α_q in eq. [1]) from males in age class 2 increased by 10% compared to the previous case with random selection (Case 1: $\alpha_2 = 4.3 \cdot 10^{-3}$; Case 2: $\alpha_2 = 4.7 \cdot 10^{-3}$). For females α_q was increased in younger ages in Case 2 as shown in Fig. 1, where the varia-

Table 1. Input parameter values.

Total population size (pre-calving)	5000
Female age structure (age classes 1-11) ^a	660·0.926 ^x ; x=age class
Total no. adult females ^b	4100
No. adult males in age class 2 and 3, resp.	244; 48
No. adult females per male	14
No. calves in each cohort	2800
No. male and female calves after slaughter	280; 700
Prop. of male and female calves retained	0.2; 0.5
Male reproductive success	No variation between adult categories
Female fecundity in age classes 2-11 ^c	0.32 + 0.15x - 0.012x ² ; x=age class
Genetic and phenotypic variances:	
Direct heritability, b_A^2	0.4
Maternal heritability, b_M^2	0.1
Direct-maternal genetic correlation, r_{AM}	-0.1
Coeff. of env. maternal effect, c^2	0.1
Phenotypic standard deviation	4.1 kg

^a From Rönnegård & Danell (2003).

^b A female is defined as adult from age class 2.

^c Derived from Rönnegård *et al.* (2002).

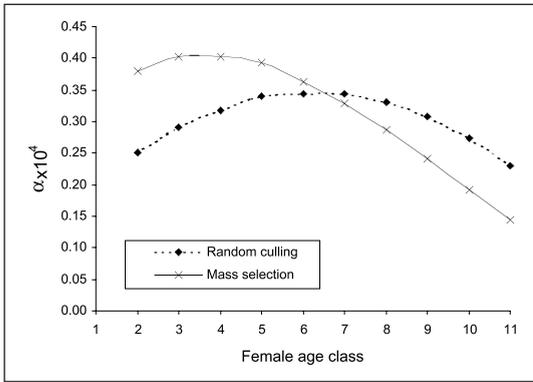


Fig. 1. Average long-term genetic contributions (α) from individual females in a specific age class assuming random culling or mass selection.

tion in α_q in Case 1 is solely due to the variation in fecundity.

In Rönnegård & Woolliams (2003) it was shown that ΔF_y was sensitive to variation in b_M^2 in small populations under intensive selection, with an increase in b_M^2 resulting in a considerable increase in ΔF_y . However, in the present case an increase of the parameter b_M^2 from 0.10 to 0.15 decreased N_e only by 2% (and increased ΔG by 4%).

The impact of the selective advantages on the long-term genetic contributions (β_q in eq. [1]) are given in Table 2, with β_q varying between males and females and between individuals at different ages (for random selection $\beta_q = 0$ in all categories). The impact of a selective advantage in males is larger than in females, because of the higher selection intensity arising from selecting fewer males, except for β_c (*i.e.* the impact of the environmental part of the maternal effect, C_d) which is not defined for males. A maternal breeding value in males is expressed in female descendants and β_M is therefore non-zero. In females the impact of a maternal breeding value is greater than an equally sized C_d (*i.e.* $\beta_M > \beta_c$). The reason for this is that a maternal breeding value is expressed both by the female and its female descendants, whereas the environmental part of the maternal effect is only expressed by the female. Also, unlike in males, β_M was greater than β_A for females, *i.e.* the maternal breeding value was a more important selective advantage for a female than for a male.

Case 3:

Two randomly mixed subpopulations, of which one is selected (open nucleus)

ΔG increased monotonically from 0 to 0.42 kg when the proportion of the total population included in the selection programme increased from zero to one (Fig.

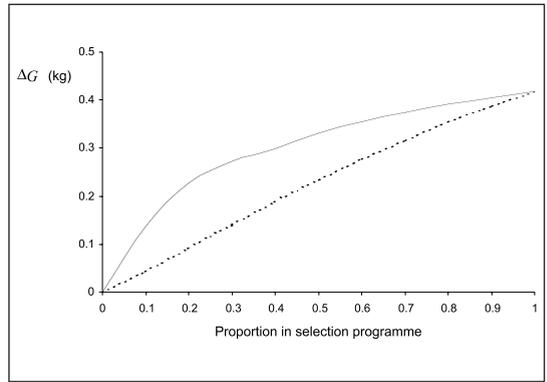


Fig. 2. Annual rates of genetic gain related to the proportion of the population included in the selection programme (---- open nucleus, — closed nucleus). Phenotypic standard deviation equal to 4.1 kg.

2), and the corresponding decrease in N_e was from 2400 to 1700 (Fig. 3). The results in Fig. 3 also apply to similar populations of different size, *i.e.* the ratio N_e/N is close to constant for other population sizes with equivalent structure. The ratio did not vary in the first two decimals for population sizes between 2000 and 10 000, as expected.

ΔG is equal in both the selected and non-selected owner flocks. However, the genetic level for a given year is higher in the selected flocks than in the non-selected flocks. The difference in genetic level was fairly constant for different proportions of the population included in the selection programme (within the range of 0.31–0.36 units of phenotypic standard deviations, *i.e.* 1.3–1.5 kg).

Case 4:

Two subpopulations, of which one is selected, and where the male calves in the randomly selected subpopulation are culled to maximise ΔG (closed nucleus)

ΔG and ΔF were calculated for a closed nucleus system for different proportions of the population included in the selection programme. In this case the number of male reindeer in the unselected owner flocks were decreased to maximise ΔG , and the number of male reindeer in the whole herding district was constant.

When the selected part of the herd becomes sufficiently small, ΔG will be increased by retaining calves at random from the non-selected part of the herd. This will be the case when the proportion of males retained in the selected part of the herd becomes greater than 0.61, which is the case when the proportion of animals in the herding district

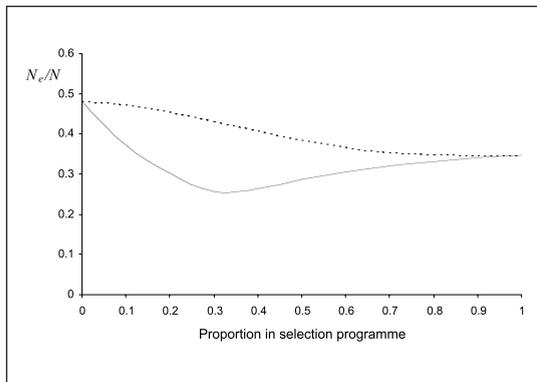


Fig. 3. Effective population size related to the proportion of the population included in the selection programme (---- open nucleus, — closed nucleus), given as proportion of the total population size.

included in the selection programme is 0.33 or less. This proportion was calculated from a difference in genetic level between unselected and selected flocks of 0.3 phenotypic standard deviations. The predicted difference in genetic level varied slightly for different proportions of the population included in the selection programme and was within the range of 0.28–0.31 phenotypic standard deviations.

ΔG was higher for a closed nucleus than for an open nucleus (Fig. 2); the difference was largest for low to moderate proportions of the herd included in the selection programme. When the proportion of the herd included in the selection programme was 0.33, the difference in ΔG between a closed nucleus and an open one was 0.13 kg (Fig. 2) and N_e reached a minimum of 1300 ($\Delta F_y = 0.78 \cdot 10^{-4}$, $L = 3.87$) (Fig. 3). For lower proportions, male calves from the non-selected part of the herd are retained and genes will thereby come from the non-selected part to the selected part of the herd because the population is randomly mixed and consequently increases N_e .

Discussion

The long-term effects of different possible breeding schemes in reindeer husbandry were studied by analysing predictions of ΔG and N_e . In the randomly mixing population the open and closed nucleus schemes were beneficial for all owners, with ΔG increasing from 0 to approximately 0.4 kg as the proportion of owners included in the selection programme increased. Over time ΔG was equal in both the selected and the non-selected parts of the herd and the genetic difference for a given year was approximately 1 kg. For a given proportion of the

Table 2. Influence of the selective advantages (A , M and C) on the long-term genetic contributions for individuals within each category, when the whole population is selected (Case 2).

	Age	Category	$10 \cdot \beta_A^a$	$10 \cdot \beta_M^b$	$10 \cdot \beta_C^c$
Males	1	1	0	0	0
	2	2	4.17	2.08	0
	3	3	3.94	1.99	0
Females	1	4	0	0	0
	2	5	0.307	0.457	0.392
	3	6	0.335	0.500	0.428
	4	7	0.344	0.515	0.438
	5	8	0.346	0.518	0.440
	6	9	0.328	0.493	0.417
	7	10	0.307	0.462	0.389
	8	11	0.276	0.416	0.349
	9	12	0.240	0.362	0.303
	10	13	0.198	0.299	0.249
	11	14	0.154	0.233	0.193

^a Regression coefficient of the direct breeding value (A) on the long-term genetic contribution, *i.e.* the first element in the vector β_q in eq. [1].

^b Regression coefficient of the maternal breeding value (M) on the long-term genetic contribution, *i.e.* the second element in the vector β_q in eq. [1].

^c Regression coefficient of the environmental part of the maternal effect (C) on the long-term genetic contribution, *i.e.* the third element in the vector β_q in eq. [1].

population included in the selection programme, the difference in ΔG between a closed nucleus scheme and an open one was up to 0.1 kg (Fig. 2, Table 3). The advantage of a closed nucleus scheme as compared to an open one was greatest in situations where the proportion included in the selection programme was around 0.3.

The results also reflect a simple practical rule in reindeer husbandry, which will be obvious in practice. In a closed selection scheme it is better to retain male calves at random from the non-selected part of the herd rather than retaining calves from the selected part that you know have lower calf weights. This is the case when the proportion of the population included in the selection programme is small (<0.4) and the proportion of male calves retained in the selected part of the herd becomes larger than 0.6.

The complexity and restrictions of a randomly bred population could possibly be controlled if the sire identities were known, by using genetic information, for example. However, the prospects of paternal test-

Table 3. Summary of annual genetic gain (ΔG) and effective population size (N_e) for the four cases modelled. The age and sex structure are the same in all four cases (see methods chapter and Table 1)

	ΔG^a	N_e
Random culling	0	2400
Mass selection	0.42	1700
Open nucleus and 50% of the population included in the selection programme	0.23 ^b	1900 ^c
Closed nucleus and 50% of the population included in the selection programme	0.33 ^b	1400 ^c

^a Annual genetic gain given in kg.

^b The same result shown in Fig. 2 at *Proportion in selection programme* = 0.5.

^c The same result shown in Fig. 3 at *Proportion in selection programme* = 0.5.

ing using genetic information is small, even though it has been used in small experimental herds (Røed *et al.*, 2002), because of the large population sizes within herding districts, and the fact that the technology would be too time-consuming and expensive.

A closed nucleus scheme will require practical solutions to obtain an economically fair system within a herding district. A possible solution would be to let the owners of the non-selected flocks to buy male reindeer from the owners of the selected flocks, using the money they earn from the extra slaughter of males. An alternative could be common ownership of all male reindeer within the herding community.

The ratio between N_e and actual size N was relatively constant as N varied within each of the four cases providing the structures remained constant (*i.e.* proportions selected and culled at different ages). For $N = 5000$, this ratio was 0.48 for the defined population structure in the absence of selection, whereas if all owners in the defined herding district applied selection then $N_e/N = 0.34$ and, in the most extreme case of a closed nucleus scheme, 0.26. Consequently, selection can have a considerable effect on N_e , but as long as the number of animals within the selected herding district is above 2000 reindeer then there is no risk that N_e will be lower than 500, which is considered as an acceptable limit in conservation biology

to uphold a viable population with sustainable genetic variation in the long term (Franklin, 1980; Mace & Lande, 1991). However, the analyses in this paper have assumed mass selection. If more refined selection methods were introduced in reindeer husbandry (*e.g.* selection based on information about relatives using an index or Best Linear Unbiased Predictors) then the effects of selection would need to be re-evaluated (see Bijma & Woolliams, 2000).

In the situation where all owners within a herding community were applying selection, ΔG was large (0.4 kg per year) compared to the realised genetic gain (0.2 kg per year) estimated by Rönnegård & Danell (2003). This difference is also reflected in the difference in heritability used in this paper (0.42) compared to the realised heritability (0.2) in Rönnegård & Danell (2003). There are several possible reasons for this difference. First of all, in age-structured populations the annual genetic gain is not constant in the first few generations even if the selection intensity is held constant (see Hill, 1974). The genetic gain in Rönnegård & Danell (2003) was estimated in the initial stage of a breeding programme before the gene flow and the genetic gain had reached equilibrium, whereas in the present paper the genetic gain at equilibrium was examined. Furthermore, the selection intensities are likely to be lower in practice (Rönnegård & Danell, 2003) than those used in the present paper. It was assumed that each cohort was selected with perfect truncation, which generally is not possible for practical reasons and results in lower selection intensities. In practice the calves cannot be gathered for evaluation at the same time. The truncation point is approximated by guessing a priori for mean weight and the mean is then recalculated as the calves are weighed (see Petersson *et al.*, 1990). A second reason for lower selection intensities in practice is that the owners partly select calves based on information other than weight, *e.g.* the dam's earlier production and manageability. Further, a longer generation interval than the one used in this paper would also result in a lower ΔG . It was assumed in the present analyses that calves were selected on weight, adjusted for the fixed effect of dam age. However, in practice calves were selected on unadjusted weight, which results in an increased generation interval of females because dams aged 6-10 years rear heavier calves than younger dams (Rönnegård *et al.*, 2002). The mean age of dams was 0.5 years lower in the present study (5.9 years in Case 1) compared to Rönnegård & Danell (2003), 6.4 years. In a separate analysis (unpubl.) it was found that not considering dam age effects could decrease ΔG by up to 10%.

It is also important to note that the models were performed assuming a good environment with low

mortality rates and moderately high calving rates, which enabled quite intensive selection. In less favourable environments ΔG will be reduced.

Environmental limitations and natural selection

There are likely environmental limits to selection response in reindeer breeding, because of the small degree of control by the herders over the environment and food intake. Control is mainly exercised by varying the animal density on ranges. Furthermore, a genetic change may imply a change in resource quality requirements of the animals. For continued improvement in calf weights it is, therefore, necessary to develop tools for monitoring and improving the environment (*e.g.* management of grazing ranges) and tools for keeping an appropriate animal density to support the capacity of the animals. Further, after several years of recording, calf selection based on dam production is possible, which is likely to result in an improvement in maternal ability and thereby reduce the increase in requirement of resources. Selection based on dam production would also reduce undesirable correlated effects to selection caused by a possible negative genetic correlation between calf weight and fitness.

In Rönnegård *et al.* (2002) the close relationship between weight and reproduction was investigated in detail, and the results showed the importance of examining both weight and reproduction in combination. Ropstad *et al.* (1991) showed that heavy female calves may reproduce prematurely as 1-year-olds and their development in weight will be retarded thereafter. Thus, it is important to follow up the reproduction and weights of the females and to examine which females die at an early age. This has been done in the Ruvhten Sijte herding district by the individual owners applying the recording system, but more systematic database tools could be used to improve the follow-up of individual weight and survival. The rut may also introduce a possible opposing force of natural selection among males, because the males, and especially heavy males, loose weight during the rut (Kojola, 1991), which may lead to increased mortality in heavy young males. Consequently, the survival of males in relation to their weight as calves should also be monitored in a reindeer selection programme.

Assumptions of no immigration from other populations and random mating

In the initial stages of a selection programme, immigration of male reindeer from surrounding non-selected herding districts may slow down the genetic gain. However, as the genetic response to selection accumulates in the selected population the male reindeer immigrants are likely to have lower selective

advantages than the average within the population. The immigrants will thereby have small influence on the long-term genetic contributions. Hence, the affect on ΔG and ΔF from immigration will be negligible when the selection programme has been applied for several generations, if the difference in genetic level between the selected and surrounding population is large.

Røed *et al.* (2002) found that female reindeer prefer to mate with heavy males, which is not in accordance with the assumption that the number of mates per male is independent of the male's weight. However, the male part of the population that was studied consisted mainly of 1-year-olds at the rut, and the variation in male weight was assumed to be so small that it would not influence mate choice.

If there are males in older age classes retained in the surrounding herding districts, then such males may have an impact as immigrants because of their larger size. The impact will be large in the first generation, but if their breeding values are inferior then the descendants will probably be culled and their long-term genetic contributions are still likely to be small. It would be possible to incorporate age-specific differences in male fecundity as a further extension to the model.

Conclusions and recommendations

The presented study has shown that the use of a herd structure with skewed sex ratio (1:14) does not result in an alarmingly low N_e in reindeer husbandry (Table 3). Mass selection reduces N_e by nearly 30%, but for herding districts with 1500 animals or more this should not result in problems due to inbreeding.

In the situation where some owners do not wish to take part in a selection programme, we recommend as a rough rule of thumb the use of a closed nucleus selection scheme, provided that the number of reindeer within the herding district is above 2000. ΔG can then be increased considerably compared to an open nucleus scheme.

For a continued improvement in productivity by selection, it is necessary to develop tools for keeping an appropriate animal density to support the capacity of the animals. We also recommend that calf selection should be partly based on dam production as soon as the needed information to evaluate dam production has accumulated. This information includes several parameters and could be handled in practice by using an index.

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Appendix A: Predicted rates of inbreeding per year

The population structure (given by the number of individuals n_q in each category q) together with the coefficients $\alpha_{i(q)}$ and β_q in

$$\mu_{i(q)} = \alpha_q + \beta_q^T (\mathbf{s}_{i(q)} - \bar{\mathbf{s}}_q)$$

are used to predict rates of inbreeding, as described in Rönnegård & Woolliams (2003). However, since they studied populations where parents are selected for reproduction, the method used to calculate the rates of inbreeding in the present paper has been slightly altered in the calculations of the cross products of eq. [A5], because both calf selection and parents being a random subset of their cohort after selection were assumed.

Let n_s be the number of individuals within the exclusive category s , *i.e.* n_s is the number of individuals with a certain life history of reproduction. Then (eq. 29 in Woolliams & Bijma, 2000):

$$E[\Delta F_s] = \frac{1}{2} \sum_s n_s E(u_{i(s)}^2) + \frac{1}{8} \sum_q n_q \delta_q \quad [\text{A1}]$$

where $\delta_q = \alpha^T V_{q,dev} \alpha$ and $V_{q,dev}$ is the difference between the variance matrix of family size from Poisson ($\delta_q = 0$ in the present paper; see Bijma & Woolliams, 2000 for a detailed description). The first term is the sum of lifetime contributions with (eq. 11 in Bijma & Woolliams, 2000)

[A2]

where n_c is the number of categories. For males the expected square contribution, with the mates accounted for, is (eq. 14 in Bijma & Woolliams, 2000):

[A3]

and for females (eq. 15 in Bijma & Woolliams, 2000):

[A4]

where \mathbf{V}^*_{qq} is the covariance matrix of selective advantages in category q , bars with subscripts m or f denote weighted averages over mate categories, and d is the mean number of females per male. Since large populations were studied, the correction for finite sample size has not been included.

The cross products caused by individuals being parents at several ages are:

[A5]

Note that there is no term $\alpha\beta$ (compare eq. 16 in Bijma & Woolliams, 2000), since the mean selective advantages are not changed between age classes.

